GÖTEBORGS UNIVERSITET

FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 48

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Contents

Some Results of the Introduction of Lake Trout (*Salvelinus namaycush* WALBAUM) into Swedish Lakes

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1. Introduction

The first introductions of the North American lake trout into Europe occurred as early as the end of the 19th century, in Swiss alpine lakes (DELACHAUX 1901). During the 1950's a brood stock was built up in Switzerland (HEINZ and LORENZ 1955). At about the same time the species was introduced into Finland, the brood stock originating from Lake Superior. Beginning in 1955 the species has now been introduced into more than 25 Finnish lakes (SORMUNEN and KAJOSAARI 1963).

The first proposal to introduce lake trout into Swedish lakes was made by Dr. O. OLOFSSON (1952), who drew attention to the successful results achieved in Switzerland. Later the idea arose that lake trout might be a good substitute for the populations of large-sized brown trout which often tended to decline in reservoirs with fluctuating water levels (SVÄRDSON 1956). It was pointed out that lake trout had a number of ecological characters that appeared to make it suitable for subarctic reservoirs, attention being drawn to its predatory habits and its ready adaption to deep and cold waters and also to the fact that its spawning habits do not imply access to running water, spawning often taking place at great depths (NILSSON and SCHUMANN 1959).

The experiences from the impounded Lake Minnewanka in the Canadian Rocky Mountains have not been encouraging. In that lake the average size of lake trout decreased after the lake was impounded. Analysis indicated that this was because the trout had to a great extent stopped feeding on the small-sized whitefish that had been their principal food before impoundment (CUERRIER 1954, RAWSON 1958, MILLER and PAETZ 1959). As yet the reason for this effect does not seem to be altogether clear, but MILLER and PAETZ have suggested that the predator and the prey had somehow become isolated from each other. Other experiences indicate more favourable circumstances. In Jackson Lake, Wyoming, for instance, where the water level fluctuates about 12 metres, the introduced lake trout grow well and give satisfactory yields (M. D. ROLLEFSON, personal communication); and in Quabbin Reservoir, Massachussets, where the species was introduced in 1953, the fish are growing well, reproducing naturally, thus providing the best sport fishing in the entire state (MULLAN and TOMPKINS 1959). In some cases

even very heavy water-level fluctuations can be endured by the lake trout without the growth being depressed. GRIMÅS and NILSSON (1962) reported on the Swiss Lake Arnensee, which, with a maximum depth of 50 metres, is brought to fluctuate 34 metres. In spite of this, introduced lake trout grow well there — up to 3,190 grammes in 6 summers — feeding mainly on fish (*Phoxinus*), planktonic *Crustacea,* and larvae and pupae of chironomids.

It soon became obvious that lake trout might be fitted for other Scandinavian water areas than reservoirs. Consequently the species has by now been introduced into many very different bodies of water, from small reclaimed ponds to the large Lake Vänern. Several attempts to introduce lake trout into the Baltic have been made by Finnish fishery managers since 1957 (SORMUNEN and KAJOSAARI 1962).

2. The Swedish introductions

The first lake-trout eggs imported into Sweden (20,000) arrived in December 1958 as a gift from the Fish and Wildlife Division of the Ontario Department of Lands and Forests. They originated from Lake Simcoe, Ontario, and gave rise to the first Swedish brood stock. Since then another four stocks have been imported, one coming from the Finger Lakes (through Dr. D. A. WEBSTER), and one from Lake Superior (through the Finnish brood stock), while two genetically undefined stocks have emanated from Wisconsin (through the U.S. Fish and Wildlife Service) and Washington respectively. The Finnish (Lake Superior) stock has been used in most of the lakes up till now.

Table 1 gives some data of the first introductions in Swedish lakes from 1959 to 1966.

The introductions induced by the Institute of Freshwater Research have been aimed, among other things, at finding out (1) whether the lake trout will grow well, reproduce and contribute to the fishing in Swedish reservoirs, (2) whether the species will utilize as food the dense populations of small-sized whitefish that characterize many lakes of the northern Swedish highlands and woodlands, and (3) whether it will find a niche in some of the deep southern Swedish lakes that are mainly inhabited by pike, perch, roach, smelt and cisco. In all the areas mentioned the fishing has either been damaged by man or has been poor for other reasons, for instance the species composition. No attempt has been made to introduce the lake trout into lakes with a trout fishery that is already considered to be satisfactory. To learn, however, how the native char (*Salvelinus alpinus* L.) will interact with its relative, a couple of introductions have also been made in lakes containing small-sized char. In addition to the Finnish experiments one introduction has been made in a Baltic bay, Bråviken.

3. Food and growth

It is a well-known fact that lake trout are pronouncedly piscivorous. Among the fish species listed as prey of lake trout in America are whitefish (*Coregonus*), smelt (*Osmerus*), alewives (*Pomolobus pseudoharengeus*), perch (*Perca flavescens*) and sculpin. In the Swiss Lake Arnensee 75 per cent of the lake trout bigger than 40 centimetres had fed on minnows (*Phoxinus*) (GRIMÅS and NILSSON 1962). Other organisms quoted as important lake trout food are *Mysis relicta* and *Pontoporeia affinis*.

The piscivorous habits are also very pronounced in the Swedish stocks. For instance, in Lake Landösjön (51) all the fish caught in July, August and November 1964 (29 specimens) and in June—July 1966 (71 specimens) had eaten whitefish. The species consumed was exclusively *Coregonus lavaretus* L. (with about 30 gillrakers), which occurs in a dwarfed but dense population (SVÄRDSON 1957). In Lake Vojmsjön (43) too, the trout had fed almost exclusively on small whitefish (approx. 95 per cent in July—August 1965 by 43 specimens), and the rest of the food was made up of pupae of *Trichoptera*. In a deep, almost isolated bay of Lake Mälaren, Lilla Ullevifjärden (57), the lake trout during May, June, July and October had fed mainly on smelt (*Osmerus eperlanus* L.). This diet was mixed with perch (*Perca fluviatilis* L.), *Mysis relicta* and the amphipod *Pallasea quadrispinosa*. Table 2 shows that fish was consumed mainly by the largest fish, *Mysis* and amphipods mainly by fish smaller than 100 grammes.

The growth of the lake trout is known to be extremely variable (MARTIN 1966) and this is true also for the Swedish stocks. In large and deep lakes such as Storsjön, Kallsjön and Landösjön the fish have generally reached a weight of about 1—1.5 kg in 6 summers. The biggest fish so far caught was a six-year-old specimen, weighing 3.6 kg. Very bad growth was noted in small reclaimed lakes without prey fish. Fig. 1 gives a detailed picture of the growth in two lakes in different parts of Sweden. A general tendency, often mentioned as characteristic of lake trout, is a relatively slow growth during the first few years of life. A tendency towards increased size variation with age is also evident. The differences between lakes may be due to many factors, such as heredity, size of the introduced fish and supply of suitable food. The last-mentioned factor has, judging from many parallel introductions of fish of identical heredity in different lakes, been of the utmost significance.

4. Vertical and horizontal distribution

The map, Fig. 2, illustrates the distribution of the recaptures of tagged lake trout introduced into Lake Storsjön in 1964. Apart from a certain concentration at the place of release, the recaptures are widely spread all over the lake.

Table 1. Introductions of lake trout into Swedish lakes and reservoirs.

Lake	River system	Surface area, km²	Main fish species	Years of introduction	Number	Stage
1 Nakerijärvi	Torneälv	7	wf, gr, bb	1966	1.400	1+
2 Vallsjärv	Kalixälv	5.5	sm, pk, bb, pc	1963	700	1+
3 Pajtasjärvi	"	28	bt, wf, gr, pk, mw, bb, bh	1966	5.200	1++
4 Stuor Tjalmejaur	Lule älv	2.8	bt, wf, pk, bb	1963	1.000	1+
5 Messaure	"	—	bt, wf, gr, pk, bb, mw	1964	500	2
6 Porsi	"	12	bt, wf, gr, pk, bb, mw	1964	500	2
7 Laddonjaure		10.6	bh, wf, pk, bb, pc	1964, 1966	3.400	1, 2
8 Yttre Huvträsket	Åby älv	0.3	bt, wf, gr, bb, pc	1964	1.700	++
9 Inre Huvträsket	"	0.7	wf, gr, pk, mw, pc	1964	2.300	++
10 St. Arbostijaure	"	1.1	wf, gr, pk, rc, bb	1964		++
11 Laggträsket	Skellefte älv	0.4	wf, pk, bb, pc	1966	2.000	2
12 St. Sikträsket	"	5.7	bt, wf, gr, pk, bb, pc	1966	8.000	++
13 Vargfors	"	8.2	bt, wf, gr, pk, rc, bb, pc	1964	2.200	++
14 Västra Verbosjön	"	6.9	bt, wf, pk, rc, bb, pc, bh	1964	3.000	++
15 Släppträsket	"	8	bt, wf, pk, bb, pc	1965	4.100	++
16 Järvträsket	Rickleån	1	pk, rc, bb, pc	1964	3.000	++
17 Lossmenträsket	Sävarån	9	wf, cc, pk, bb, rc, pc	1964	4.600	1+
18 Tavelsjön	Tavelån	20	wf, pk, sm, rc, bb	1966	5.000	+
19 St. Tjulträsket	Umeälv	5.4	bt, ch, gr	1966	6.000	1
20 Fjosocken	"	12	bt, wf, pk, bb, pc		2.000	1
21 Abmoträsket	"	9.5	wf, pk, bb, pc	1964	5.000	+
22 Yttersjön	"	1.4	wf, pk, rc, bb, pc	1964	1.500	2
23 Storuman	"	156.5	bt, ch, wf, gr, pk, pc	1965	2.000	++
24 Gäutajaure	"	32	bt, ch, wf	1965	3.000	++
25 Laisan		18	bt, ch, wf, gr	1964, 1965	10.500	++
26 Lillarmsjön	Hörneån	3	cc, wf, pk, rc, pc	1965	5.000	++
27 St. Arasjön	Öre älv	9	wf, pk, rc, bb, pc	1964	3.000	2
28 Vänjaurträsk	"	1.5		1966	3.000	++
29 Storlögdasjön	Lögde älv	12.3	bt, wf, gr, pk, bb, pc	1963	5.000	+
30 Önskasjön	Husumån	7	cc, wf, pk, rc, bb, pc, rf, bh, sm, ee	1964	6.400	1, 2
31 Inre+Yttre Lemelsjöarna	"	12	cc, wf, pk, rc, bm	1964	2.000	2
32 Storsjön	Gide älv	6	bt, wf, pk, rc, pc	1965	2.000	+
33 Bergsjön	Moälven	0.7	bt, wf, gr, sm, pc	1961	2.650	1

No. Lake	River system	Area	Species	Year	Number	Result
34 St. Arksjön	Ångermanälven	—	bt, wf, pk, rc, bb, pc	1964, 1965	1.500	+
35 Lavsjön	"	—	bt, wf, pk, rc, bb, pc	1964, 1965	4.100	++
36 Malgomaj	"	92.7	bt, ch, wf, gr, pk, rc	1965	29.000	++
37 Tåsjön	"	45.4	bt, wf, gr, pk, bb, pc, rf	1961	3.000	1
38 Ormsjön	"	—	bt, wf, pk, rc, bb, pc	1964	ca 5.000	1, 1+
39 Bomsjön	"	25.0	bt, wf, pk, rc, bb, pc,	1964	4.000	++
40 Jansjön	"	4	wf, pk, sm, rc, bb, pc, rf	1964	2.000	++
41 Betarsjön	"	34.4	bt, cc, wf, cm, pk, rc	1963, 1964	29.500	++
42 St. Skirsjön	"	9.3	bt, wf, pk, rc, bb, pc	1964	15.000	++
43 Vojmsjön	"	78	bt, ch, wf, pk, mw, bb, pc	1964	3.500	2
44 Näversjön	Indalsälven	3.2	bt, wf, gr, pk, rc, bb, pc	1961		
45 Gussjön	"	5.1	bt, ch, cc, pk, rc, ee, bb, pc, wf, br	1963, 1965	6.000	+, 1
46 St. Hasslingen	"	1.2	bt, wf	1964	5.000	++
47 Alsensjön	"	4.0	bt, wf, gr, pk, bb, pc	1964	4.500	++
48 Juveln	"	35.8	bt, ch, gr, bb, pc	1964	3.000	++
49 Gesunden	"	29.5	bt, wf, gr, pk, sm, pk, rc, bb, pp, pc, rf, bh	1964	10.000	+
50 Storsjön	"	456	bt, ch, wf, gr, pk, rc, bb, pc	1962, 1964, 1966	21.550	1, 1+, 2
51 Landösjön	"	49	bt, wf, gr, pk, bb, pc	1961, 1963, 1965, 1966	10.600	+, 1, 1+
52 Kallsjön	"	155	bt, wf, gr, rc, mw, bb	1961, 1963, 1964, 1965, 1966	85.200	1, 1+
53 Helgesjön	Ljungan	5.8	bt, ch, wf, pk	1963, 1965	15.600	1
54 Storsjön	"	456	bt, ch, gr, pk, pc	1966	5.000	1
55 Ansjön	"	8.3	bt, wf, pk, rc, mw, ee, bb, pc	1964	3.500	+
56 Trängslet	Dalälven	38	bt, gr, pk, rc, bb, pc	1966	13.000	1
57 Lilla Ullevifjärden	Mälaren	1.6	wf, cc, sm, pk, rc, rd, bm, ee, bb, pc, rf	1964, 1966	10.000	1
58 Immeln	Skräbeån	24	bt, wf, pk, rc, ee, bm, bb	1964, 1965	10.000	+
59 Ånimmen	Vänern—Götaälv	16.4	cc, sm, bl, bm, ee, bb, pk, bm, mw, ee, bb, pc, rf, sb	1964	1.000	+
60 Anten	"	19.3	cc, sm, bl, bm, ee, bb, pk, rc, pc, rf	1964	1.000	++
61 Övre Gla	"	10	wf, sm, pk, sc, mw, ee, bb, pc, rf	1964	2.000	1
62 Mjörn	"	55.5	cc, pk, rc, bl, bm, sm, ee, bb, pc	1964	2.000	+
63 Vänern	"	5 500	cc, wf, sm, pk, bm, ee, bb, pp, pc	1963, 1964	3.330	1
64 Ränken	"	14.5	bt, cc, sm, pk, rc, bl, bm, ee, bb, bh	1964	1.000	+
65 Värmeln	"	78.8	bt, cc, wf, sm, pk, rc, bl, bm, mw, ee, bb, pp, pc, bh, rd	1964, 1965	7.000	++
66 Fryken	"	45.9	bt, wf, pk, bm, ee, bb, pp, pc, bh, cc, rc, bl, mw	1964	6.000	++
67 Visten	"	33.4	bt, wf, cc, sm, pk, rc, bl, bm, ee, bb, pc, rf, bk	1965	1.000	++
68 Höljesjön	"	17	bt, wf, gr, pk, rc, mw, ee, bb, pc	1965	7.500	+, 1+
69 Rådasjön	"	10.6	bt, wf, gr, pk, rc, mw, ee, bb, pc	1965	4.000	++

Abbreviations: bt=brown trout, ch=arctic char, cc=cisco (*Coregonus albula*), wf=whitefish, gr=grayling, sm=smelt, pk=pike, rc=roach, rd=rudd, bl=bleak, bm=bream, mw=minnow, ee=eel, bb=burbot, pp=pike-perch, pc=perch, rf=ruff, bh=bullhead, sb=stickleback, +=fingerling, 1=yearling, etc.

Table 2. The food of lake trout of different size in Lilla Ullevifjärden in
1966. Mean percentage of stomach volume.

	<100 g	101—200 g	201—300 g
Perch	—	8.7	5.0
Smelt	28.6	87.0	95.0
Mysis	67.0	4.3	—
Amphipoda	4.3	—	—
Cyclops	0.1	—	—
Number of specimens	13 (6 empty)	39 (16 empty)	12 (4 empty)

Judging from this and several other plantings, tagged fish can spread very rapidly from the place of release, and this may be the reason why there are no indications that scattered planting has any substantial advantages over more concentrated planting (WEBSTER *et al.* 1959).

It is a well-known fact that lake trout are generally deep-swimming fish, although it has been shown that in arctic lakes such as Great Bear Lake they can be caught in shallow water even in the middle of the summer (MILLER and KENNEDY 1947). A cold-stenothermal adaptation seems to be the most important of the factors governing this habit. It has been shown by test fishing that lake trout are caught in deep water during the summer when there is a thermal stratification (MARTIN 1952, WEBSTER *et al.* 1959).

Laboratory experiments have revelated that lake trout have very low optimum and lethal temperatures (GIBSON and FRY 1954), and a comparison between experimental data and catch data in nature indicates that "optimum temperature" under natural conditions is low, around 8—15°C (FERGUSON 1958).

Fig. 3 shows the vertical distribution of the catch of lake trout in two Swedish lakes, Vojmsjön (43), which is a cold northern lake, and Lilla Ullevifjärden (57) in southern Sweden, which has pronounced thermal stratification. It is obvious that the fish are much more evenly distributed in the homothermal Lake Vojmsjön than in the stratified Lilla Ullevifjärden, where most of the trout have been caught at depths between 15 and 25 metres. The tendency of the fish to be absent at great depths in late autumn in Lilla Ullevifjärden is certainly due to oxygen deficit that develops every summer in this lake, extending in late autumn from the greatest depth to about 25 metres. Data from other lakes confirm the picture obtained, and on the whole the Swedish lake trout have hitherto been caught in relatively deep water, in most lakes at 15—25 metres.

5.   Recapture and survival

The species has been introduced in all different stages up to two-year-old (two-plus) fish. Fish released as newly hatched fry have been recaptured
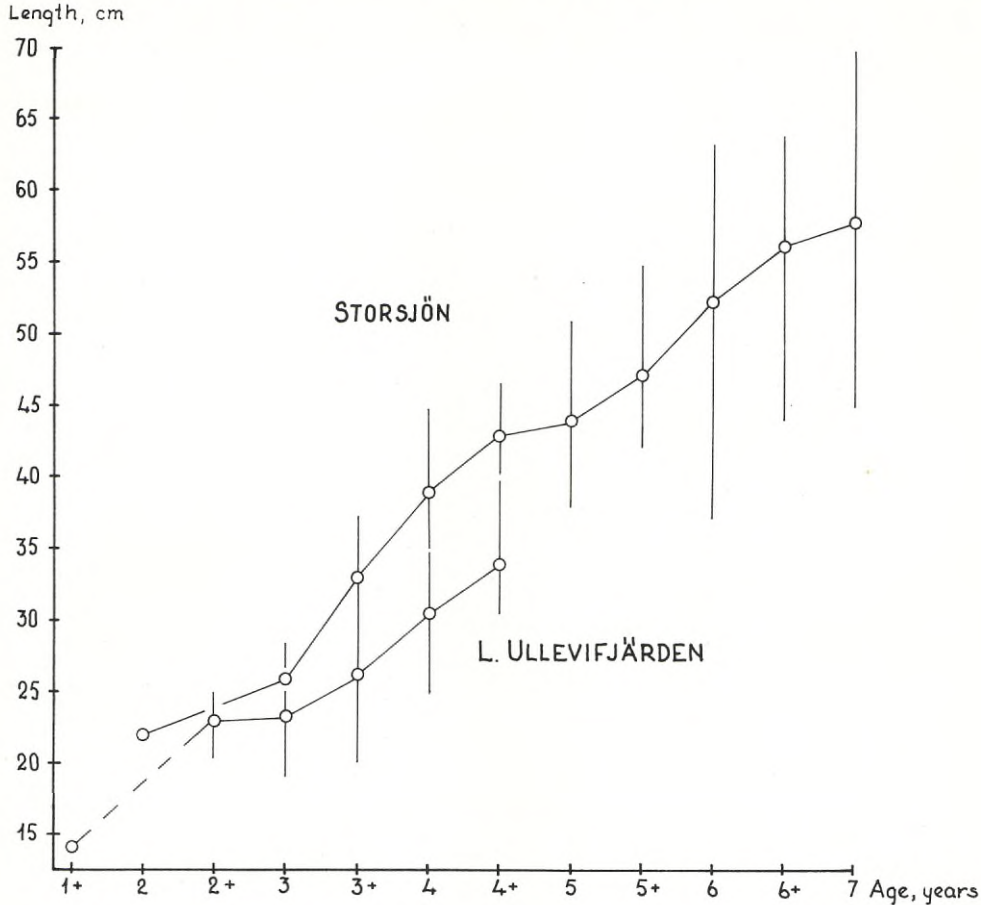
Fig. 1. The growth of lake trout in Lakes Storsjön and Lilla Ullevifjärden. Vertical lines indicate total variation in length.

only in small reclaimed waters, where, however, they seem to have had good survival. No attempts to release fry into large unreclaimed lakes have been made, as the general experience in America indicates that this practice is ineffective (DYMOND 1957). The success of release is highly dependent on the size of the fish. Experiments with stocking of lake trout in the southern part of Lake Superior (PYCHA and KING 1967) have indicated that successful releases were obtained only with fish larger than 50 per kg (22 per lb). On the whole, American experiences indicate a much higher survival of yearlings (one-plus fish) than young of the year. For instance, in Cayuga Lake the representation of stocked yearlings in the catch was fourfold as compared to fingerlings (WEBSTER *et al.* 1959).

The Swedish experiences are still too recent to be conclusive. The releases of one-summer-old fish have hitherto not been encouraging. In Lakes Gesun-
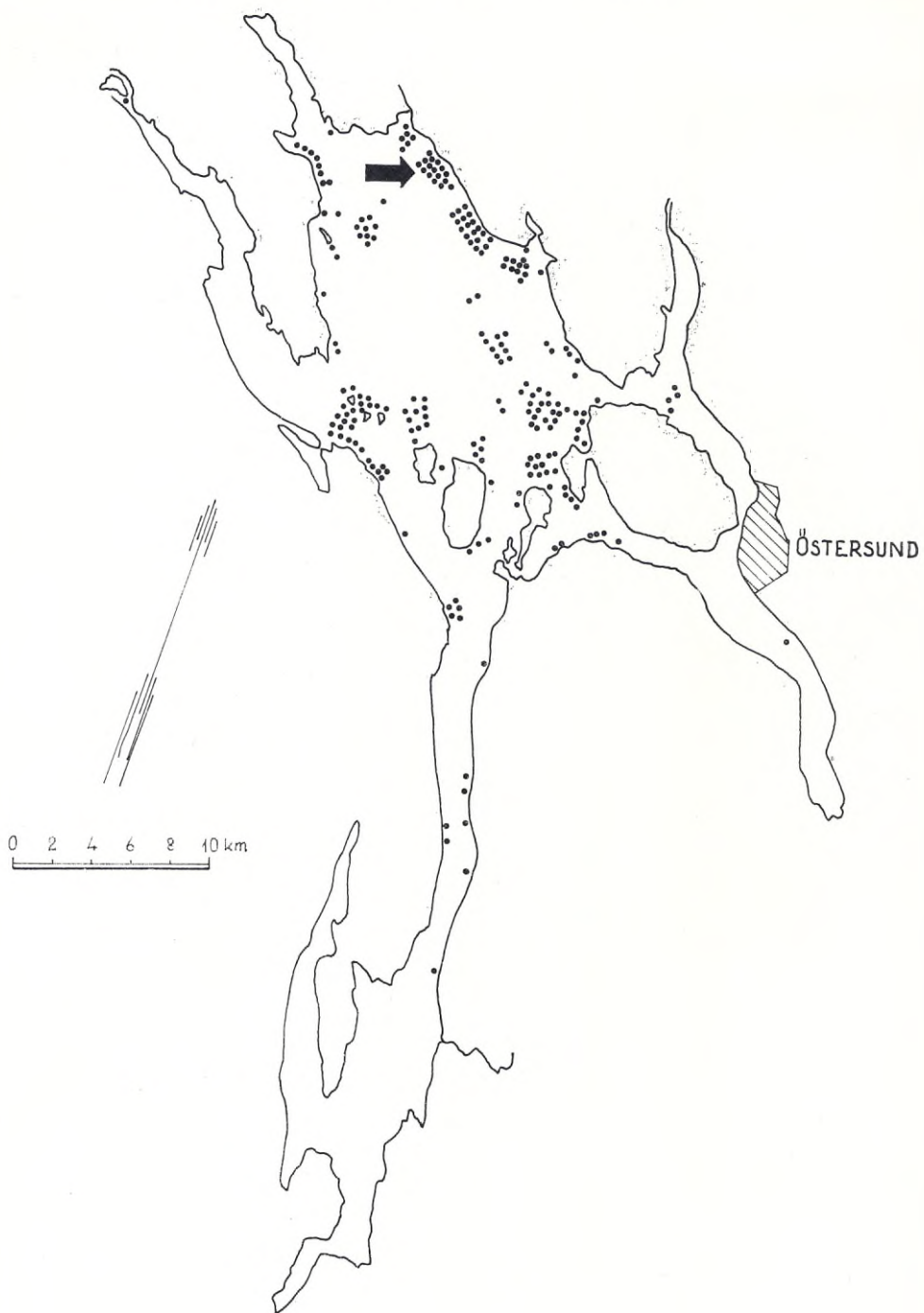
Fig. 2. Recaptures of tagged lake trout in Lake Storsjön 1964—1967. Arrow indicates place of release.
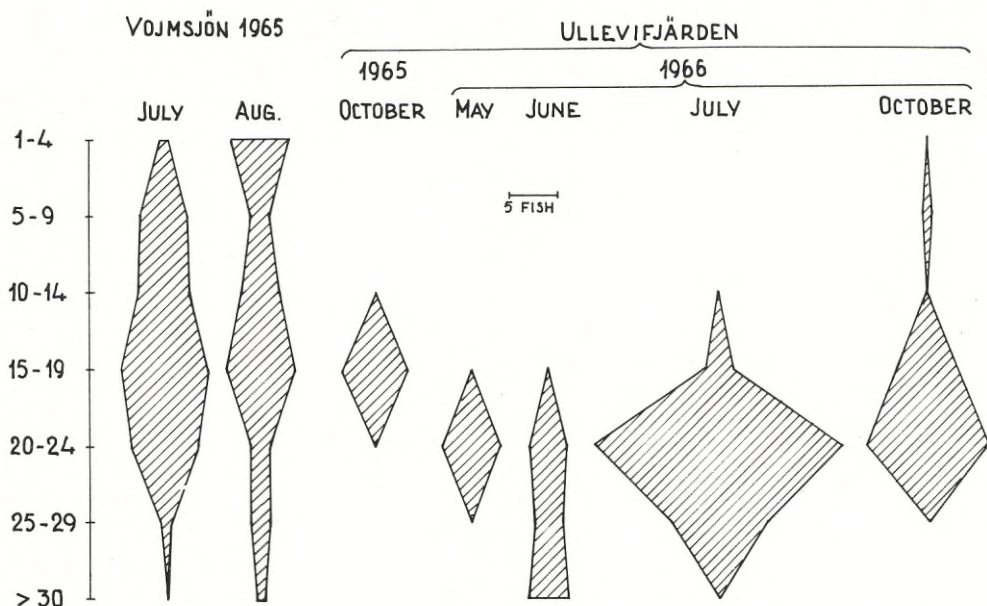
Fig. 3. Vertical distribution of the catch of lake trout in Lakes Vojmsjön and Lilla Ullevifjärden.

den (49) and Ansjön (55), for instance, where the fish were introduced in 1964, no recapture at all has been reported, in spite of special test fishing operations. Some plantings of yearlings seem also to have failed, as for instance in Tåsjön and Vänern, where no recaptures (except during the few days after release) have been reported. Long and otherwise difficult transportations may in many cases have, through stress phenomena, caused or added to the bad results.

One of the best statistics on the recapture of unmarked yearling fish is that from Lilla Ullevifjärden where 5,000 fish were released in 1964. Since then more than 140 fish were recaptured up to June 1967, which means nearly 3 per cent in three and a half years.

The most rewarding recaptures have hitherto been obtained by planting two-year-old fish. Some of these plantings have been controlled by tagging (using the CARLIN tag). It has then appeared that the tagged fish experience a high early mortality when the tags get outangled with the fishermen's gill-nets. For this reason, and probably owing to some tag losses as well, later (and heavier) recaptures are made of untagged released fish. On the other hand, untagged fish are often not reported. Keeping these errors in mind, however, it is possible to calculate approximately the reward from the release of the hatchery-reared fish.

Table 3 gives the data on the best-rewarding release of tagged lake trout

Table 3. The recaptures of tagged lake trout in Lake Storsjön.

Total length, centimetres	Number tagged	Mean weight, grammes	Number recaptured	per cent recaptured	Mean weight, grammes
20	7	81	5	71	514
21	19	85	11	58	763
22	16	88	9	56	653
23	19	93	13	68	1,243
24	19	101	12	63	1,122
25	7	106	7	100	1,041
26	2	123	1	50	2,000
27	2	173	1	50	860
Σ	91		59	64,8	959

in Sweden so far experienced. From 91 (two-plus) fish stocked in July 1962 into Lake Storsjön (50), Central Sweden, 59 were recaptured up to July 1st, 1967, which means 65 per cent, or calculated as weight, a yield of 62.2 kg per 100 released fish. This is an enormously high recovery rate and the weight is above average for salmon smolts released into the Baltic (CARLIN 1963). The released fish were quite large (average length 224 mm, size ranging from 20 to 27 cm). The table gives further evidence for the significance of the size of the fish, when released. It seems that larger stocked fish not only give a higher percentage return, but also give heavier recaptures.

If the fish are grouped to those below and above 22 cm the following result appears:

20—22 cm	42 tagged	25 recaptured	(59.5 %)	average weight 0.674 g
23—27 cm	49 ,,	34 ,,	(69.4 %)	,, ,, 1.170 g

It seems as if something special favoured the survival and growth of fish, released at a size of 23 cm and above. To judge from the stomach analyses the diet of the lake trout is often changed to fish at roughly that size.

PYCHA and KING (1967) calculated that 17—20 fish per lb was a size close to the optimum for a "successful" release of lake trout into Lake Superior. The present data indicate that it sometimes may be rewarding to stock even much larger fish provided that the cost of rearing can be kept moderate.

6. Spawning

No natural spawning has hitherto been observed in Swedish lakes. In a rearing pond in Bonäshamn, where the first brood stock from Lake Simcoe is held, spawning occurred in the autumn of 1965, and fry were caught in the following spring. More than 100,000 eggs were fertilized in the autumn of 1966 and twice that number is reported in 1967.

7. Summary

1. Beginning in 1959 about 70 Swedish lakes have been stocked with the North American lake trout (*Salvelinus namaycush*), the chief aim being to improve fishing in impounded or otherwise non-productive lakes.

2. The fish were mostly caught at considerable depths (15—25 metres) but there is a tendency towards a more even vertical distribution in cold homothermal lakes.

3. The lake trout have fed mainly on fish (whitefish, smelt and perch), in the younger stages on crustaceans (*Mysis* and *Pallasea*), and the growth has been very variable, in the best case 3.6 kg in 6 years.

4. Survival has hitherto been low in fish released as young of the year but very good in fish released as two-year-olds. Yearlings have given intermediate results. The best-rewarding release was made in Lake Storsjön with two-plus fish, ranging from 20 to 27 centimetres. The recovery of this lot in the first five years was 65 per cent and the weight of recapture was comparable to salmon smolt releases in the Baltic.

5. No natural reproduction has hitherto been observed in the lakes.

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Growth, Weight and Year-Class Fluctuations in the Pike-Perch (Lucioperca lucioperca L.) of Lakes Hjälmaren and Mälaren

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Contents

Introduction

In three of the four big lakes in southern Sweden the pike-perch (*Lucioperca lucioperca* L.) is the most important fish from a commercial point of view. Since this species also seems to stand the pollution of lakes better than do most other significant species and its importance is thus increasing, more knowledge about its growth and survival was needed.

In 1955, therefore, two stations were set up, one in Lake Hjälmaren and the other in Lake Mälaren. At these, annual samples were taken and fishing by means of a set of gill-nets of differing meshes was performed. There are no official statistics of the yield in Swedish lakes, as fishery rights are privately owned and — even in the big lakes where off-shore fishing is free for everyone — any fisherman can catch fish and sell it directly to the market. The experimental fishing must therefore, apart from giving samples for age determination, also indicate the frequency of fish in the lake.

Lake Hjälmaren has an area of 480 km² and lies 22 metres above sea level. It has a maximum depth of 25 metres, but most of the lake is considerably shallower than this. It runs through the Eskilstunaån River down to Lake Mälaren. This lake is bigger, its area being 489 km², and its maximum depth is 64 metres. Mälaren lies only 0.5 metre above the Baltic Sea and empties into the Baltic through the short Norrström River in the centre of the city of Stockholm.

Table 1. The catch of pike-perch, Lake Hjälmaren 1955—1965.

Year	Stretched mesh 133 mm				Stretched mesh 109 mm				Stretched mesh 92 mm				Stretched mesh 75 mm			
	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort
	number	kg			number	kg			number	kg			number	kg		
1955	—	—	—	—		—	—	—		—	—	—	7	2.55	0.36	0.70
1956	—	—	—	—	1	0.30	0.30	0.09	21	13.45	0.64	1.91	49	20.80	0.42	4.45
1957	2	2.90	1.45	0.20	5	4.55	0.91	0.50	19	12.10	0.64	1.90	23	12.45	0.54	2.30
1958	—	—	—	—	—	—	—	—	19	12.60	0.66	1.90	30	15.70	0.52	3.00
1959	—	—	—	—	3	2.95	0.98	0.33	3	2.50	0.83	0.33	16	7.40	0.46	1.78
1960	2	7.70	3.85	0.20	—	—	—	—	6	3.60	0.60	0.60	13	5.80	0.45	1.30
1961	—	—	—	—	—	—	—	—	3	1.80	0.60	0.30	9	4.20	0.47	0.90
1962	2	2.00	1.00	0.20	—	—	—	—	1	0.95	0.95	0.10	12	5.05	0.32	1.20
1963	1	3.05	3.05	0.10	1	0.70	0.70	0.10	20	13.35	0.67	2.00	37	17.40	0.47	3.60
1964	1	0.65	0.65	0.10	4	2.90	0.73	0.40	27	16.25	0.60	2.70	29	13.90	0.48	2.90
1965	1	2.15	2.15	0.10	5	4.20	0.84	0.50	10	6.15	0.62	1.00	20	8.10	0.41	2.00
Total	9				19				129				245			

Year	Stretched mesh 67 mm				Stretched mesh 60 mm				Total		
	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort	Number	kg	Average weight
	number	kg			number	kg					
1955	15	4.30	0.29	1.50	13	3.68	0.29	1.30	35	10.53	0.30
1956	35	11.80	0.34	3.18	28	8.70	0.31	2.56	134	55.05	0.41
1957	9	3.45	0.38	0.90	17	5.10	0.30	1.70	75	40.55	0.54
1958	6	2.15	0.36	0.60	8	1.75	0.22	0.80	63	32.20	0.51
1959	23	8.85	0.38	2.56	22	6.80	0.31	2.44	67	28.50	0.43
1960	15	4.45	0.30	1.50	8	2.05	0.26	0.80	44	23.60	0.54
1961	10	2.30	0.23	1.00	16	3.70	0.23	1.60	38	12.00	0.32
1962	16	5.00	0.31	1.60	13	3.35	0.26	1.30	44	16.35	0.37
1963	25	9.85	0.39	2.50	17	4.70	0.28	1.70	101	49.05	0.49
1964	32	12.30	0.38	3.20	18	5.95	0.33	1.80	111	51.95	0.47
1965	19	6.80	0.36	1.90	14	3.75	0.27	1.40	69	31.15	0.45
Total	205				174				781		

Material and methods

The locations selected for the two fishing stations were Mellanfjärden, which is a part of the western end of Lake Hjälmaren, and Lambarfjärden, a wider area at the eastern end of Lake Mälaren. The distance between the two stations, as the crow flies, is about 130 km. The water depths are 1.5—2.0 metres at the Hjälmaren-station and 15—25 metres at the station in Lake Mälaren. All gill-nets were made of twisted nylon and were 30 metres long. The depth of the nets was 5 feet in Hjälmaren and 20 feet in Mälaren.

Table 2. The catch of pike-perch, Lake Mälaren 1955—1965.

Year	Stretched mesh 133 mm				Stretched mesh 109 mm				Stretched mesh 92 mm			
	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort
	number	kg			number	kg			number	kg		
1955	—	—	—	—	4	3.10	0.78	0.33	16	9.20	0.58	1.33
1956	—	—	—	—	—	—	—	—	10	5.65	0.57	0.83
1957	2	2.00	1.00	0.18	6	4.05	0.68	0.55	29	18.90	0.65	2.64
1958	1	0.30	0.30	0.10	7	13.00	1.86	0.70	37	22.10	0.60	3.70
1959	1	1.55	1.55	0.09	6	4.60	0.77	0.55	19	11.10	0.58	1.73
1960	1	0.65	0.65	0.13	9	9.30	1.03	1.13	25	17.80	0.71	3.13
1961	1	0.30	0.30	0.10	9	6.85	0.76	0.90	18	10.90	0.61	1.80
1962	1	5.70	5.70	0.11	3	3.85	1.28	0.33	5	2.65	0.53	0.56
1963	3	8.50	2.83	0.25	1	1.10	1.10	0.09	20	11.95	0.60	1.67
1964	2	8.35	4.18	0.15	6	5.30	0.88	0.46	22	16.20	0.74	1.69
1965	5	6.30	1.26	0.50	6	7.65	1.28	0.50	10	7.03	0.70	0.83
Total	17				57				211			

Year	Stretched mesh 75 mm				Stretched mesh 60 mm				Total		
	Catch		Average weight	Number fish/effort	Catch		Average weight	Number fish/effort	number	kg	Average weight
	number	kg			number	kg					
1955	32	10.65	0.33	2.67	—	—	—	—	52	22.95	0.44
1956	13	5.30	0.41	1.08	—	—	—	—	23	10.95	0.48
1957	60	28.45	0.47	5.45	—	—	—	—	97	53.40	0.55
1958	42	21.55	0.51	4.20	—	—	—	—	87	56.95	0.65
1959	40	19.65	0.49	3.64	28	8.00	0.29	2.55	94	44.90	0.48
1960	52	25.50	0.49	6.50	51	15.25	0.30	6.38	138	68.50	0.50
1961	38	16.60	0.44	3.80	79	17.75	0.22	7.90	145	52.40	0.36
1962	16	6.55	0.41	1.78	42	9.75	0.23	4.67	67	28.50	0.43
1963	48	20.95	0.44	4.00	28	10.35	0.37	2.33	100	52.85	0.53
1964	35	19.30	0.55	2.69	12	5.15	0.43	0.92	77	54.30	0.71
1965	7	3.70	0.53	0.58	22	5.65	0.26	1.83	50	30.33	0.61
Total	383				262				930		

The set contained nets varying from 60 to 133 mm, stretched mesh. This represents a considerable contrast to the nets used for the commercial catch, which is taken predominantly in nets of 109 mm stretched mesh.

In the years 1955—65, fishing was performed in Lake Hjälmaren during the first half of September and in Lake Mälaren during the first half of October; 9—11 nights a year were fished in Hjälmaren and 8—13 nights a year in Mälaren.

In all 781 pike-perch were caught and studied in Lake Hjälmaren and 930 specimens were taken in Lake Mälaren. All fish, specified as to nets, number and weight, are recorded in Tables 1 and 2.

The reading of the scales was done several times, principally by G. Molin,

and the scales from Hjälmaren were found to be more easily interpreted than those from Mälaren. Annuli are laid down in this species in May—June, when the new season of growth begins (FREIDENFELT 1922). FREIDENFELT's critical study was made in Lake Hjälmaren and his pioneer work was of much value to us.

No back-calculation of the growth before capture was performed in this study.

Growth

The pike-perch were taken in the last part of the growing season (Hjälmaren) or when growth was probably terminated for the year (Mälaren). In Table 3 the average total length of the captured fish is given separately for males and females.

In Lake Hjälmaren males are shorter than females in four age groups out of five. In the deviating group, age 7 summers, the total number of fish is small and the difference obviously insignificant.

In Lake Mälaren males are again shorter than females in three age groups out of five. In one of the other two groups the length is similar and only in one age group, 5 summers, are males slightly longer than females.

In the recent synopsis of biological knowledge on the pike-perch (DEELDER and WILLEMSEN 1964) no reference is given to a more rapid growth rate of the female sex. In other species, of course, such as pike (*Esox lucius*) and perch (*Perca fluviatilis*), this phenomenon is wellknown, and according to our data the same tendency, although rather slight, may occur also in the pike-perch. A bulkier body in the case of the female has probably not caused selection by the nets, since the catches were taken in autumn and many immature specimens are involved.

Since no back-calculation was performed, the growth data in Table 3 are selected in a high degree by the fishing intensity within each lake. In Lake Hjälmaren the pike-perch are 314 mm long in September of their third growth season, while in Lake Mälaren, a month later, they are even shorter, i.e. 281 mm. The apparent later annual increment in Lake Hjälmaren is small, which is clearly due to the intensive selection by the fishery, which leaves only the smallest fish of each group to live until the next age group. In Lake Mälaren the fishing intensity is probably less high, and the annual increments of growth are here apparently bigger.

FREIDENFELT (1922) made some back-calculations, using direct proportionality for the relation scale-fish length, and he found the following data:

Age 1 year	7.5—11 cm	average 9.0 cm
„ 2 „	16.0—21 „	„ 19.0 „
„ 3 „	24.0—32.5 „	„ 30.5 „
„ 4 „	32.5—38.5 „	„ 36.0 „
„ 5 „	36.0—45.0 „	„ 43.5 „
„ 6 „	47.0—51.5 „	„ 46.0 „

Table 3. Total length in mm of the pike-perch at different ages (summers).

Summers	3			4			5			6			7		
Sex	♂♂	♀♀	Tot.	♂♂	♀♀	Tot.	♂♂	♀♀	Tot.	♂♂	♀♀	Tot.	♂♂	♀♀	Tot.
Hjälmaren	310	317	314	359	367	364	397	409	401	398	413	406	470	421	436
numbers	(80)	(93)	(173)	(114)	(165)	(279)	(86)	(107)	(193)	(53)	(59)	(112)	(4)	(9)	(13)
Mälaren	278	285	281	334	344	339	392	389	391	420	420	420	460	467	464
numbers	(85)	(83)	(168)	(128)	(99)	(227)	(155)	(139)	(294)	(87)	(95)	(182)	(24)	(19)	(43)

For the age groups three and four summers, i.e. fish that are just being recruited to the fishery, FREIDENFELT's data are very similar to our data from the same lake for a period, some 40—50 years later. Thus in spite of the increase of fishing pressure within the lake, the growth rate seems to have been rather stable.

In Lake Mälaren the average growth rate is slightly slower in young fish and, making allowance for the fact that selection by the fishery is less severe in this lake, the apparent better growth of older fish may be illusory.

Previous studies on pike-perch growth in Swedish lakes, apart from FREIDENFELT's, have given the following results:

	Number of summers					
	3	4	5	6	7	8
Lake Toften (ALM 1919)	23	29	34	39	44	48 cm
Lake Yxtasjön (ALM 1922)	—	38	42	49	52	52 ,,
Lake Ymsen (VALLIN 1929)	34	43	50	55	60	64 ,,

The pike-perch in Lake Ymsen displays a growth rate which is better than the average for 24 German lakes (BAUCH 1953). However, it is inferior to the extremely fast-growing pike-perch of the Bay of Stettin (NEUHAUS 1934) and the Bay of Riga in the brackish Baltic (MÄÄR, 1947).

It is known that slow-growing populations of pike-perch occur in some of the most northerly lakes in which the species can live in Sweden. However, exact growth data have not so far been published. On the whole the species has a comparatively uniform growth rate in a wide range of habitats and it seems to have almost no tendency to appear in dwarf populations, so numerous in other Scandinavian freshwater fish species.

Weight

In Tables 4 and 5 the weights of 900 pike-perch from Lake Hjälmaren and 969 specimens from Lake Mälaren are given by nearest centimetre class and by sex. If these weights are compared to that given by DEELDER and WILLEMSEN (1964) which represents an average for several studies, the pike-perch of Lake Mälaren can be said to have normal weight, while those from Lake Hjälmaren are clearly lighter. There is no significant weight difference between males and females.

Table 4. The weight of pike-perch at various lengths. Lake Hjälmaren 1955—1965.

Cm	♀ av. weight	♀ number	♂ av. weight	♂ number	Total av. weight	Total number
18	25	(2)	25	(1)	25	(3)
22	30	(1)	75	(1)	53	(2)
23	—	—	90	(2)	90	(2)
24	80	(1)	—	—	80	(1)
26	150	(1)	—	—	150	(1)
27	150	(1)	150	(1)	150	(2)
28	169	(9)	168	(7)	169	(16)
29	212	(10)	189	(9)	201	(19)
30	218	(17)	212	(21)	215	(38)
31	227	(22)	233	(20)	230	(42)
32	258	(30)	258	(31)	258	(61)
33	281	(33)	273	(18)	277	(51)
34	316	(42)	313	(26)	315	(68)
35	332	(25)	346	(23)	339	(48)
36	370	(36)	380	(26)	375	(62)
37	410	(27)	395	(26)	403	(53)
38	445	(40)	456	(40)	450	(80)
39	473	(27)	489	(21)	481	(48)
40	518	(42)	533	(30)	525	(72)
41	591	(36)	578	(22)	585	(58)
42	615	(34)	619	(25)	617	(59)
43	678	(20)	688	(13)	683	(33)
44	719	(23)	733	(21)	726	(44)
45	774	(10)	854	(4)	814	(14)
46	881	(5)	757	(3)	819	(8)
47	913	(3)	925	(1)	919	(4)
48	963	(2)	950	(1)	956	(3)
49	950	(1)	1,100	(1)	1,025	(2)
50	1,600	(1)	—	—	1,600	(1)
52	1,400	(2)	—	—	1,400	(2)
59	—	—	2,150	(1)	2,150	(1)
60	2,400	(1)	—	—	2,400	(1)
67	3,050	(1)	—	—	3,050	(1)
Total		505		395		900

It is surprising that the weight of the Lake Hjälmaren pike-perch is lower, since this population has a more rapid growth rate (at least in young fish) and this lake is rather eutrophic. However, it has been reported (N. JOHANS-SON, verbal communication) that one as yet unidentified parasite, the egg of which is found in the intestines, has been found in considerable numbers in pike-perch from Lake Hjälmaren, and the fishermen report that in early spring the condition of many fish is quite low.

Since our material is large enough we have divided the weight data for all fish into two periods, i.e. 1955—60 and 1961—65 (Table 6). It then emerges that during the time in question the weight was deteriorating in Lake Hjälmaren but improving in Lake Mälaren. This tendency aggravates the difference in weight between the lakes. It is hoped that a more thorough study on the parasite can be started in the near future (N. JOHANSSON, verbal communication).

Table 5. The weight of pike-perch at various lengths. Lake Mälaren
1955—1965.

Cm	♀ av. weight	♀ number	♂ av. weight	♂ number	Total av. weight	Total number
19	—	—	60	(1)	60	(1)
20	—	—	85	(1)	85	(1)
24	127	(6)	132	(7)	130	(13)
25	141	(7)	143	(6)	142	(13)
26	156	(9)	157	(14)	157	(23)
27	197	(14)	171	(14)	184	(28)
28	193	(21)	193	(22)	193	(43)
29	214	(11)	208	(14)	211	(25)
30	242	(21)	229	(21)	236	(42)
31	256	(12)	259	(26)	258	(38)
32	293	(16)	301	(19)	297	(35)
33	331	(20)	327	(13)	329	(33)
34	356	(26)	333	(20)	345	(46)
35	388	(19)	392	(26)	390	(45)
36	416	(32)	422	(37)	419	(69)
37	447	(20)	468	(32)	458	(52)
38	498	(45)	481	(43)	490	(88)
39	534	(21)	537	(23)	536	(44)
40	581	(36)	595	(30)	588	(66)
41	634	(25)	636	(27)	635	(52)
42	683	(23)	666	(20)	675	(43)
43	717	(22)	748	(14)	733	(36)
44	747	(17)	812	(22)	780	(39)
45	819	(11)	856	(6)	838	(17)
46	974	(7)	907	(17)	941	(24)
47	1,037	(5)	1,117	(3)	1,077	(8)
48	1,016	(7)	1,075	(7)	1,045	(14)
49	1,117	(4)	1,125	(2)	1,121	(6)
50	1,175	(2)	1,167	(3)	1,171	(5)
51	1,117	(3)	1,500	(1)	1,309	(4)
52	1,675	(2)	1,450	(3)	1,563	(5)
53	—	—	1,350	(1)	1,350	(1)
54	1,650	(1)	1,550	(1)	1,600	(2)
55	1,500	(2)	—	—	1,500	(2)
56	—	—	1,625	(2)	1,625	(2)
61	2,700	(1)	—	—	2,700	(1)
77	—	—	5,300	(1)	5,300	(1)
86	7,100	(2)	—	—	7,100	(2)
Total		470		499		969

Maturity

Every specimen of pike-perch caught in our set of gill-nets was inspected
as to maturity. It was determined by field inspection whether the fish would
spawn next spring or not. In the latter case it was noted as juvenile. If re-
corded as »mature» this referred to the next spring when the age would be
in even years. In Table 7 the data have been grouped according to age at
maturity. A few males, but no females, were mature when three years old.

Maturity comes rather gradually at 3—8 years of age for the males and
at 4—8 years for the females. The size at maturity is mostly 40—42 cm.

Table 6. Change of weight in two lakes 1955—60 to 1961—1965.

Cm	Hjälmaren				Mälaren			
	1955—1960		1961—1965		1955—1960		1961—1965	
	av. weight	number	av. weight	number	av. weight	number	av. weight	number
18	—	—	25	(3)	—	—	—	—
19	—	—	—	—	60	(1)	—	—
20	—	—	—	—	85	(1)	—	—
22	75	(1)	30	(1)	—	—	—	—
23	—	—	90	(2)	—	—	—	—
24	—	—	80	(1)	131	(5)	126	(8)
25	—	—	—	—	131	(4)	147	(9)
26	150	(1)	—	—	162	(3)	169	(20)
27	150	(1)	150	(1)	173	(9)	192	(19)
28	185	(7)	157	(9)	183	(13)	201	(30)
29	194	(11)	204	(8)	189	(3)	216	(22)
30	227	(22)	204	(16)	243	(15)	230	(27)
31	242	(28)	210	(14)	255	(15)	260	(23)
32	269	(30)	247	(31)	285	(14)	305	(21)
33	295	(27)	264	(24)	308	(16)	344	(17)
34	325	(32)	307	(36)	338	(28)	362	(18)
35	367	(17)	316	(31)	365	(23)	412	(22)
36	382	(38)	369	(24)	416	(40)	424	(29)
37	421	(25)	387	(28)	455	(23)	462	(29)
38	456	(38)	445	(42)	486	(43)	496	(45)
39	496	(16)	470	(32)	535	(26)	540	(18)
40	542	(27)	505	(45)	574	(48)	605	(18)
41	617	(23)	557	(35)	624	(30)	652	(22)
42	624	(22)	612	(37)	665	(34)	685	(9)
43	711	(12)	657	(21)	685	(22)	741	(14)
44	729	(19)	730	(25)	753	(22)	802	(17)
45	813	(4)	802	(10)	848	(9)	843	(8)
46	825	(4)	813	(4)	923	(17)	984	(7)
47	944	(4)	—	—	1,037	(4)	1,084	(4)
48	975	(2)	925	(1)	1,008	(9)	1,101	(5)
49	1,025	(2)	—	—	1,138	(4)	1,100	(2)
50	—	—	1,600	(1)	1,167	(3)	1,175	(2)
51	—	—	—	—	1,175	(2)	1,250	(2)
52	—	—	1,400	(2)	—	—	1,563	(5)
53	—	—	—	—	—	—	1,350	(1)
54	—	—	—	—	1,600	(2)	—	—
55	—	—	—	—	—	—	1,500	(2)
56	—	—	—	—	1,650	(1)	1,600	(1)
59	—	—	2,150	(1)	—	—	—	—
60	2,400	(1)	—	—	—	—	—	—
61	—	—	—	—	—	—	2,700	(1)
67	—	—	3,050	(1)	—	—	—	—
77	—	—	—	—	—	—	5,300	(1)
86	—	—	—	—	—	—	7,100	(2)
Total		414		486		489		480

In Lake Hjälmaren more than half of the males are mature at age 5, compared with age 6 in Lake Mälaren. Of the females a significant majority are mature at age 6 in Hjälmaren whereas only every second female fish mature in Mälaren. It can be said, therefore, that maturity comes roughly one year later in Lake Mälaren, where the growth during the first few years is also inferior.

Table 7. Age at maturity of pike-perch in Lake Hjälmaren and Lake Mälaren.

		Hjälmaren							Mälaren				
Age	Average length	♂ Juv.	♂ Mature	♀ Juv.	♀ Mature	Total	Age	Average length	♂ Juv.	♂ Mature	♀ Juv.	♀ Mature	Total
2	210	2	—	3	—	5	2	241	1	—	1	—	2
3	314	77	4	92	—	173	3	281	84	1	83	—	168
4	364	83	30	156	10	279	4	339	106	22	96	3	227
5	401	36	50	63	44	193	5	391	84	71	97	42	294
6	406	12	42	18	41	113	6	420	25	62	47	48	182
7	436	—	4	—	9	13	7	464	6	18	2	17	43
Total		210	130	332	104	776	Total		306	174	326	110	916

A positive correlation between early maturity and better growth has been summarized for the species by DEELDER and WILLEMSEN (1964) and for related species as well by ALM (1959).

Age distribution

The age distribution (summers) of the catch is given in Tables 8 and 9.

One-summer-old pike-perch have not been caught with the gear used. However, in November 1909, Dr. I. ARWIDSSON, as reported by FREIDENFELT (1922), caught some one-summer-old pike-perch in Lake Hjälmaren by means of a seine. They were 50—105 mm total length, average length 82 mm.

A single two-summer-old pike-perch was caught by us in Lake Mälaren, and 5 specimens were taken in Lake Hjälmaren. As seen from the tables the catch from Lake Hjälmaren is younger, 4-summer-old fish being the most numerous age group, while 5-summer-old fish dominate in Lake Mälaren. Fish 10 summers old or older were met only twice in Hjälmaren but were encountered 6 times in Mälaren.

The lower age of the fish in Lake Hjälmaren corresponds to the more rapid growth as well as the more intensive fishing there. The higher fishing intensity is attributable mainly to the fact that Hjälmaren has a greater part of its area open to free fishing owing to the topography of the shores and the legislation on offshore fishery rights.

Relative strength of eight year-classes

The main purpose of this study was to investigate what factors might influence the numerical strength of the year-classes of the pike-perch. Since the fishing intensity is high, there are proposals from anglers and commercial fishermen for various types of new restrictions on the fishery

Table 8. Catch by age (summers). Lake Hjälmaren.

	2	3	4	5	6	7	8	9	10	Total
1955	—	34	1	—	—	—	—	—	—	35
1956	—	10	123	1	—	—	—	—	—	134
1957	—	12	9	51	2	—	—	1	—	75
1958	—	5	28	12	18	—	—	1	—	63
1959	2	40	13	10	1	1	—	—	—	67
1960	—	24	18	—	—	—	1	—	1	44
1961	—	29	9	—	—	—	—	—	—	38
1962	—	2	39	2	1	—	—	—	—	44
1963	1	7	17	73	2	—	—	—	1	101
1964	2	9	14	23	63	—	—	—	—	111
1965	—	1	8	21	26	12	—	1	—	69
Total	5	173	279	193	113	13	1	2	2	781
%	0.6	22.2	35.6	24.7	14.5	1.7	0.1	0.3	0.3	100.0

or for modifying the restrictions now in force, i.e. a legal size limit of 40 cm and a closed season for pike-perch during its spawning period.

In order to arrive at an estimate of the size of the year-classes, as represented in our experimental fishing, the following procedure was adopted.

In Lake Hjälmaren the number of efforts varied from 9 to 11 during the different years. The catch in this lake was, however, smoothed out as if 10 nights of fishing had occurred in each year. The total real catch of 781 pike-perch thus was modified to 776 specimens, the age of which is given in Table 10.

In the same way, the effort in Lake Mälaren has been smoothed to 12 annual nights of fishing. The number of pike-perch is thereby increased from the 930 actually caught to 1078.9 fish, the quantity which it is assumed would have been taken, had fishing been going on for 12 nights in every year. The age distribution of these fish, based on the real proportion, is given in Table 11.

Now, by adding the number of all pike-perch belonging to the same year-class that were caught during four successive seasons (ages 3—6 summers), a relative index of the year-class strength was obtained. Eight different year-classes, those of 1953—60, could be compared in this way and they are included in Table 12. Since the nets with small meshes were not used in Lake Mälaren in the period 1955—58, which obviously means smaller catches of young fish in these years, all small-meshed nets were excluded, as an alternative, from both lakes. This changed the relative magnitude of the year-classes, and gives a further possibility of comparison.

As can be seen from Table 12 in Lake Hjälmaren two year-classes, those from 1953 and 1959, ranked far above the others. In Lake Mälaren 1953 and 1959 were again very rich, but 1955 had joined their group. The classes 1956, 1954 and 1958 were rather poor in both lakes.

Table 9. Catch by age (summers). Lake Mälaren.

Year	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
1955	—	21	15	8	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	52
1956	—	—	20	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23
1957	—	7	18	67	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	97
1958	1	7	15	29	32	1	1	—	—	—	—	—	—	—	—	—	—	—	1	87
1959	—	6	16	59	10	3	1	—	—	—	—	—	—	—	—	—	—	—	—	94
1960	—	19	33	17	59	8	1	—	1	—	—	—	—	—	—	—	—	—	—	138
1961	—	78	26	24	8	8	1	—	—	—	—	—	—	—	—	—	—	—	—	145
1962	—	27	26	4	6	2	1	—	—	—	—	—	—	—	—	—	—	—	—	67
1963	—	1	27	58	10	3	—	—	—	—	1	1	1	—	—	—	—	—	—	100
1964	—	2	6	23	43	1	—	—	1	—	—	—	1	—	—	—	—	—	—	77
1965	—	—	25	2	5	13	5	—	—	—	—	—	—	—	—	—	—	—	—	50
Total	1	168	227	294	182	43	9	—	2	—	1	1	1	—	—	—	—	—	1	930
%	0.1	18.1	24.4	31.6	19.6	4.6	1.0	—	0.2	—	0.1	0.1	0.1	—	—	—	—	—	0.1	100.0

Table 10. Catch in Lake Hjälmaren, recalculated to a constant effort of ten nights a year.

Year	2	3	4	5	6	7	8	9	10	Total
1955	—	34.0	1.0	—	—	—	—	—	—	35.0
1956	—	9.1	111.7	0.9	—	—	—	—	—	121.7
1957	—	12.0	9.0	51.0	2.0	—	—	1.0	—	75.0
1958	—	5.0	28.0	12.0	18.0	—	—	—	—	63.0
1959	2.2	44.4	14.4	11.1	1.1	1.1	—	—	—	74.3
1960	—	24.0	18.0	—	—	—	1.0	—	1.0	44.0
1961	—	29.0	9.0	—	—	—	—	—	—	38.0
1962	—	2.0	39.0	2.0	1.0	—	—	—	—	44.0
1963	1.0	7.0	17.0	73.0	2.0	—	—	—	1.0	101.0
1964	2.0	9.0	14.0	23.0	63.0	—	—	—	—	111.0
1965	—	1.0	8.0	21.0	26.0	12.0	—	1.0	—	69.0
									Total	776.0

In Lake Hjälmaren the two best year-classes are roughly ten times as rich as the poorest class, while in Lake Mälaren the ratio between the best and the poorest is 3 or 4: 1. The factors causing the differences in survival of the year-classes must thus be more potent in Hjälmaren than in Mälaren.

The pike-perch and the water temperature

The pike-perch has a geographical distribution which indicates a preferred habitat of warm, eutrophic lakes with a high turbidity. In Sweden the species spread to a southern and lower eastern part of the country from the fairly warm big Ancylus lake which once covered the Baltic basin. During the following more saline stages of the Baltic, the pike-perch was probably ousted from parts of its Scandinavian area. This seems to be the reason for the many highly successful artificial introductions which have been made in this century into eutrophic lakes at a fairly low altitude. Above the 90— 100 metre altitude, however, many introductions of fingerlings in various lakes have given a very few big fish, which have not been capable of re-producing their kind. A certain sensitivity to cold water is thus indicated for the young stages of this fish already from fishery-management experience.

WILLEMSEN (1958) has proved by experiment that the embryonic development of this species is abnormal below 9°C and, again, WIDERBERG (1941) found unsuccessful hatching when the water was below 10°C. Thus it is fairly evident that on the lee-side of the lake, windy days in spring could bring deeper and colder water to the spawning grounds, jeopardizing the hatching of the pike-perch. The warmer the spring and the deeper a thermo-cline, the less would be the risk appearing for the embryonic development.

In Table 13 the deviation from normal temperature is given according to

Table 11. Catch in Lake Mälaren, recalculated to a constant effort of twelve nights a year.

Year	2	3	4	5	6	7	8	9	10	11	12	13	14	15	20	Total
1955	—	21.0	15.0	8.0	6.0	2.0	—	—	—	—	—	—	—	—	—	52.0
1956	—	—	20.0	3.0	—	—	—	—	—	—	—	—	—	—	—	23.0
1957	—	7.6	19.6	73.1	3.3	2.2	—	—	—	—	—	—	—	—	—	105.8
1958	1.2	8.4	18.0	34.8	38.4	1.2	1.2	—	—	—	—	—	—	—	1.2	104.4
1959	—	6.5	17.5	64.4	10.9	3.3	—	—	—	—	—	—	—	—	—	102.6
1960	—	28.5	49.5	25.5	88.5	12.0	1.5	—	1.5	—	—	—	—	—	—	207.0
1961	—	93.6	31.2	28.8	9.6	9.6	1.2	—	—	—	—	—	—	—	—	174.0
1962	—	36.0	34.6	5.3	8.0	2.7	1.3	—	—	—	1.3	—	—	—	—	89.2
1963	—	1.0	27.0	58.0	10.0	3.0	—	—	—	—	—	—	1.0	—	—	100.0
1964	—	1.8	5.5	21.2	39.7	0.9	—	—	0.9	—	—	0.9	—	—	—	70.9
1965	—	25.0	2.0	5.0	13.0	5.0	—	—	—	—	—	—	—	—	—	50.0

Total 1,078.9

the official meteorological stations at Örebro (close to the part of Hjälmaren where the fishing took place) and Stockholm (close to the Mälaren fishing station).

April was, by far, warmest in 1953 and 1959, May warmest in 1954 and 1960, June very warm in 1953 and 1960, July was warm in 1955 and August in 1955 (exceptionally so) and 1959. The whole period April-August was, by far, warmest in the years 1953 and 1959. These were the very best year-classes in Lake Hjälmaren, and two of the three best years in Lake Mälaren. There can hardly be much doubt that a high temperature during the first summer of the pike-perch's life is favourable to survival.

The year 1955 proves to be an interesting one. The spring and early summer were cold, but from late June onwards the temperature was very much above normal. This year gave only an intermediate year-class in Lake Hjälmaren but a very rich one in Lake Mälaren.

The coldest years were 1956, 1958, 1957 and 1954 (especially at Örebro). They all gave poor year-classes in both lakes.

HAVINGA (1949) found in Holland that the year-classes of pike-perch became rich when May was warm. In Germany TESCH (1962) found the March temperature to be especially important. DEELDER and WILLEMSEN (1964) also concede the influence of climate, but they stress the independence of neighbouring lakes.

Discussion: Climate and fish population fluctuations

Water temperature may, in northern regions, influence the life of the freshwater fish in several ways and there is considerable evidence of its significance for population fluctuations.

First, the *distribution* of the fish within a lake may be influenced. SØMME

Table 12. Relative strength of eight year-classes of pike-perch.

Order	Hjälmaren				Mälaren			
	All nets		Small-mesh nets excluded		All nets		Small-mesh nets excluded	
1	1953	214.7	1953	131.5	1959	225.9	1955	178.5
2	1959	204.0	1959	114.0	1955	178.5	1953	152.5
3	1960	68.0	1960	27.0	1953	152.5	1959	113.2
4	1957	63.4	1955	26.8	1960	97.2	1954	65.3
5	1955	51.1	1954	24.3	1957	92.8	1956	61.0
6	1958	39.2	1957	22.6	1958	75.0	1957	49.2
7	1954	31.2	1958	15.0	1954	65.3	1960	47.5
8	1956	19.4	1956	8.4	1956	61.0	1958	30.6

(1941) in his important book on the brown trout (written in Norwegian and therefore not so widely known as it deserves to be) tells of the spring movements of the trout in the Hardangervidda mountain plateau. When the ice is melting in very late spring or early summer, the trout accumulate in the surface water, preferably along the northern shore, where the sun has warmed the water most. The fish also aggregate at the mouth of small becks, again preferably at those coming from mountain basins where the sun may heat the water strongly. While the surface of the lake may have a temperature of 0—4°C, the water of the becks may be at 20°C and it spreads over the lake surface. The trout, also, are concentrated at the mouth of the becks and move on the surface of the water, with the dorsal fin rising above the lake surface. It can be proved from their stomach contents, according to SØMME, that the trout in these cases do not feed from the fauna of the becks but concentrate in the warmest water.

There is much circumstantial evidence, from the fishermen's experience, that many species of fish have temperature-directed movements all the year round, though the phenomenon seems to be especially conspicuous in the high mountain lakes.

The *growth* of fish may also be strongly influenced by temperature. This seems to have been first observed and recognized by HUITFELDT-KAAS (1927) who noted as early as 1907 that in that summer, which was a cold one, the trout grew less than normally. He made notes on the phenomenon several times in 1911 and 1917 and in his mature work (HUITFELDT-KAAS 1927), based on scales of 13,500 Norwegian freshwater fish, he devoted a chapter to growth irregularities caused by climate. He found that the growth of trout (*Salmo trutta*) in Lakes Nedre Leirungen and Tyin, 30 km apart, had a parallel trend and that it was also parallel to the average air temperature deviation from normal values during July, August and September. The small growth increment during 1907 was especially evident. He also found the growth of whitefish in Lake Drengen to be correlated to the summer temperature during the period 1906—12. The cisco of Lake Mjøsa also had,

Table 13. Deviation from normal values of the monthly average air temperature at Örebro and Stockholm during the summers of 1953—1960.

Year	April		May		June		July		Aug.		April—Aug.	
	Ö	S	Ö	S	Ö	S	Ö	S	Ö	S	Ö	S
1953	+2.8	+3.1	+1.0	+1.1	+3.0	+3.6	−0.2	+0.4	+0.3	+0.9	+6.9	+9.1
1954	+−0.0	−0.5	+2.0	+2.3	+0.1	+1.0	−1.4	−0.4	+0.1	+0.4	+0.8	+2.8
1955	−1.0	−1.9	−2.1	−1.6	−0.7	−0.5	+2.5	+2.7	+3.7	+4.4	+2.4	+3.1
1956	−1.3	−2.1	+1.7	+2.2	+−0.0	+0.4	−0.6	−0.8	−1.8	−1.4	−2.0	−1.7
1957	+0.7	+0.2	−0.7	−0.2	−0.5	−0.4	+0.5	+0.8	+−0.0	+0.3	+−0.0	+0.7
1958	−0.9	−1.1	−0.2	+0.4	−0.3	+−0.0	−0.7	−0.4	−0.3	+−0.0	−2.4	−1.1
1959	+2.6	+2.2	+1.2	+1.4	+1.1	+1.5	+1.6	+2.4	+3.4	+3.4	+9.9	+10.9
1960	+0.7	+0.6	+2.0	+2.1	+2.0	+3.0	−1.2	−0.7	+−0.0	+0.3	+3.5	+5.3

Ö = Örebro, S = Stockholm

according to HUITFELDT-KAAS, a growth rate that fluctuated from year to year, owing partly to the temperature but also to other factors, i.e. population pressure.

OLOFSSON (1932) found that the whitefish (*Coregonus*) of several northern Swedish lakes had a broad zone of growth on their scales in the autumn of 1930 but a very small one in 1931. The summer of 1930 was warm, but that of 1931 was cold and it followed a very late spring. A few fish, rather old ones, had a broad zone at the margin of the scale when caught in the autumn of 1931 and OLOFSSON concluded, without doubt correctly, that these fish had not grown at all during the cold summer. SEGERSTRÅLE (1932, 1933, 1947) found the same growth difference in several fish species, mostly bream, in the brackish water of the Finnish archipelago during 1927 and 1928. The former year had the warmest, the latter the coldest summer in 35 years. The correlation between growth increments and average July—August temperature was extremely good and SEGERSTRÅLE (1947) said he could estimate from the scales the average temperature to within 1°C.

After this group of pioneering work in all the Fennoscandian countries further authors made contributions. SVÄRDSON (1951) confirmed OLOFSSON's findings that *Coregonus* had an above average growth in 1930 but found that in the same lake the fish did not display a good growth in the equally warm summer of 1947. RUNNSTRÖM (1957) found the brown trout of Lake Rensjön to accelerate its growth in July 1948, when temperature was above normal, whereas in the next year, which was much colder, the trout achieved much more of the season's growth in August. The increments of the two years were almost equal. Again, RUNNSTRÖM (1964) found the growth of trout and char in Lake Ransaren better in warm years. NORDIN (1963) noted a very good growth of *Coregonus* in the hot summer of 1959.

It is often taken for granted that a better growth of a fish in a warm year is due to the presence of more food organisms in the lake, since the general production is higher in such years. Though obviously this may play a part, the temperature may exert a rather direct influence on the metabolism of the fish, just as the fish grows in summer but not in winter in a lake where there is abundant food even in the cold season of the year. LECREN (1958) and KEMPE (1962) demonstrated that the annual growth of the perch and roach was correlated to the number of days with a water temperature above a certain threshold value (cf. VARLEY, 1967).

If growth accelerates, *survival* too is most probably improved (SVÄRDSON 1962). From five years' tagging of natural smolts in a sea-trout river in southern Scania, it was found that in 1962, when according to lighthouse measurements the Baltic water in the vicinity was rather cold, both the postsmolt growth and survival were below average and this was most pronounced in the survival of the smallest smolts (SVÄRDSON, 1966). This indicates, that the influence of high temperature on survival (probably acting

through less predation) may last for a considerable period of the fish's life and not be active only during the presumed "critical period" of the fry. The hot summer of 1947 caused a rich year-class of *Coregonus,* which may have, by competition, led to growth not above average (SVÄRDSON 1951). The warm June of 1953 produced an extremely rich year-class of Baltic whitefish at the south-eastern coast of Sweden (SVÄRDSON 1961), and this gave rich yields in the commercial fishery for many years. Again, in the same year, the whitefish of Lake Vättern experienced a very rich year-class (SVÄRDSON 1963), giving good yields for a couple of years and low yields for char, as these two fish species react antagonistically to each other. In more northerly lakes, like Storsjön and Hornavan, rich year-classes in whitefish also appeared in 1953 (SVÄRDSON, unpublished, NORDIN 1963).

RUNNSTRÖM (1957) found the trout of Lake Rensjön to have rich year-classes in the years 1943, 1947 and 1953, all of which had a warm June. LECREN found the year-classes of perch richer than normal in several different lakes of one region in the warm year of 1949 (LECREN 1955).

Returning now to the pike-perch in Lakes Hjälmaren and Mälaren, it is in conformity with the rule that the very best year-classes were born in springs when water temperature was high (1953 and 1959). The year 1955, however, demonstrates that the survival rate late in the first summer may also be of importance and that, if the mortality in the first part of the summer has not been too high, the strength of the year-class can be "repaired". It would seem that this occurred in 1955 in Mälaren but not in Hjälmaren. The more open topography of this latter lake probably gives a pronounced mortality of eggs or fry of pike-perch in cold and windy weather, if cold water is drawn to the shores. The amplitude of rich and poor year-classes is also bigger in Lake Hjälmaren, and this may be due to the same cause. This illustrates the difference between lakes, mentioned also by DEELDER and WILLEMSEN (1964).

Summary

1. Samples of some 1,700 pike-perch, taken from the big Lakes Hjälmaren and Mälaren during 1955—65 were examined and their age, growth and weight recorded.

2. In both lakes growth was found to be slightly better in females. Growth was faster in Hjälmaren than in Mälaren, but weight was higher in Mälaren. Maturity occurs in ages 3—8 for the males and 4—8 for the females, and comes roughly one year later in Lake Mälaren, where growth is slower.

3. The relative strength of eight year-classes was estimated and found to be very much the same in the two lakes. Two early and warm summers created rich year-classes, and a cold summer gave very poor survival.

4. The pike-perch is rather sensitive to the temperature of the water, but in northern regions quite a number of other species also react strongly to temperature as regards movements, growth and survival.

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The Grayling, Thymallus thymallus (L.), of the Sundsvall Bay Area

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1. Introduction

In Sweden the grayling, *Thymallus thymallus* (L.), is a typical northern fish with a coherent distribution in rivers from the Dalälven in the south to the Finnish border in the north. South of this area there is grayling in the water system of the Motala Ström (Lake Vättern) and in the Klarälven. Earlier it was present in the Lagan on the Swedish west coast but it is said to have now completely disappeared from that river.

In the northern distribution area the grayling is a fish for rivers as well as for lakes. In the more southerly part of the area it appears only in rivers, but further to the north it is also common in lakes with clear, not too acid water; in such lakes it is found up to the western mountains. Some lakes in this mountain area have dense populations of grayling and offer very comprehensive angling.

In addition to this freshwater presence the grayling is also very common along the coast of northern Sweden. There is a coherent distribution along the coast from just south of Sundsvall Bay northwards around the Gulf of Bothnia and far down the Finnish coast. In certain areas this stock can be very abundant and earlier there was commercial fishing for grayling in many places along the coast. South of the coherent presence along the coast there is local occurrence of grayling around river mouths, for instance, those of the Ljusnan and Dalälven rivers.

As in other rivers in northern Sweden the grayling has been very common in the Indalsälven, especially in parts with fast-running water. In parts with a very slow current its presence has been less conspicuous but by no means unusual. During the time when fishing with "otters" was allowed the method was used intensively for grayling on a 25-kilometres-long calm stretch of the river with rather deep water and only sandy bottoms. The catches were said to be good; moreover the fish were bigger there than in stretches with rapids.

Apart from the use of otters, angling with worms was the most important mode of fishing. Especially in springtime this type of angling for so-called "ice grayling" could give very good catches. This spring-time angling was

directed at grayling which before and during spawning time were collected in smaller areas.

Otter fishing in running water was finally forbidden and since then the fishing for grayling has mostly changed to angling from the shore of from boats with flies or worms or to harling, generally with two or three rods. Boat fishing with one long line having many wet flies has also been common. Since 1945 fishing with fly rod and dry flies has occurred to a certain extent. Spinning has also produced some grayling, and bigger fish, especially, have been taken on small spinners.

No considerable catches have been made with nets, which indeed could not be used in places where grayling was common. Seine netting for white-fish (*Coregonus*) during late summer and early autumn has given only small catches of grayling.

Sundsvall Bay, into which two big rivers, the Indalsälven and the Ljungan, discharge, (Fig. 1), and where the salinity is very low, has had a large abundance of grayling. The fishing for grayling at the coast was practiced with nets or otters (personal communications from JOHN BERGSTEN, KARL KARLSSON, and several other fishermen). From about 1945 on fishing with fly rods and dry flies has occurred (PETERSON 1958).

From what has been said above it should be clear that the grayling has not been an economically valuable fish. It has rarely been caught for sale, but is a typical fish for the household (PETERSON 1962). On the very few occasions when grayling has been marketed it has been offered together with whitefish and generally, indeed, it has been sold as a whitefish. As a fish for the household, however, or for the angler the grayling is of great value. In many places it is the only game fish which appears numerous enough to give good catches in a short time and at the same time takes a fly or another bait under very different conditions.

It has been a common opinion that the grayling stock in the river has been recruited from the fish which in the spring migrates from the coast to the river for spawning. Fry and young fish, it is said, go down to the coast and return as adults for spawning. The big fish present in the river would accordingly be fish which had stayed in the river after spawning. In an article on grayling signed "PHOXINUS" (1939) such views are also put forward concerning the migration of grayling between lakes and rivers. If the grayling's possibilities to migrate between coast and river were cut off, as they were of for example at Bergeforsen in the Indalsälven from 1954, the stock of grayling both at the coast and in the river would suffer.

2. Material and methods

The collection of the material took place during the years 1951—62. In all the investigation covered 615 grayling, 575 from the Indalsälven and 40 from

the coast. Of the grayling from the river 307 were preserved in formalin and carefully examined, while from the remaining 268 fish scale samples were taken, length and weight were noted, and the sex was determined. Among some of these fish the stomach contents have been examined in the field.

The catch during 1951—54, totalling 395 fish, was taken along the whole river from the channel downstream of the power station at Hölle right to the river mouth, a distance of nearly 90 kilometres. The grayling caught during 1955—62 were all taken just below the power station at Bergeforsen. Of the fish from the sea 26 were preserved and from the remaining 14 fish scale samples were taken, length and weight were recorded, stomach contents were examined and sex was determined in the field.

A further 375 grayling were tagged in the river and 10 at the coast. This material has not been used when calculating growth.

The material from the river 1951—59 and from the sea was taken with fly rod. The selectivity of this fishing tackle could of course be discussed, especially as regards younger fish (see below). As a result of specialization on certain food among some individuals, the fishing method may be selective. On the other hand, the investigation shows that grayling with only bottom animals in the stomach can be taken on a dry fly. Smaller fish up to one year old, were taken by electrofishing and in a trap for salmon smolts in the mouth area of the river (LINDROTH 1953, 1954, JOHANSSON 1956). Part of the one-summer-old material was placed at my disposal by Fishery Officer C.-G. HAMMARLUND from his investigations in the river. The catch of the fish from the years 1955—62 were made partly in the so-called central fishery at Bergeforsen and partly with gill nets just below the power station.

The fish used for the tagging experiments were partly taken by fly rod in the upper part of the river and at the coast, and partly in the central fishery at Bergeforsen.

As a routine length and weight were measured, stomach contents were examined, sex was determined and age and growth were reckoned by scale reading. Further, the gillrakers were counted (left anterior gillbow) on all preserved fishes, and on some of them the scales in the lateral line were counted. On the fish, preserved in formalin, the weight has been reduced by 10 per cent to make it comparable with the weight of fresh material (ANDRÉN 1953).

For age determination the scales were taken on the left side of the body between the posterior half of the dorsal fin and the lateral line. The annuli seem to be formed during May or the beginning of June. There is no annulus on the scales of a one-year-old grayling caught in April or May, but it is always found on fish of the same year-class caught in June. ROSÉN (1920), on a grayling caught on May 1, found "the border zone" (the annulus) partly formed; he says that at the end of June there were a couple of circuli
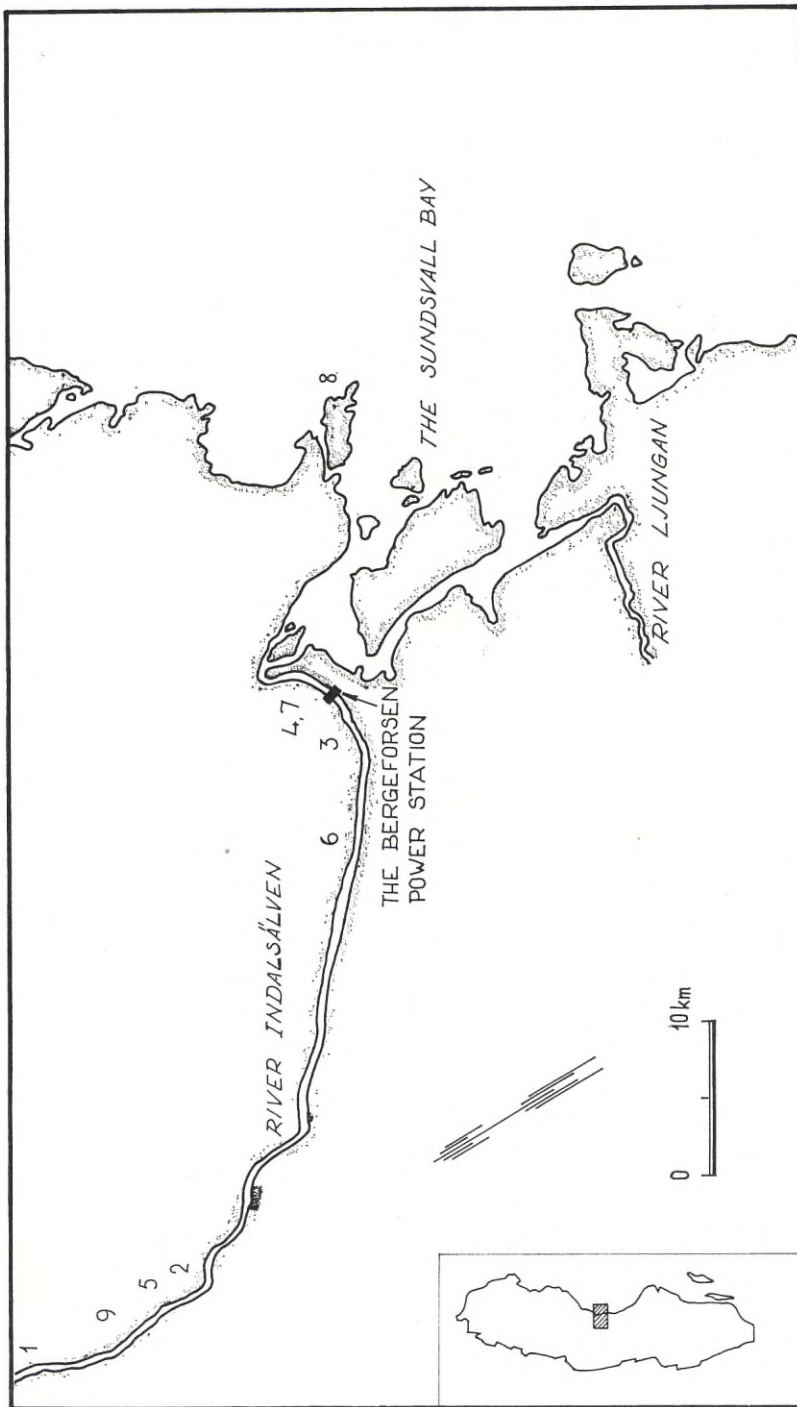
Fig. 1. Map, showing River Indalsälven and the Sundsvall Bay Nr 1—9 places where tagged graylings were released (see table).

outside the border zone. BROWN (1943) found on Montana grayling, (*Thymallus signifer*) that the annulus is generally formed between April 15 and May 15.

No noteworthy scale erosion in connection with the spawning seems to appear in grayling in this area. The same thing has been observed by, for example, PLATT (1936) and JONES (1953) in grayling in British rivers and BROWN (1943) in American grayling.

3. Ecology of the young grayling

The grayling spawn in the river a short time after the breaking up of the ice. From catches made just below the power station at Bergeforsen it is obvious that ripe females can be found at the end of April at a water temperature of 3—4°C and at beginning of May, also at a temperature of about 4°C, spawning grayling can be found. The largest number of spawning fish is generally found about the middle of May at a water temperature of 5—6°C. FABRICIUS and GUSTAFSON (1955), in their study of the spawning of the grayling in Hegledbäcken, found a considerably later spawning. In that brook, where the temperature varies substantially between day and night, the most intensive spawning took place at a temperature of about 10°C, the variation during 24 hours was 4.0—11.6°C. In the mouth of the Indalsälven River there is practically no temperature variation at all between day and night, but at the time of the most intensive spawning the water temperature rises about 0.3°C from one day to the next.

It seems to take about three weeks to hatch the grayling eggs, while the water temperature increases from 5 to 12°C. The newly hatched fry swims fairly soon after the hatching, but it seems to remain near the bottom, where it can stay behind stones (LINDROTH 1957). It is very common to find grayling fry, only a few weeks old, in small pools apart from the river. These pools are formed in connection with falling water in the early summer. This observation, confirmed by electrofishing, indicates that young grayling lack the ability of young salmon and brown trout to find their way out from such pools before they are altogether cut off from the river (LINDROTH 1953).

There was a drift of young grayling out from the river to the sea, in any case before the construction of the power station at Bergeforsen. Between July 3 and July 17 1953 17 young grayling with a length of 32—55 millimetres were caught in a smolt trap in the river mouth. A further 8 young grayling with a length of 58—91 millimetres were caught between August 3 and October 19. The trap was constructed to catch fish of the size of salmon smolt, i.e. more than 120 millimetres. The collecting fence and the meshes in the corf were not fitted to catch very small fish, so the number of small grayling caught there during their first summer must probably have been very small as compared with the total number of migrating fish.
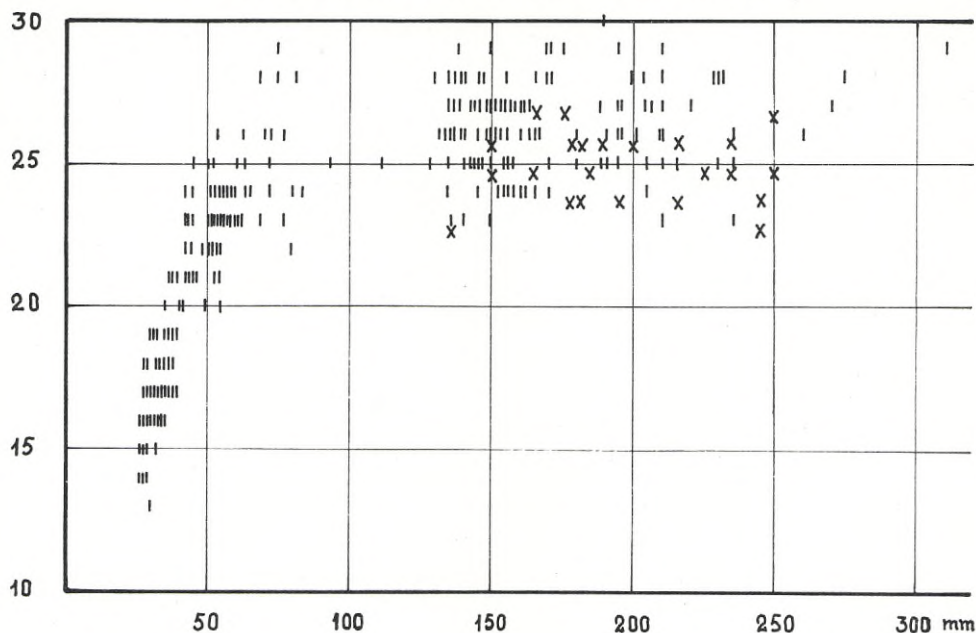
Fig. 2. Number of gillrakers compared with body length in grayling from River Indals-
älven (I) and the coast (X).

In the young grayling the first scales appear along the lateral line when
the fish is about 37 millimetres long. GUSTAFSON (1949) found that the scales
were first formed at a size of 33.5 millimetres, but it is not possible to find
any scales on grayling from the Indalsälven at that size. BROWN (1943) found
scales on Montana grayling at a length of 35.5 millimetres. The number of
circuli increase from 2 at a body length of about 40 millimetres to 8—10 at
a length of 70 millimetres and 10—12 at an age of one full year and a length
of 90 millimetres.

The number of gillrakers increases rapidly (Fig. 2) and already during the
first summer they reach full number as in whitefish (SVÄRDSON 1951, LIND-
ROTH 1957). In the smallest fish investigated, 25—30 millimetres, the number
varies between 13 and 18, and already at a length of 70 millimetres the
number reaches 23—29, i.e. that of the adult fish.

Sex determination has been made in fish less than one full year old, and
it has been possible to determine the sex in fish from about 50 millimetres
in length. The sex ratio seems to be close to 1:1; from 63 fish investigated
and belonging to age group 0+ there were 34 males and 29 females. In the
size in question there were a few in which sex could not be determined.

The types of locality where the young grayling spend their first summer
may be rather different, as it seems that their plasticity in choice of biotope
is greater than that of young salmon and brown trout. Usually they are

found on the same sort of bottoms as are salmon and brown trout of the same age, i.e. on bottoms with coarse gravel and small stones and with a rather rapid current. But even during their first summer they can be found on bottoms with very big stones and a rather slow current, but very rarely in nearly stagnant water. MÜLLER (1961) has found the same behaviour in grayling from the River Lule älv. He has found them in areas with a water speed of 0.5 metre per second as well as in currents of less than 0.2 metre per second, though in the latter case only on stony bottoms. One peculiarity of the grayling during its first year is that, if frightened, it hides under stones as do salmon and brown trout of the same age. This has also been reported by LINDROTH (1955). This is the reason why it has been possible to catch young grayling by electrical fishing. Older grayling, when frightened, always swim off very rapidly, often with the current.

Nothing is known about spawning places for grayling in the Sundsvall Bay. In the northern part of the Gulf of Bothnia many spawning places for grayling are known at the coast. One very well known spawning place is around the island of Holmön off the mouth of the River Ume älv (RIMFÄLT and others, personal communication). Great numbers of grayling eggs were taken there earlier for different hatcheries. Further north, too, in the archipelago off the coast of Norrbotten, many spawning places are known (ROSÉN 1920, MÜLLER 1960 and several others). It is also known that the grayling may spawn in lakes, e.g. Lake Vättern (ANONYMUS 1938, ECKERBOM 1938).

That young-of-the-year of grayling must occur also in the Sundsvall Bay is clear. As stated above, a number of migrating young grayling were caught in a smolt trap just at the river mouth (LINDROTH 1953, 1954 and JOHANSSON 1956). ROSÉN (1920) says that the fry of coast grayling that hatch in the river probably stay there for some time before migrating to the archipelago off the coast. Owing to the catching methods used for coast grayling in this investigation, fly rod, it has not been possible to catch grayling younger than 1+. Young of that age, however, are common.

4. Dominance of immature fish

Nearly all grayling one year and older, caught during 1951—54 both in the river and at the coast, were taken with fly rod. They may be looked upon as fairly representative of the year-classes older than one year. The catches during the years 1955—62 from the area below the power station at Bergeforsen are not representative of the different year-classes as the fishing methods used catch only adult fish, owing to mesh sizes, etc. The total material during the years 1951—54 is distributed among the different age groups as follows:
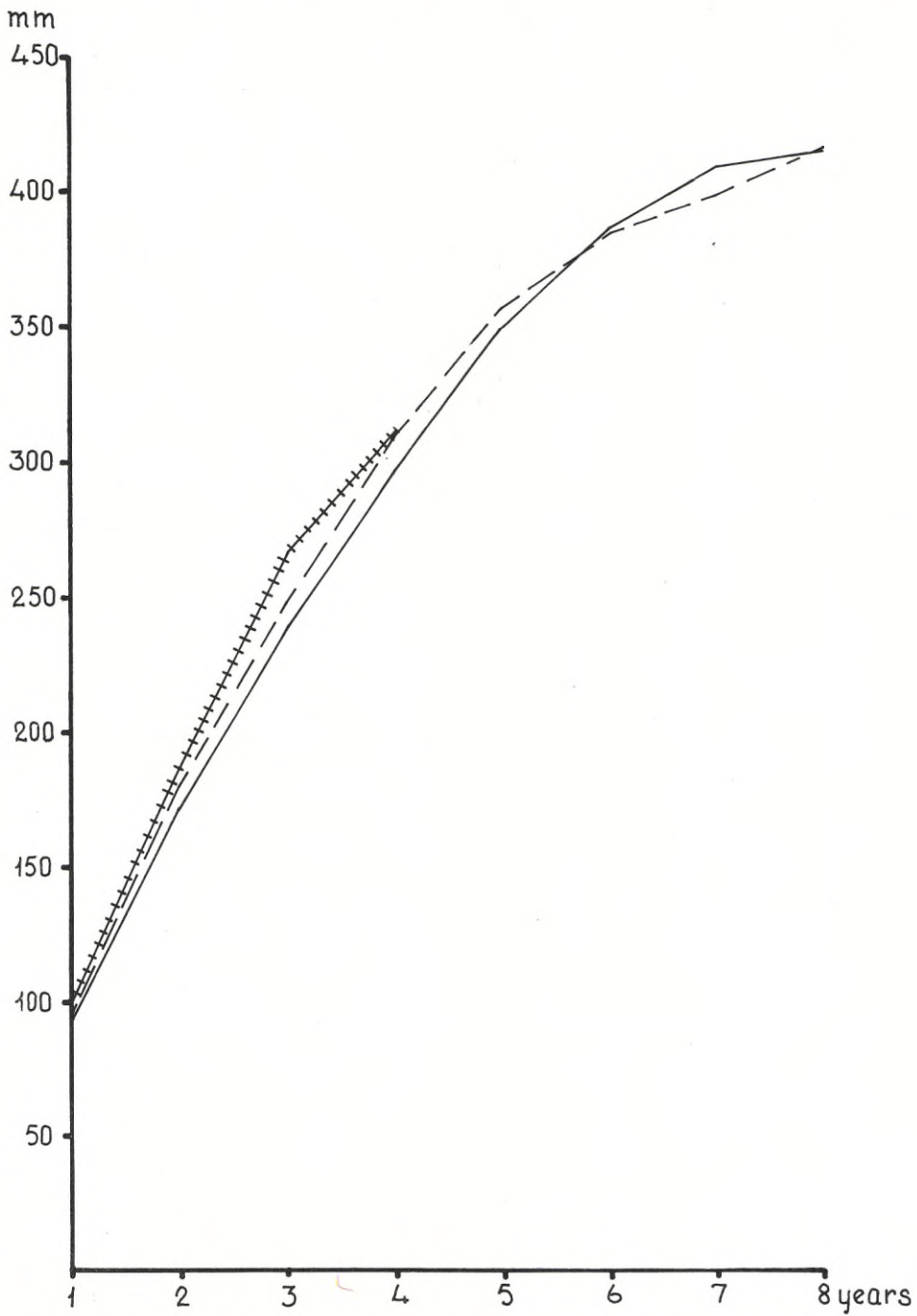
Fig. 3. Growth in grayling from the river (———), below the Bergeforsen power station (— — —) and the coast (+++).

Indalsälven River			The Baltic Sea		
Age group	Number	%	Age group	Number	%
1+	74	36	1+	10	25
2+	62	30	2+	23	57.5
3+	33	16	3+	5	12.5
4+	22	11	4+	2	5
5+	6	3		40	100
6+	3	1.5			
7+	3	1.5			
8+	1	1			
	204	100			

The table shows that by far the greater part of the catches consists of one and two-year-old fish, both in the river (at least 66 %) and in the sea (83 %). These fish have not yet reached sexual maturity. Concerning catches with other fishing-tackles, it may be mentioned that when fished with a long rod and wet flies or worms the percentage of young fish was still higher. The depth conditions in the river were in fact often of such a kind that an angler fishing from the shore, or even when wading, could not reach the deep water, where the bigger fish preferred to stay. That type of angling was very often done in shallow water, where only young fish were to be found. Only when fishing from a boat was the distribution of age groups the same as when fishing a fly rod. In the River Indalsälven a great part of the grayling stock is caught before the first spawning (PETERSON 1948, PRITT 1888, SØMME 1936). The Indalsälven may, at the time of the damming at the power station at Bergeforsen in 1955, have been one of Sweden's richest grayling rivers and therefore the intensive fishing of young fish had not affected the reproduction.

5. Maturity

The age at which the grayling of the Indalsälven reaches sexual maturity has not been investigated, but in the material from 1955 to 1962, which should be a mixed stock of grayling from both river and coast, the youngest spawning males as well as females have been 5 years old. As already stated, the catch has been made with wide-meshed nets which do not allow the catching of smaller and younger grayling. GUSTAFSON (1949) found that among the grayling in Lake Storsjön the males reached sexual maturity at an age of only two years and the females at three years. SØMME (1936) considers that the grayling in northern Norway first spawn at an age of 5 or 6 years and thereafter spawn every year. PLATTS (1936) says that the grayling in the English rivers spawn for the first time when 3 years old and thereafter every year. SEGERSTRÅLE (1947) states that the males as well as the females are mature at an age of 5 years and a length of 35—39 centimetres; five years is a very high age for first spawning, but according to SEGERSTRÅLE it is true for grayling from both rivers and coast. MILLER (1946) has found that arctic grayling is mature at an age of 3 or 4 years.

6. Growth

The growth of the grayling from the three different groups can be seen in Fig. 3. The main growth occurs during June and July. The annual growth of the grayling from the river and from the area below the power station at Bergeforsen is rather uniform, being slightly better in the latter. The grayling from the sea has a better growth, 8—10 centimetres a year, compared with 6—9 centimetres for fish from the river. That the grayling from below Bergeforsen shows a better mean growth than the grayling from the upper part of the river may be due to a considerable presence of fish from the coast in the grayling population of the mouth area in the spring. The growth at the coast seems to correspond with observations from Lake Storsjön (GUSTAFSON 1949).

A comparison of different growth data is given in Table 1.

As can be seen, there are considerable differences due, however, partly to differences in the back calculations. The growth of the grayling in the Indalsälven is a little better than that of the grayling from the River Pasvigsälv in northern Finland (SEGERSTRÅLE 1947) and also than in the Lule älv with tributaries (MÜLLER 1957, 1960). Comparison with the data given by MÜLLER is difficult, as he seems to have used constructed years; he assumes that the grayling was born on July 1 and then counts the growth in periods of 12 months. His fish are given as "after the first year" and "after the second year", which in reality means fish of age groups 1+ and 2+.

The English grayling seems to grow much better in the first year than all the other populations (PLATTS 1936). It is somewhat dubious, however, if the scale reading was interpreted in the same way.

There seems to be slightly better growth of the male grayling. The difference, however, may be due to chance or some sort of selection in the sampling. ROSÉN (1920) holds that the female grayling from the coast may possibly grow better, but both HUITFELDT-KAAS (1927) and SØMME (1936) have found better growth in the males than in the females. BROWN (1943) has not found any difference in neither length nor weight between the sexes in American grayling.

The difference in growth between particular years can be quite large (Table 2) but a year with poor growth in young fish does not always give poor growth also in older fish. (See the years 1949—50 for grayling from the upper river and 1953—54 from the mouth area.)

The proportion between length and weight in all three groups can be seen in Fig. 6. There is also a comparison made with grayling from England (PLATTS 1936) and Finland (SEGERSTRÅLE 1947).

Table 1. Growth of grayling in different rivers. Length in millimetres.

	Length (in mm) at age										
	1	2	3	4	5	6	7	8	9	10	11
River Indalsälven	94	172	239	296	349	386	408	413	—	—	—
River Pasvigsälv	70	149	233	305	—	—	—	—	—	—	—
River Lule älv (Porsi)..	77	154	204	253	298	332	360	403	—	—	—
River Test	158	286	356	387	413	432	—	—	—	—	—
Great Bear Lake	93	155	231	285	325	353	378	399	410	436	454

7. Food

Investigations have been made of the stomach contents in all preserved material and also in a considerable proportion of other fish. (Table 3).

The dominating food in grayling of age group 0+ and 1+ consist of terrestrial insects but also in 2+ fish these insects form an important part of the food. In older fish from the river larvae of *Trichoptera* are the most important food, the grayling change to become bottomfeeding. Among the insects, taken from the water surface, ants sometimes can be very numerous; up to 50 may be found in one single fish. They appear mostly during swarming time, but before and after that time wingless ants are common in the food. Among winged insects mosquitoes, gnats and flies dominate, but also for example *Homoptera* are common. Water insects are less common, but *Corixa* and *Gyrinus* occur. Plankton can only be found in age group 0+ and then mostly in fish caught in locked pools. Copepodes form the dominating group. Chironomides are an important part of the food; they are eaten by fish up to age 5+ in this material. Of less importance are larvae of gnats (*Simulium*), they occur sporadically up to age 2+ in the river grayling. Among the larger insect larvae the *Trichoptera* dominate; they are the most important food in older fish. In addition *Ephemeroptera* and *Plecoptera* are common in the food, especially in the 0+ group. Older fish often eat molluscs; up to five of these have often been found in one fish. Grayling of the sizes included here are hardly piscivorous; only some few small fish (bullheads or lamprey larvae) have been found in the stomach contents.

In grayling from the coast, fish are more common. Young perch up to 50 millimetres are the most common but small sticklebacks are also taken. In the grayling caught in the spring below the power station eggs of salmon, brown trout and whitefish and once grayling have occurred in great numbers. In fact fish ova seem to be the most important part of the food in that area in the spring, followed next by larvae of *Trichoptera*. Newly hatched fry of salmon, brown trout and whitefish can also be found among the stomach contents. In one grayling 50 ova or fry of salmon or trout have been found and even a greater number of whitefish ova may occur. The occurrence of
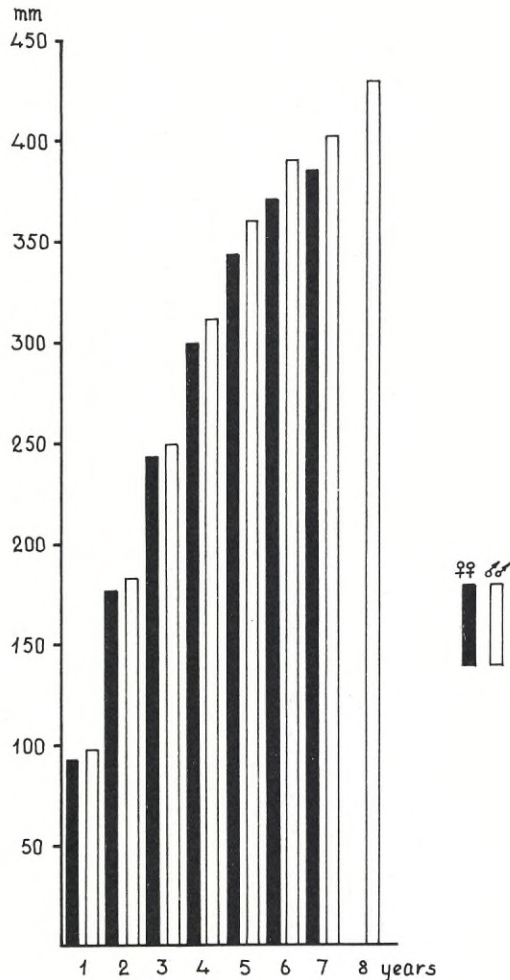
Fig. 4. Difference in length between the sexes in grayling from below the power station at Bergeforsen.

salmon and trout eggs can be explained as a result of the sorting of eggs in the salmon hatchery, where eggs with high mortality often are refused and washed out through the outflow to the river. Eggs and yolk-sac fry from natural spawning are normally hidden in the gravel and are inaccessible to the grayling. The whitefish eggs, on the other hand, originate from natural spawning as a great number of whitefish spawn on the sandy bottoms below the power station.

Besides these common food objects in grayling, some more peculiar items can be mentioned. In two grayling there were found 50 and 30 hair-worms (*Gordius aquaticus*) respectively in the stomachs; in the one with the greater number the whole gut was full of the animals in an undigested state. The same strange choice of food has been found in whitefish in Lake Brunträsket
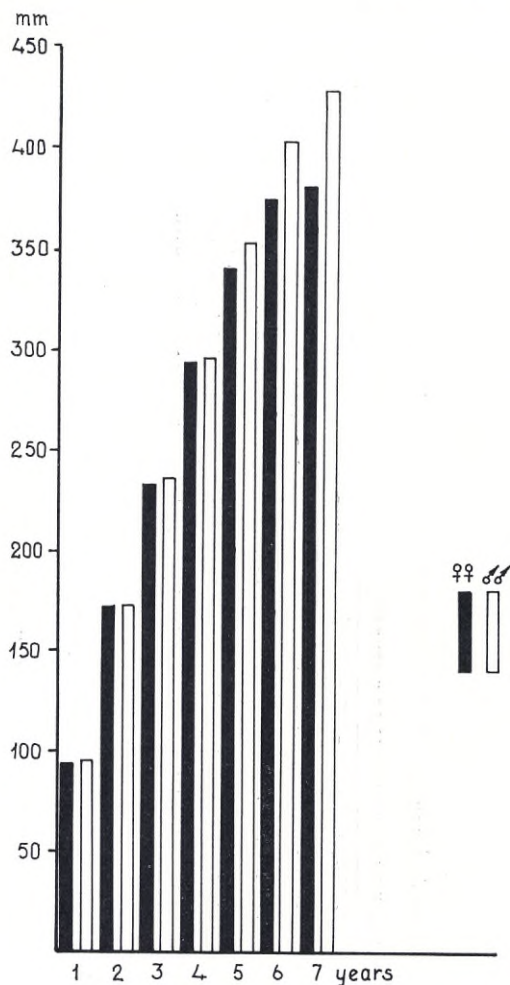
Fig. 5. Difference in length between the sexes in grayling from River Indalsälven.

in Malå in northern Sweden, where in the spring hair-worms were very common in the food (PETERSON 1949). More or less by mistake, small pieces of wood, fir needles, seed, other pieces of plants and green algae might have been taken when the fish were feeding. A blue-coloured piece of a feather, apparently a part of an angler's fly, has also been found.

Only 6 fish of 335 have been quite empty; 5 were in age group 0+ and of these 4 were taken in a closed pool and 1 in the smolt trap mentioned earlier. The sixth was a 4+ fish taken on a fly in the upper part of the river.

Specialization on one kind of food is rather common. In the 0+ group it has been either on winged insects or on copepodes, in other age groups on winged insects or *Trichoptera*.

As can be seen above, the grayling find their food among several groups

Table 2. Mean length in millimetres at the beginning of the growth in the year of (A The River, B below the power station, C the coast).

Year-class	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961
1944 A	135	203	265	312	333	361	388	413	—	—	—	—	—	—	—	—	—
1945 A	—	116	189	254	313	362	392	415	—	—	—	—	—	—	—	—	—
1946 A	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1947 A	—	—	—	102	173	244	303	340	389	—	—	—	—	—	—	—	—
1948 A	—	—	—	—	98	171	240	299	371	—	—	—	—	—	—	—	—
1949 A	—	—	—	—	—	95	170	238	268	—	—	—	—	—	—	—	—
B	—	—	—	—	—	89	150	200	257	323	355	377	393	—	—	—	—
C	—	—	—	—	—	92	176	238	315	—	—	—	—	—	—	—	—
1950 A	—	—	—	—	—	—	96	174	232	330	—	—	—	—	—	—	—
B	—	—	—	—	—	—	89	168	239	272	327	349	366	375	—	—	—
C	—	—	—	—	—	—	106	207	276	—	—	—	—	—	—	—	—
1951 A	—	—	—	—	—	—	—	91	165	—	—	—	—	—	—	—	—
B	—	—	—	—	—	—	—	93	175	253	310	358	391	414	425	—	—
C	—	—	—	—	—	—	—	100	183	—	—	—	—	—	—	—	—
1952 A	—	—	—	—	—	—	—	—	88	—	—	—	—	—	—	—	—
B	—	—	—	—	—	—	—	—	91	166	228	284	331	362	382	—	—
C	—	—	—	—	—	—	—	—	104	—	—	—	—	—	—	—	—
1953 B	—	—	—	—	—	—	—	—	—	97	184	249	306	356	386	413	431
1954 B	—	—	—	—	—	—	—	—	—	98	183	241	316	362	400	411	
1955 B	—	—	—	—	—	—	—	—	—	—	104	194	269	331	376	405	
1956 B	—	—	—	—	—	—	—	—	—	—	—	96	179	252	316	367	

of animals. However, the older fish seem mainly to seek animals living on the bottom, *Trichoptera,* molluscs, and so on; but at the same time winged insects are frequently taken from the surface. This feeding from the bottom at a depth of often more than 2 metres obviously does not prevent the grayling from rising to the surface to snap at a rapidly floating food object (dry fly).

Other investigations have generally shown the same choice of food in grayling from other localities. Some differences may be mentioned here. From the Dalälven River TRYBOM (1908) mentions that he found fish remains in many graylings. Young whitefish of up to 50 millimetres in length, perch (*Perca fluviatilis*), roach (*Leuciscus rutilus* L) and alburn (*Alburnus alburnus* L) of the same size, and bullhead (*Cottus gobio* L) up to 60 millimetres were found, sometimes in quite large numbers. In a grayling female, 300 millimetres in length, he once found not less than 19 young roaches. The smallest grayling in which he found fish remains was only 105 millimetres. Among other differing stomach contents, he twice found small crayfish (*Astacus fluviatilis* L).

TRYBOM's investigation was first meant to show the predation on salmon and brown trout in younger stages in the lower part of the Dalälven. He found that during the spawning times of those two species their eggs form the main food for the grayling which was in the spawning area. He fished

gr.

1500

x—————x RIVER INDALSÅLVEN
□—————□ BELOW THE POWER STATION
•—————• COAST
△—————△ FINNISH COAST
○—————○ RIVER TEST

1000

750

500

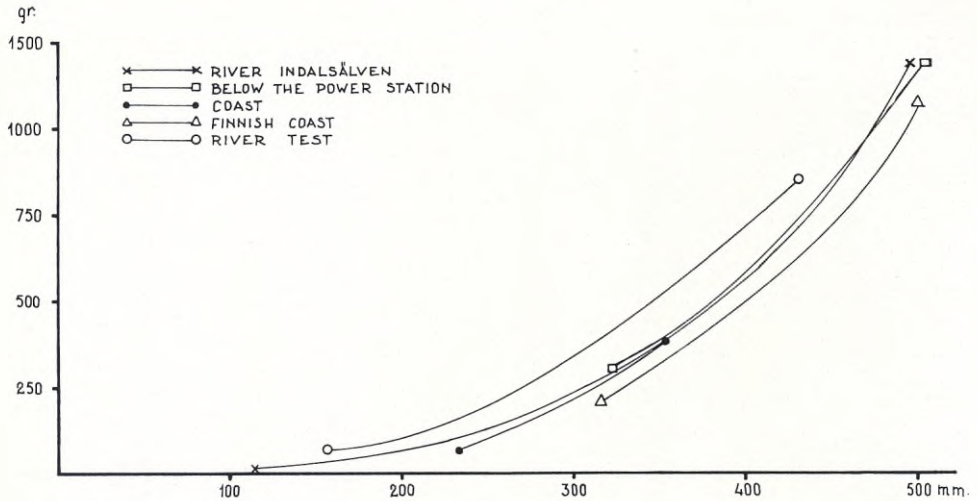250

100   200   300   400   500 mm.

Fig. 6. Length-weight relation in grayling.

for grayling only within these spawning areas, using a small-meshed seine net. To some extent he also found eggs of whitefish in grayling but they were never so numerous as salmon and trout eggs.

TRYBOM also made investigations in the spring and the early summer to see to what extent the grayling also took fry of salmon and trout, but he could find no evidence of this. His material was rather small. TRYBOM however states that the numbers of salmon and trout eggs taken by grayling is so great that this fish must be looked upon as the most serious enemy of the salmon and the trout. "The grayling annihilates as many salmon as can be hatched in a medium-sized hatchery", he says in his report.

From the Dalälven River EKMAN (1906) also found that most of the grayling bigger than 220 millimetres and also many smaller ones had eggs of salmon or trout in the stomach. In one fish of 335 millimetres he found no fewer than 150 eggs in the stomach and 25 still undigested eggs in the gut. HULT (1947) found in a grayling of 400 millimetres, caught in the Dalälven on June 5, 1946, a roach with a length of more than 120 millimetres. This must be considered as an exceptionally big prey for a grayling of that size.

From northern Sweden ROSÉN (1920) has found the same kind of food as has been reported here in the grayling from the coast. He also found fish, among others sticklebacks (*Gastereostus sp.* L) in the food. MÜLLER (1957, 1960) has found in grayling of age group 0+ from the River Lule älv a different food from what is found in the Indalsälven. He mostly found zoo-plankton in the youngest fish, but that can be explained by the fact that his graylings in group 0+ were caught in areas with a very low water velocity. In older fish the grayling from the Lule älv seem to take more winged

Table 3. Stomach contents of grayling from river Indalsälven (A), Below the power station (B), and the coast (C). Number of fish with different groups of food animals in stomach content.

Age group	Number examined	Terestrial insects	Aquatic insects	Plankton	Chironomidae	Simulium	Ephemeroptera and Plecoptera	Trichoptera	Molluscs	Fish	Eggs of salmon or trout	Eggs of Coregonus	Empty	Specialists in one kind of food	Miscellaneous
0+ A ..	168	113	10	35	52	7	45	13	—	—	—	—	5	64	6
1+ A ..	61	57	3	—	16	6	6	26	4	—	—	—	—	22	—
1+ C ..	10	7	6	—	6	—	—	3	3	4	—	—	—	—	—
2+ A ..	42	26	1	—	6	6	2	22	10	—	—	—	—	16	1
2+ C ..	16	13	11	—	6	—	—	3	9	9	—	—	—	2	—
3+ A ..	20	4	—	—	2	—	1	14	7	1	—	—	—	12	1
4+ A ..	12	3	—	—	1	—	4	7	3	1	—	—	1	4	—
4+ B ..	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
5+ A ..	3	1	—	—	1	—	—	2	1	1	—	—	—	—	1
5+ B ..	69	—	—	—	—	—	—	38	2	2	12	15	11	39	6
6+ A ..	2	1	—	—	—	—	—	1	1	—	—	—	—	1	—
6+ B ..	60	1	—	—	3	—	—	29	4	5	11	27	2	29	8
7+ A ..	1	—	—	—	—	—	—	—	1	—	—	—	—	—	1
7+ B ..	25	1	—	—	—	—	—	12	2	1	4	11	3	10	3
8+ B ..	4	—	2	—	—	—	—	2	—	—	1	1	1	1	—

insects than do grayling of the same age from the Indalsälven. Here, too, the difference may be due to catches in different habitats. MÜLLER never found fish in the food of the grayling from the Lule älv.

In Norway SØMME (1936) found the same food in grayling as is reported here from the Indalsälven. Though he examined unusually big grayling he never found fish in the food. SEGERSTRÅLE (1947), from an investigation of grayling from the Finnish coast, also reports about the same food, but in wintertime only he found fish, viz. ten-spined stickleback (*Gastereosteus pungitius* L). However, his material is rather small.

British investigations (PRITT 1888, PLATTS 1936 and RADFORTH 1940) confirm that grayling take most of their food from the bottom after they have passed the youngest stage. In grayling from the River Tweed, for instance, 94,5 % of the total stomach contents consisted of bottom animals. Gnat pupae form an important part of the food in older fish also. Fish was never found in the English grayling, but PRITT says that minnows (*Phoxinus phoxinus* L.) are used as a bait when fishing for bigger grayling in the River Wye in Derbyshire and the River Yore. SOMMANI (1953), who investigated the food of young grayling in some waters in Italy, found that plankton is the main food for grayling during the first summer. In arctic grayling MILLER (1946) found that terrestrial insects are the dominating group of animals in the food.

8. Movements

As already mentioned in the Introduction, there was a movement of grayling between the coast and the upper parts of the river before the construction of the power station at Bergeforsen. To learn something about how extensive this movement was, a number of grayling were caught when spawning below the power station at Bergeforsen, tagged and then released at different places along the river. Further tagging has been done in the upper part of the river with grayling caught on angling. Furthermore a few grayling caught at the coast have been tagged and then released there.

Common to all the taggings is a relatively high rate of recapture, which indicates a high fishing intensity. The poorest recapture of grayling put out in the river is from June 18, 1956, a tagging which only gave 24 % of recaptures. Probably the fish were in poor condition after being kept in a basin for a long time. The very poor recapture at the coast may be partly due to the low fishing intensity in that special area (military area with entry forbidden).

All taggings of grayling caught during spawning migration (material: below Bergeforsen) have given recaptures both in the river and in the sea (Table 4).

From tagging no. 1, at Hölle, with fish from below Bergeforsen one fish was caught at the coast 9 days later and 100 kilometres from the place of release. From the same tagging another fish was caught 14 months later just at the releasing place. Because of the beginning of the damming at Bergeforsen during 1954 that fish could not have left the river and turned back again to spawn in 1955. It had stayed in the river more than one year. From the tagging at Järkvissle (no. 2), the first recaptures came after about 10 days, upstream of the place of release, but three weeks later one of the tagged grayling was taken at the coast about 60 kilometres south of the mouth of the river. It was a migration of about 120 kilometres in 21 days. Another fish was caught 14 months later, just at the place of release. From tagging no. 3, at Svedje, it may be noted that only 5 days later one fish was caught at the coast, 35 kilometres from Svedje and 20 kilometres from the river mouth. One year later, one of these grayling was caught 65 kilometres upstream of the releasing place. From tagging no. 4, at Bergeforsen (below the dam) recaptures can be noted at the coast a few days after release, but there are also recaptures just below the place of release after 4 months.

From the "pure" river grayling in tagging no. 5 — the fish were caught by angling, tagged and immediately released at the same place — all recaptures during 3 years after the tagging had been made very close to the releasing place. Tagging no. 6, at the Kävsta Bridge, gave after only 3 days one recapture 20 kilometres south of the river mouth, 45 kilometres from the releasing place. On the other hand, 6 weeks after release two grayling were

Table 4. Recaptures of grayling.

Tagging nr	Day	Number tagged	Mat.	Place	Number	%	River Number	%	Coast Number	%
1	10.6.54	14	B.-f.	Hölle	11	79	4	36	7	64
2	10.6.55	50	B.-f.	Järkvissle	29	58	15	52	14	48
3	17.6.55	40	B.-f.	Svedje	24	60	7	29	17	71
4	17.6.55	41	B.-f.	Småholm.	22	54	11	50	11	50
5	17—18.9.55	29	I	Hölle-Liden	12	41	12	100	0	0
6	18.6.56	58	B.-f.	Kävstabr.	14	24	7	50	7	50
7	27.6.56	134	B.-f.	Småholm.	58	43	27	47	31	53
8	7.56	7	K	Tynderö	1	14	0	0	1	100
9	2—9.9.56	9	I	Boda	3	33	3	100	0	0

Mat. B.-f.=caught below the power station
    I=caught in the river
    K=caught at the coast

taken 35 kilometres above that place and one year afterwards one fish was taken 5 kilometres upstream.

Tagging no. 7, below Bergeforsen, gave 10 recaptures at the coast during the months April—June in the following year. This catching time coincides with the spawning time during the year of tagging and may therefore possibly indicate that the grayling do not spawn every year.

The recaptures from taggings nos. 8 and 9, fish caught by angling, are all very close to the releasing places. This can be said of all taggings of fish taken at other times than in connection with spawning migrations. The migrating fish, on the other hand, have proved partly to stay in the river, in spite of possibilities of leaving it, and partly also to return to the sea, very quickly sometimes. When the taggings were done in 1954 and 1955 the damming at Bergeforsen was only partly up but was still high enough to stop all fish from passing upstream. In 1956 the damming was completed (23 metres) and fish passing down had to go through the spillways or the timber flume. Fish caught the year after the tagging above Bergeforsen cannot have been in the sea and turned back for another spawning.

GUSTAFSON (1949) found from his tagging in the Svartbäcken, Lake Storsjön, that the recaptures of the grayling returning to the lake took place close to the spawning river. Only two recaptures were made as far as 12 kilometres from the river mouth. The other 33 fish were taken within a radius of 4 kilometres from the tagging place. The grayling migrating for spawning in the mouth area of the Indalsälven is not so stationary; the recaptures are spread over an area within 20 kilometres north and 60 kilometres south of the river mouth. The latter is about the southern limit of

the coherent grayling population at the Swedish coast. On the other hand, the grayling seems to be very stationary during the other parts of the year. It is also obvious that some of the grayling, migrating from the sea to the river for spawning, can stay there for at least one year.

9. River and sea-going grayling as subpopulations

LINDROTH (1957) has shown that the whitefish caught at the coast of the Sundsvall Bay belong to two different populations. There is one whitefish spawning at the coast having a low number of gillrakers, and secondly a river-spawning species with more gillrakers. The average numbers of gill-rakers are about 28 and 31, respectively. As it was conceivable that a similar condition might also prevail in the grayling at the coast and in the river, the gillrakers were counted in some fish.

The average number of gillrakers is 25.1 in grayling caught at the coast and 26.2 in grayling caught above Bergeforsen (25 and 116 specimens respectively, all more than 100 millimetres and all caught at other times than spawning migrations). See Fig. 2. Though the difference seems to be statistically significant (P < 0.001) it is not possible to state that there are two different subpopulations. SVÄRDSON (1966) has shown that there are fewer gillrakers in younger than in older whitefish from the same stock and the same may be also the case in grayling. The grayling sampled from the sea is generally younger than that from the river.

The scale numbers at the lateral line have also been counted but no real difference has been found between grayling from the sea and grayling from the river. The number varies between 85 and 101, the counting being done in fish of age group 1+ and older (the highest number was found in a fish of age group 1+).

The tagging experiments have shown some tendency among the grayling from the sea to stay in the river after spawning. No spawning places are known at the coast within the Sundsvall Bay.

From all this it can be concluded that there is no evidence for the existence of different genetic subpopulations in the river and the sea.

10. Summary

1. The grayling has occurred and partly still occurs in great numbers in the lower part of the Indalsälven River and in Sundsvall Bay. The presence of a spawning migration between coast and river has long been known and it was possible to confirm this by taggings. It was not possible to find any real difference between an entirely river-living population on the one hand and a coast-living but river-spawning population on the other.

2. The habitat, growth, food, scale formation of the young grayling, as well as its drift down to the sea is discussed.

3. The growth of the grayling is rather rapid, with a uniform growth rate up to an age of 5—6 years. Very young fish in the age groups 1+ and 2+ dominate the angler's catch, fish 5+ and older are rarely caught. The males seem to grow somewhat better than the females.

4. The dominating food is terrestrial insects in younger fish and large insect larvae (mainly *Trichoptera*) in older fish. Plankton may appear in young fish of age group 0+. In rare cases fish may be found in older grayling, more commonly in the sea than in the river. Eggs are frequently eaten.

5. There is some movement in grayling during spawning time, but at other times the fish seem to be very stationary.

6. There is a difference as to the number of gillrakers between grayling caught in the river and at the coast respectively. This does not, however, prove the existence of two different subpopulations as the gillraker difference may be due to different age of the fish.

11. Acknowledgements

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On the Problem of Sibling Species and Possible Intraspecific Variation in Fourhorn Sculpin, Myoxocephalus quadricornis (L.)

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Introduction

The spread of glacial relicts, including the fourhorn sculpin (*Myoxocephalus quadricornis* (L.)), has been studied in Scandinavia for a hundred years. Recently there was published a new hypothesis (Segerstråle 1957, 1962) which sets out to explain the present distribution of the sculpin. The hypothesis is founded on some recent discoveries by Russian glaciologists.

In the early part of the Wisconsin (Würm) glaciation, the fauna of the brackish estuary of the Onega river was trapped by glaciers coming from the NW and thus cutting off the connection with the White Sea. The water of the Onega formed an ice-dammed lake, which gradually was pushed upstream. This Onega Valley Ice Lake persisted during the whole glaciation, and in postglacial times was the starting point for the spread of the glacial relicts, among them the fourhorn sculpin. In Sweden the fourhorn sculpin is present in some twenty deep lakes of the southern and central parts of the country and also in the Baltic.

The lake populations of sculpin have been found to differ in roe colour. Svärdson (1958, 1961) considers that the fact that the fourhorn sculpin fall into two groups where roe colour is concerned suggests a genetic difference and two independent and subsequent invasions.

The first invasion was the sculpins which had been trapped in the Onega Valley Ice Lake and isolated there and thus evolved to the so-called 'relictus' type, with yellow roe. When the glaciers began melting, this type spread over the Baltic drainage area by entering the Finnish Bay of the Baltic via Lakes Onega and Ladoga. The sculpin was also able to survive the Wisconsin glaciation outside the Onega Valley Ice Lake at the Siberian coast further east.

Shortly after the 'relictus' type had entered the Baltic, a short-term marine connection probably occurred between the Baltic and the Arctic Ocean. A second invasion by the green-egged 'quadricornis' type then occurred which replaced the 'relictus' type, except in lakes which had been inaccessible owing to upwarping of land. In Lake Fryken, fourhorn sculpin with

both egg colours have been reported. This suggests two sympatric populations, behaving as two species according to the hypothesis.

In order to examine the amount of genetic divergence between these two invasions of sculpin as well as the possible splitting up of the groups after they had reached their present geographical distribution, we have used as parameters of genetic transformation the protein 'pictures' obtained by starch gel electrophoresis. Since the proteins are primary products of the genes, differences in protein patterns which are not due to, for instance, food or disease will consequently reflect differences in the various genotypes. The investigation of various tissues by means of numerous histochemical staining methods may thus give a good picture of the magnitude of genetic transformation of the various populations of a species as well as the splitting of a genus.

Material

The present investigation is based on material collected from four lakes of central Sweden and from the Baltic, and the field work was performed during the autumn and winter of 1966.

The lakes investigated were Mälaren, Vättern, Orsasjön and Siljan. Attempts were also made to obtain fish from Lake Fryken, but without success.

The sculpin populations in the Baltic and in Lake Mälaren have a greenish or green-blue egg colour and thus belong to the *'quadricornis'* type according to SVÄRDSON's hypothesis. In Lakes Vättern, Orsasjön and Siljan, on the other hand the egg colour is yellow and these fish are thus of the *'relictus'* type.

In Lakes Vättern and Mälaren all fish were obtained at a depth of about 40 m, in Lakes Orsasjön and Siljan only between 80 and 90 m.

Methods

The methods employed in the present study are described elsewhere (NYMAN 1967). To summarize, they are a combination of electrophoresis on starch gel and various histochemical staining methods, and the buffers used in gel and electrode vessels have been those described by SMITHIES (1955), POULIK (1957), ASHTON & BRADEN (1961) and BURSTONE (1962).

Blood was taken by cardiac puncture by means of a scalpel and collected in heparinized tubes. The mucus was removed at the site of injection in order to prevent clotting. The micro-centrifuge of the Beckman Spinco Analytical System was employed when the haemoglobin was separated from the serum (20 s). The livers and the roe were washed in a physiological saline to remove excess blood and then homogenated in a glass homogenator cooled with an ice-water mixture, buffered with TRIS (POULIK 1957), after which the cell

Table 1

Prealbumin	polymorphism
Albumin	homogeneity
Transferrin	,,
Ceruloplasmin	,,
Alpha-glycerophosphate dehydrogenase	,,
Lactate dehydrogenase	,,
Haptoglobin	,,
Haemoglobin	,,
Catalase	,,
Leucine aminopeptidase	,,
Alkaline phosphatate	,,
Acid phosphatase	,,
Esterase	,,
Peroxidase	polymorphism

debris was spun down (20 min). The tissues were either treated and analysed simultaneously or stored in dry ice or in a freezer, at a temperature below —25°C.

The electrophoresis was performed for 1 hour 45 min at a constant voltage of 400 V. Some 25 samples could be tested at the same time, ensuring a good comparison.

Results

Three different tissues of fourhorn sculpin were tested. The major interest has been devoted to the blood, and the various histochemical staining methods employed have revealed the protein patterns of the protein groups presented below. (Table 1).

From Table 1 it can be seen that the proteins of sculpin blood are very homogeneous, i.e. with two exceptions there is no variation between the populations of different lakes, and thus no differences between the 'relictus' and the 'quadricornis' types.

One enzyme (peroxidase) was, however, found to be polymorphic with three different possible patterns, and by adopting a hypothesis that two allelic co-dominant genes are responsible for the segregation of these patterns the distribution of the three types was calculated and tested according to the HARDY-WEINBERG law of phenotype distribution in a randomly mating population. The three peroxidase patterns shown in Fig. 1 are thus termed S/S, the 'slow' homozygote, F/F, the 'fast' homozygote and F/S, which represents the heterozygote pattern.

Blood serum was obtained from 84 sculpin, distributed among the various lakes and the Baltic as presented in Table 2.

Table 2

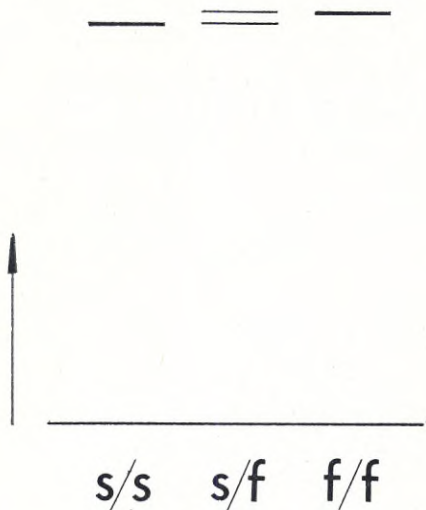| 'Quadricornis' type	Baltic	46	sculpin
	Lake Mälaren	14	,,
'Relictus' type	Lake Vättern	12	,,
	Lake Orsasjön	9	,,
	Lake Siljan	2	,,

Fig 1. The three patterns of blood-serum peroxidase. s/s='slow' homozygote, f/f='fast' homozygote, s/f=heterozygote.

s/s s/f f/f

Apart from the Baltic population, collected at the Askö Laboratory (University of Stockholm), the samples are too small for proper tests including chi-square analysis, but the phenotype distribution is shown in order to give some information on the trend of the gene frequencies (Table 3).

A good resemblance between observed and expected values seems to support the two-allelic theory, which is furthermore indicated in the chi-square value for the Baltic population ($\chi^2=0.27$, 1 degree of freedom, P 0.50 —0.75). Although no frequency differences seem to exist between the two types of sculpin, the gene frequency trend in Lake Vättern differs from the other populations.

The other polymorphism is located in the prealbumins (Fig. 2). Here the genetic background has another mechanism, since only two possible

Table 3

The Baltic (p(F)=0.23)	obs.	exp.	Lake Mälaren (p(F)~0.25)	obs.	exp.
F	3	2	F	2	1
F/S	15	16	F/S	3	5
S	28	27	S	9	8

Lake Vättern (p(F)~0.75)	obs.	exp.	Lake Orsasjön (p(F)~0.28)	obs.	exp.
F	7	7	F	1	1
F/S	4	4	F/S	3	4
S	1	1	S	5	5

Lake Siljan	obs.	exp.
F	—	—
F/S	1	—
S	1	—

Fig. 2. The two patterns normally occurring in the amido-black dyed serum proteins. N=the most frequently occurring type, D=the rare type.

N D
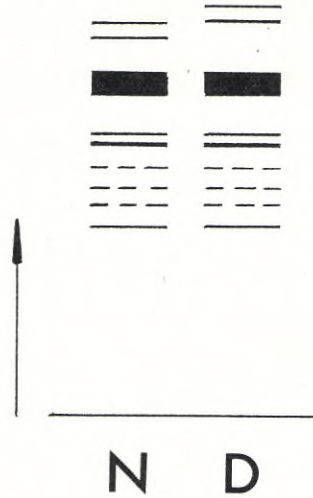
patterns exist. The frequency of the common pattern is found to be about 0.9, with no marked differences between the various populations.

The amido-black dyed proteins, the esterases and the peroxidases of sculpin liver do not show any kind of variation, except for quantitative differences in the esterase patterns (Fig. 3). No association with sex or geographical origin was noted.

Tests of the proteins of roe of different colour did not reveal any variation associated with colour. In the amido-black dyed roe proteins, one deviating pattern was detected, but this was evidently due only to a difference in concentration (Fig. 4).
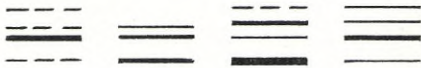
Fig. 3. Four normal patterns of liver esterase. The differences are evidently due to variations in concentration.
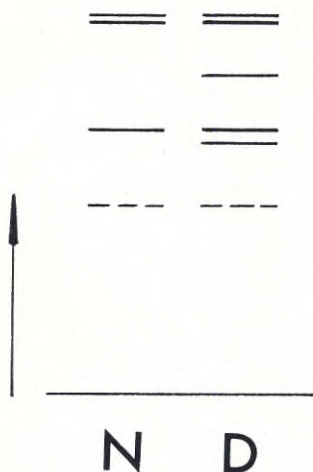
Fig. 4. Amido-black dyed roe proteins. N=the normal pattern, D=a deviating pattern.

N   D

To sum up the results, only two types of variation were detected, none of them apparently associated with either type of sculpin, and the same genes are present in all populations investigated where these proteins are concerned.

Discussion

Since the fourhorn sculpin is a pronounced deep-water-living animal which seems to migrate to shallow water only in the spawning season, one might expect a high degree of spatial isolation between populations of different bodies of water. Consequently most lake-dwelling populations can be considered as closed with respect to the inflow of alien genes from other demes. Such closed populations are thus good sources for speciation, since the environment of any lake differs at least slightly from all others, producing different selection pressures upon the genes incorporated in the local gene pools. Since the probability that the same mutations will occur in the same sequence in different populations is almost nil, recombination will subsequently produce different gene pools and the different populations will begin to diverge from one another. Such diverging phenotypes also exist in *Myoxocephalus quadricornis,* where the Baltic brackish water form is closest in resemblance to the arctic marine ancestor, and where the lake forms differ to some extent in eye size, body size and horn size. It has, however, not been tested to what extent this phenotypical variation is reflected in the gene pools.

MAYR (1963) has stressed the great importance of geographical isolates as the main source for the process of speciation. The rate at which this process works depends on the following three factors, as was pointed out by MAYR: "(1) the frequency of barriers, that is, of factors producing geographical
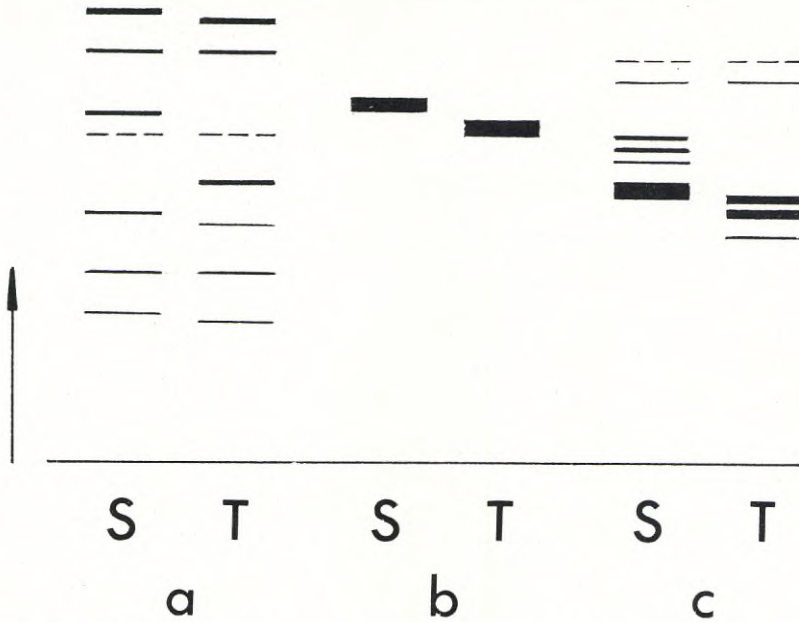
Fig. 5. Protein variations in three 'protein systems' of Atlantic salmon (S) and brown trout (T). a=blood-serum proteins (amido-black), b=blood-serum esterase, c=liver esterase.

isolates, (2) the rates at which geographical isolates become genetically transformed and more specifically at which they acquire isolating mechanisms, and (3) the degree of ecological diversity offering vacant ecological niches to newly arising species."

In our case we face geographical isolates which are rather perfect, owing to the above-stressed deep-water life of these animals. The rate of genetic transformation is a far more complicated problem, since the process of speciation shows an enormous variation even between closely related species. Very rapid speciation is found in, for instance, desert springs of the Great Basin region of North America (HUBBS & MILLER 1948, MILLER 1948, 1961), and at the other end of the time scale we have dipnoan fishes with very slight phenotypical change since the Carboniferous (SCHAEFFER 1952).

From the results presented above it would seem evident that the rate at which new genes become incorporated in the sculpin gene pools is low, since no protein system tested shows any qualitative variation. Consequently there seems to be little evidence for any higher degree of genetic difference between the sculpin populations examined.

The homogeneity of the protein patterns of sculpin also seems to support the investigations by TÅNING (1952), which showed that most meristic characters in fish are affected by the environment and are thus non-genetic.
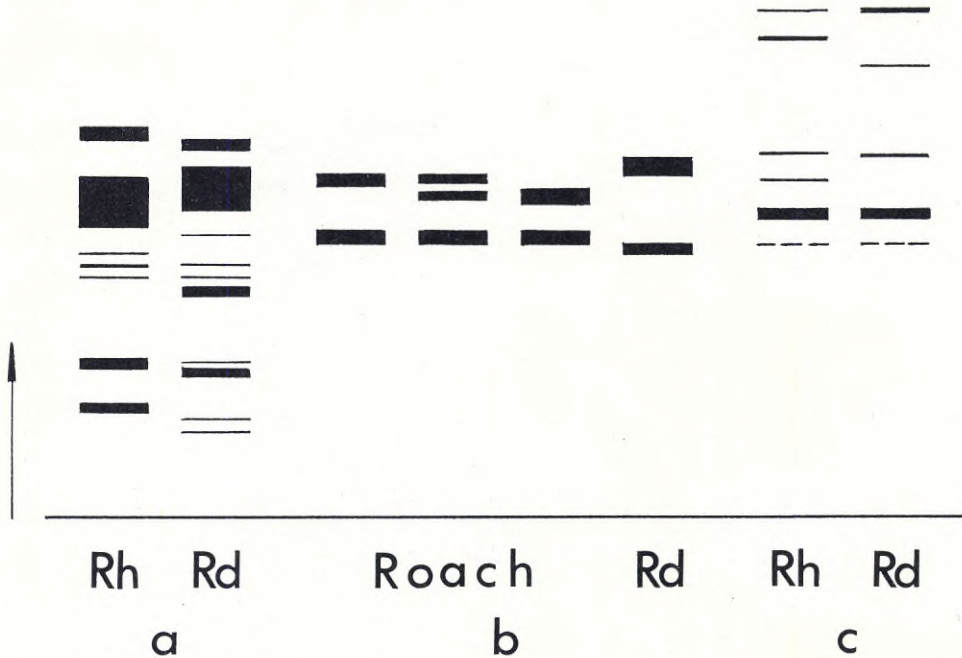
Fig. 6. Protein variations in three 'protein systems' of roach (Rh) and rudd (Rd). a=blood-serum proteins (amido-black), b=blood-serum esterase (three genotypically different patterns in roach), c=liver esterase.

For that reason it may be assumed that much of the morphological variation found in the sculpin populations is non-adaptive.

The reason why these populations seem to diverge at such a low rate may be explained as follows. We have already concluded that the sculpin populations of most lakes can be considered to be closed, i.e. all new genetic material is incorporated by means of mutation. The environmental conditions for a deep-water animal like the sculpin will probably not differ very much in different bodies of water, many of the ecological factors, e.g. temperature, predators and possible competitors, being almost identical. Since as a general rule environmental conditions have a much greater influence on speciation than mutation, part of the genetic stability will be due to the rather homogeneous environment, in the first place since the isolation during the Wisconsin (Würm) glaciation and in the second place during the isolation after the retreat of the ice cap with the upwarp of land, when the connections between the Baltic drainage area and the various lakes were broken.

Another factor to be taken into account is the possible presence of a 'strong' genetic homeostasis, i.e. the capacity of genetic mechanisms to resist changes of the epigenotype (the total developmental system, according to MAYR). It is thus probable that we are here dealing with a 'conservative'

genotype with narrow limitations as to incorporation of new genes. From the discussions above it may seem justifiable to conclude that probably very few genes account for the genetic difference between the two possible sibling species of fourhorn sculpin, despite their long isolation. Nevertheless this can not, of course, be taken as proof of the non-existence of sympatric sibling species, according to the discussions above the state of affairs in fourhorn sculpin differs strongly from the situation in other closely related species of fish. Below, a few examples are presented where there exist large [inter-specific] differences between species of the same genera, viz. *Salmo* and *Leuciscus,* the two species of each genus having very similar ecological demands and both pairs occurring in the same bodies of water. In Fig. 5 the protein patterns of salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) are compared, and in Fig. 6 the patterns of roach (*Leuciscus rutilus* L.) and rudd (*Leuciscus erythrophthalmus* L.).

Summary

A pair of hypothetical sibling species of fourhorn sculpin (*Myoxocephalus quadricornis* (L.)), one with green, the other with yellow roe were investigated as to possible genetic divergence.

Proteins, the primary products of the genes, were used as parameters, and they were examined by employing an electrophoretical method based on starch as supporting medium.

The results indicate a stable genotype in the fourhorn sculpin, neither inter- nor intraspecific differences being found between the two possible sibling species. For comparison, a few examples are shown where congeneric species with very similar ecological demands have large qualitative differences.

Acknowledgements

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The fertility of Fourhorn Sculpin, *Myoxocephalus quadricornis* (L.)

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Introduction

The following studies were carried out in December 1966 at the Askö Laboratory, the Swedish marine station in the Baltic, in an attempt to contribute to the knowledge of fertility of the species. The egg number in a 23-cm-long pecimen was earlier estimated by Ekman (1899) at 3000—3500.

Material and methods

The investigation is based on material collected at a depth of 35—40 metres in the vicinity of Askö, where the fourhorn sculpin is frequent.

The spawning took place from the end of December to the end of January. The fish were trapped in gill-nets and the eggs were counted in December, a week before the culmination of the spawning. The culmination was estimated by counting the percentage of spawned fish, trapped in gill-nets.

Mature eggs are relatively large, measuring 2.4—2.9 mm in diameter. This made it easy to investigate the relation between the number of eggs and length and weight of fish.

The eggs were pressed out and after that the remaining eggs in the ovary were counted. No difficulty was met in separating the mature eggs destined

Table 1. *Myoxocephalus quadricornis,* average number of eggs for 25 g weight groups.

Weight group g	Number	Average weight	Average egg number	F/g
25— 49	2	47	1,030	21.9
50— 74	10	66	1,257	19.0
75— 99	6	89	1,666	18.7
100—124	10	114	1,978	17.3
125—149	8	139	2,480	17.8
150—174	7	163	3,075	18.8
175—199	7	186	3.466	18.6
200—224	3	208	4,017	19.3
225—249	3	246	4,433	18.0
250—	7	264	4,455	16.9

Table 2. *Myoxocephalus quadricornis,* average number of eggs for
2 cm length groups.

Length group cm	Number	Average length	Average egg number	F/L
15.0—16.9	4	16.5	1,135	69
17.0—18.9	7	18.0	1,329	74
19.0—20.9	11	20.1	1,636	81
21.0—22.9	16	21.9	2,470	116
23.0—24.9	13	23.9	3,470	145
25.0—26.9	9	25.9	3,945	152
27.0—28.9	3	28.0	4,870	174

for the approaching spawning period from the bulk of small immature
oocytes.

Counting was carried out on 63 females 16.5—28.7 cm long and weighing
45—278 g.

The eggs of each fish having been preserved separately in alcohol, the
eggs were weighed exactly and 10 per cent of the egg mass was weighed
exactly and counted.

To check the accuracy of the method all eggs were counted in 10 cases.
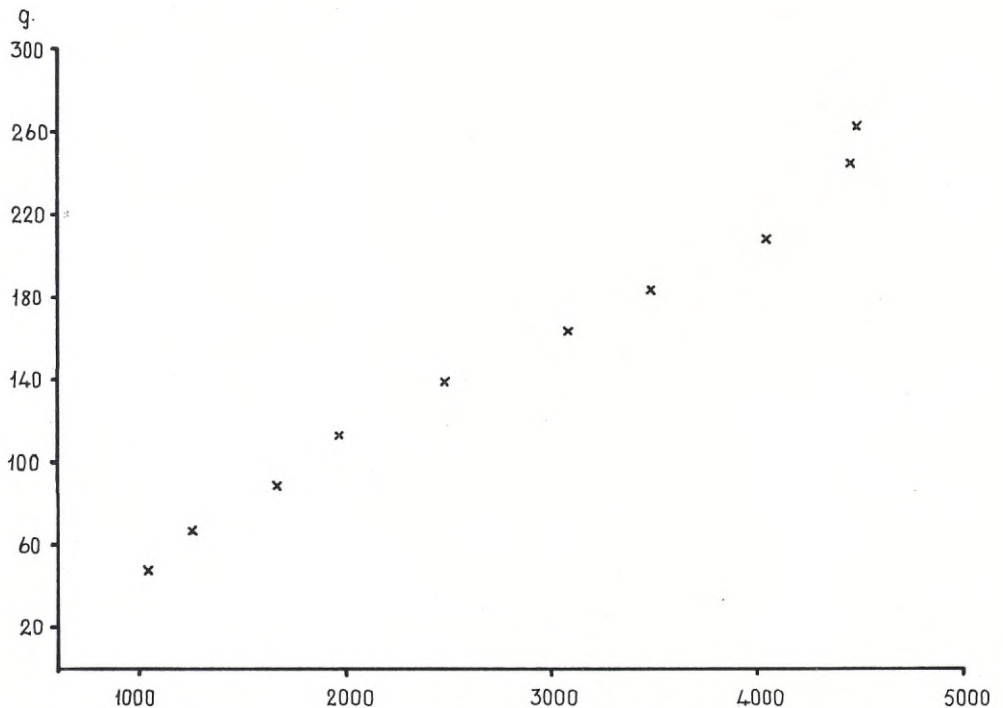The accuracy was ±2 per cent.

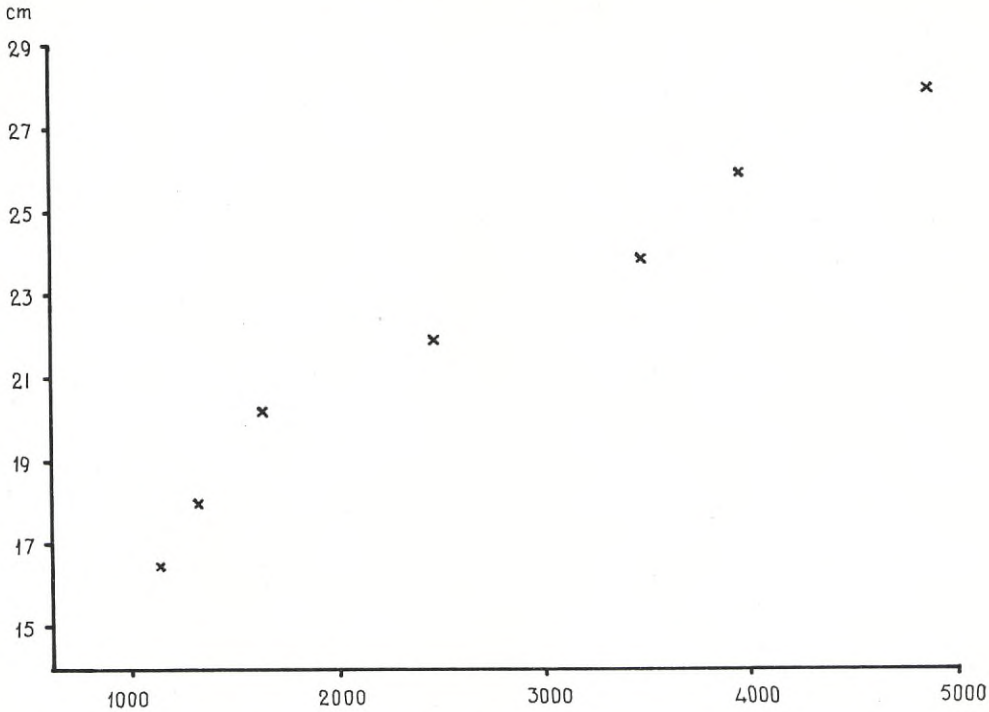Fig. 1. *Myoxocephalus quadricornis.* Relation between egg number and weight of fish.

Fig. 2. *Myoxocephalus quadricornis*. Relation between egg number and length of fish.

Results and discussion

The egg number per fish varies from 792 to 5,900; it increases with increasing weight and length.

As can be seen from Tables 1 and 2 the quotient F/g is remarkably constant. The quotient F/L, on the other hand, increases rapidly with increasing length from 69 to 174.

In Fig. 1, the mean numbers of the weight groups are plotted in a coordinate system and in Fig. 2 the mean numbers in length groups are plotted.

The fertility of *Myoxocephalus scorpius* (L.) and *Taurulus bubalis* (Euphr.) has been determined by F. LAMP (1966), who in his investigation found that there was no linear relation between egg number and weight or length respectively. By plotting the mean numbers in coordinate system he showed that the regression curves cut the ordinates at a point above the zero point. From the course of this curves he suggested that the regression for both relations was well represented by a parabola.

This may be true for the fourhorn sculpin in the case of the length group, but in the weight group the relation seems to be linear. (Figs. 1 and 2).

The fertility compared with *M. scorpius* is much lower. The highest egg number counted in this species was 28,930. *T. bubalis* had about the same quantity as *M. quadricornis* but in *T. bubalis* the eggs are extruded in two portions at different times and only the first portion was counted (LAMP 1966).

The low fertility of *M. quadricornis* is balanced by the aggressive watch over the egg mass by the males.

The last statement is based on observations of egg-guarding males in aquaria, which will be published separately.

Material and methods

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Lethal Limits of Temperature for Fourhorn Sculpin
Myoxocephalus quadricornis (L.)

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Introduction

Lethal temperatures have been given quantitative assessment in the laboratory in various ways. Such measurements have been the temperature reached before death when heated at certain constant rate (Huntsman and Sparks, 1924), the average survival time at a given constant temperature (Loeb and Wasteneys, 1912), and the temperature at which a given percentage survive for a given length of time (Hathaway, 1927).

For any environmental factor the range within which life of an organism is possible may be divided into two zones. The first is the zone within which an animal can live free from lethal effects. This is the zone of tolerance. It is bounded by upper and lower incipient lethal levels where for instance temperature is just beginning to have a lethal effect. The incipient lethal temperature rises as the acclimation temperature rises, but in the case of upper lethal temperatures, a point is reached where further rise in acclimation temperature fails to raise the incipient lethal temperature. The latter temperature is termed the ultimate upper incipient level. It is the highest level to which a fish can be acclimated. At temperatures beyond the incipient lethal level, fish can live for a certain finite period. This is termed the resistance time. No attempt has been made in the present investigation to determine the resistance time.

These definitions are a restatement of facts which have been mentioned previously by Fry, Hart and Walker (1946). The studies here reported concern the lethal temperature relations of the fourhorn sculpin, *Myoxocephalus quadricornis,* which has an arctic distribution and a relict occurrence in the Baltic Sea and in a few lakes in Scandinavia, Finland and Russia.

Material and Methods

The present studies were carried out at the Askö Laboratory, the Swedish marine station in the northern part of the Baltic in June—Sept. 1966 and Jan.—Feb. 1967. The sculpins were trapped in gill-nets at a depth of 35—40 metres, where the temperature was 2—5°C and the salinity 6—7 ⁰/₀₀.

Table 1. Relation between upper lethal temperature and acclimation temperature of the fourhorn sculpin.

T°C=temperature of the experimental aquarium. No.=number of fish per aquarium. %=percentage mortality.

	Acclimation temperature								
T° C.	2° C. No. %	5° C. No. %	10° C. No. %	16° C. No. %	18° C. No. %	19° C. No. %	20° C. No. %	22° C. No. %	24° C. No. %
17	8 25	— —	— —	— —	— —	— —	— —	— —	— —
18	8 25	8 13	— —	— —	— —	— —	— —	— —	— —
19	8 63	16 50	— —	— —	— —	— —	— —	— —	— —
20	— —	16 87	6 17	— —	— —	— —	— —	— —	— —
21	— —	8 87	16 25	— —	— —	— —	— —	— —	— —
22	— —	8 100	8 63	— —	— —	— —	— —	— —	— —
23	— —	— —	8 100	6 33	6 0	— —	— —	— —	— —
24	— —	— —	— —	6 50	6 0	10 0	6 0	— —	— —
25	— —	— —	— —	6 100	6 100	10 60	6 33	4 25	— —
25.5	— —	— —	— —	— —	— —	— —	6 66	6 66	8 25
26	— —	— —	— —	— —	— —	8 100	— —	6 100	8 87
Lethal temp.	18.5	19	21.5	24	24.5	25	25.5	25.5	25.5

Half degrees only.

In the part of the Baltic in question the temperature and salinity conditions at such a depth vary very little during the year.

The method of lethal-temperature determination employed was essentially that used previously by BRETT (1941, 1944) and FRY, BRETT and CLAWSON (1942) which in turn was adapted from HATHAWAY (1927). For reasons of comparison and in order to establish a clearly defined and easily determined index, the lethal temperature was defined by BRETT (1941) as the temperature at which 50 per cent of the fish will die if exposed for a period of 14 hours.

Previous to determining the lethal effects of temperature the fish were acclimated to various constant temperatures. The temperature was increased

Table 2. Relation between lower lethal temperature and acclimation temperature of the fourhorn sculpin.

T°C=temperature of the experimental aquarium. No.=number of fish per aquarium. %=percentage mortality.

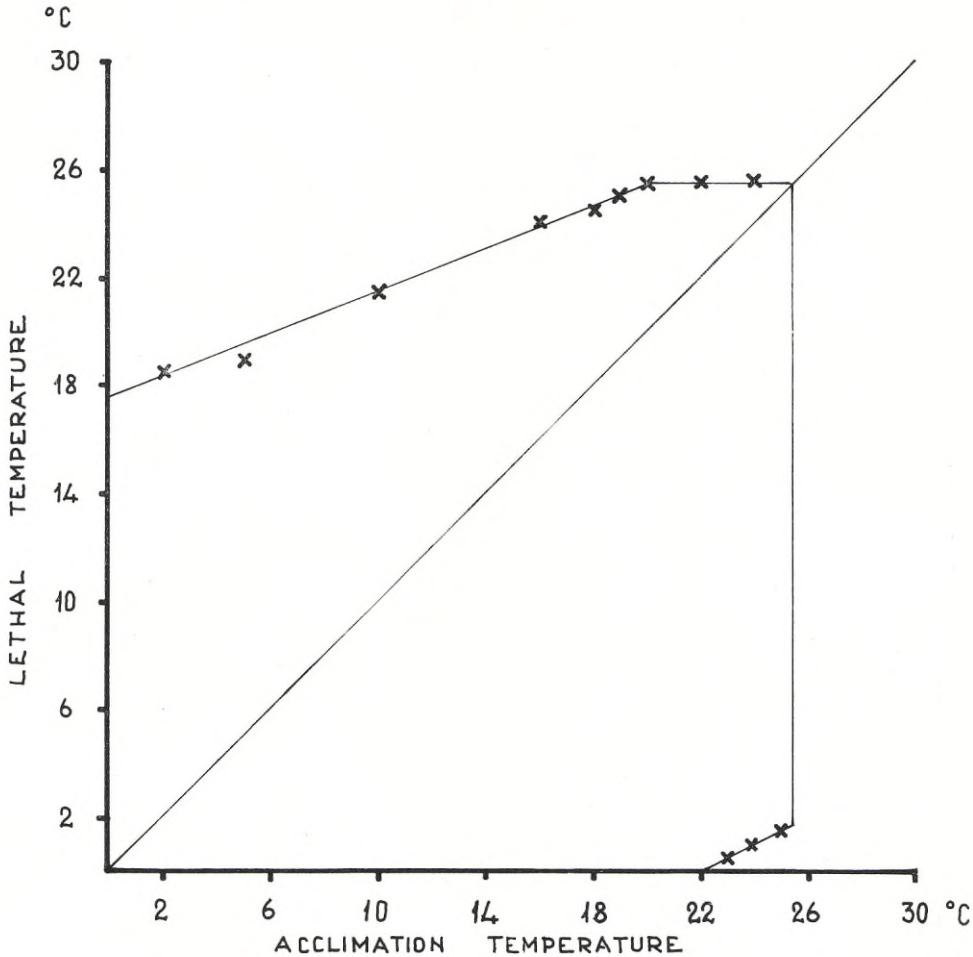|	Acclimation temperature			
T° C.	22° C. No. %	23° C. No. %	24° C. No. %	25° C. No. %
0	4 25	4 100	4 100	4 100
1	4 0	4 0	4 50	4 75
2	4 0	4 0	4 25	4 25
Lethal temp.	—	0.5	1	1.5

Half degrees only.

Fig. 1. The relation between temperature of acclimation and the temperature at which
50 per cent of the fourhorn sculpin can survive for 14 hours.

1°C daily until the acclimation temperature was reached. The acclimation
temperatures investigated were 2, 5, 10, 16, 18, 19, 20, 22 and 24°C.

To determine the effects of a given temperature, a sample of adult fish
was taken from the acclimation tank and placed directly in a temperature-
controlled aquarium. To obviate oxygen deficiency, compressed air was
bubbled into each aquarium, and the percentage of oxygen present was
recorded at different times for each aquarium throughout the experiment.
As a rule, three aquaria, differing in temperature by 1°C, were used and the
experiment was continued for a period of 14 hours. The period mentioned
can be regarded as for all practical purposes equivalent to infinity so far as

the direct lethal effects of temperature are concerned. This conclusion is pointed to by experiments of HATHAWAY (1927) and BRETT (1941).

Attempts to feed the fish were made, but with little or no success. The possibility that this might have been a factor affecting the lethal temperature was considered. In order to ascertain wether there were grounds for such a hypothesis, the experiment with fish acclimated to 5°C was repeated with non-starved and 20-day-starved fish. No appreciable difference in the lethal temperature was obtained. An experiment by BRETT (1944) points to the same conclusion.

The problem regarding differences in lethal temperature between young and adult fish could not be solved because no young fish were trapped.

No attempt was made to determine lethal temperatures below the freezing point of water.

Results

1. Upper and lower incipient lethal temperature.

The relation between the 50 per cent lethal temperature and the acclimation temperature is shown in Fig. 1, in the manner first used by FRY *et al.* for *Carassius*. This method of illustrating the data by plotting the upper and lower lethal temperatures against acclimation temperature offers a good picture of the thermal range for any species. The following characteristics could be pointed out:

a. A rising upper incipient lethal temperature with rising acclimation temperatures up to a certain level. This relation is linear up to 20°C. An increase of about 2.5°C in the acclimation temperature results in an increase of 1°C in the upper lethal temperature. From the figure it can be seen that the upper lethal temperature of the fourhorn sculpin varies from 17.5° to 25.5°C.

b. Above a certain acclimation temperature there is no further increase in the upper incipient lethal temperature. This plateau is termed the ultimate upper lethal temperature and is situated at 25.5°C. It is also the ultimate temperature to which the species can be acclimated.

c. The lower lethal temperature was above 0°C when the sculpins were acclimated to temperatures above 22°C. The lower lethal temperature changes more markedly in response to a change in the temperature of acclimation, as has been pointed out earlier by FRY *et al.* (1942).

The relation between lower lethal and acclimation temperature is probably linear, but the slope is steeper than that of the upper lethal temperatures. A difference of 2°C in acclimation temperature results in a change in the lower lethal of about 1°C.

2. Thermal tolerance.

The thermal tolerance of this population of fourhorn sculpin is shown in the figure in the manner originally adopted for *Carassius* by FRY *et al.* (1942).

The thermal tolerance is the zone bounded by the upper and lower incipient lethal temperatures; it can best be expressed by measurement of the area contained by the trapezoid and is a measure of its eurythermicity. The area contained by the trapezoid expressed quantitatively is 568 units, expressed as degrees centigrade squared.

Discussion

Compared with other species of fish investigated, it seems quite clear that the fourhorn sculpin has a very small eurythermicity. In fact the fish concerned has the least range of thermal tolerance of all species published by BRETT (1956), with the exception of five *Oncorhynchus* species where only freshwater fry stages have been examined.

The habitat of the sculpin is quite in accordance with its thermal tolerance, for the fourhorn sculpin has a relict occurrence in Finland, Russia and in about twenty deep Swedish lakes (NYBELIN 1956), where the temperature during the year is practically stable at a depth below 30 metres. The same is the case with regard to the Baltic population, which is present up to a few metres only after the turnover in the autumn, when a state of homothermy prevails.

Summary

1. The lethal temperature and thermal tolerance were investigated in the Baltic population of fourhorn sculpin, *Myoxocephalus quadricornis*.
2. Fish acclimated from 2° to 20°C showed a linear increase in lethal temperature from 17.5° to 25.5°C.
3. Further acclimation above 20°C did not increase the lethal temperature above 25.5°C.
4. The lower lethal temperature was above 0°C when fish were acclimated above 22°C.
5. The thermal tolerance, expressed in degrees centigrade squared, was 568 units.
6. Compared with other species investigated, the fourhorn sculpin had a very small eurythermicity.

Acknowledgement

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The Influence of Predation by Brown Trout on Asellus in a Pond

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Introduction

In Billingedammen, a pond some 20 kilometres from the most easterly part of Lake Vänern in central Sweden, studies are being made of the growth of the brown trout (*Salmo trutta* L.) and its relation to the environmental conditions, especially the supply of food. The trout live almost exclusively on the bottom fauna, where the water slater, *Asellus aquaticus,* is dominant. The trout population is probably of very ancient date, for nothing is known of any introduction.

Before the start of the present investigation in 1961, fishing had been carried on a small scale for several years. Since 1963 more than 100 trout have been marked and checked individually with regard to growth and choice of food. In order to avoid killing the fish, their stomachs have been evacuated and the contents subsequently examined. The average weight of the trout slightly exceeds 500 grammes, the maximum weight being about 1300 grammes.

At an early stage it became clear that the intensity of trout predation is subject to a seasonal variation that is roughly parallel to the changes in the biomass of *Asellus*. The maximum occurs in late winter and early spring, and a pronounced decline sets in. The minimum is reached in June—July, and is followed by a gradual increase during autumn and winter. The causes thereafter of the parallelism of food supply and intensity of predation are the object of continued investigations. As a link in these investigations the importance of predation for the population dynamics of *Asellus* has been made the subject of special experimental studies, partly by placing in the pond cages preventing predation, partly by dividing the pond into two zones, one with, the other without fish (Fig. 1). The first-mentioned experiment has been concluded and will be dealt with in the present paper. A more detailed account of the environmental conditions, the bottom fauna, predation, and the growth of trout in Billingedammen will be given elsewhere. Here these questions are only touched upon slightly, and mainly for the period of the experiments with the cages, i.e. from July 1965 to December 1966.

Material and methods

The temperature of the water was determined by means of a thermistor and a Ruttner sampler. The qualitative and quantitative mapping of the vegetation was carried out by means of 100 m² squares pegged out in the pond (Fig. 2). The quantitative determination of the mass of the plants in the bottom samples was effected by compressing the fresh material in a container and making an approximate measurement of the volume. For the quantitative examination of the bottom fauna an EKMAN bottom sampler was used. Two samples were taken every month in 14 of the sampling squares indicated in Fig. 3. Each of the figures given from the cages is based upon two samplings (Figs. 6—9). Mean values are based upon 6—12 samples from each cage (Fig. 10), 14 samples from the zones and 28 bottom samples from the whole pond. Altogether, the bottom fauna material here presented comprises 640 samples. The sifting of the bottom samples was carried out with a 0.6 mm mesh. The material was preserved in alcohol and its fresh weight determined with a precision of ± 0.1 mg. The contents of the stomachs were obtained by slowly injecting water into the stomach until everything was washed out. The volume of the material was determined by the displacement of fluid in a measuring cylinder. The stomach contents of more than 1000 trouts were analysed and 51,840 prey animals were counted during the period here discussed.

The trout were caught in nets and, during spawning time (Oct.—Nov.), in traps in the spring brook (see below). After being anaesthetized with MS-222 SANDOZ (Tricaine-Methansulfonate) they were weighed to the nearest gramme and measured with a precision of 1 mm. Immediately after evacuation of the stomach they were released. This treatment did not seem to harm the trout. Every fish was recaught very many times, and in one instance a fish released in the morning was caught again on the evening of the same day with more than 300 animals in its stomach. The scales were sampled about once a year. The fish were marked with a red-hot wire.

The cages are made of wire netting with 10 mm mesh. Cage 4 measures 3×2 m, its boundary on one side being formed by an island. Cage 5 measures about 5×14 m with natural boundaries along the longer sides (Fig. 1). Cage 9 measures 2×2 m. The mesh of the wire permits the passage of all bottom fauna while excluding the trout.

In the middle of May 1966 Billingedammen was divided into two zones by a net placed across its centre. Thereafter the trout were transferred from zone 2 to zone 1. Although the net were carefully attached to the bottom by a diver, some isolated trout have succeeded in returning to zone 2. Nets were, however, placed at regular intervals in zone 2 throughout the ice-free seasons, and returning fish were been relatively easily transferred to the appropriate zone.
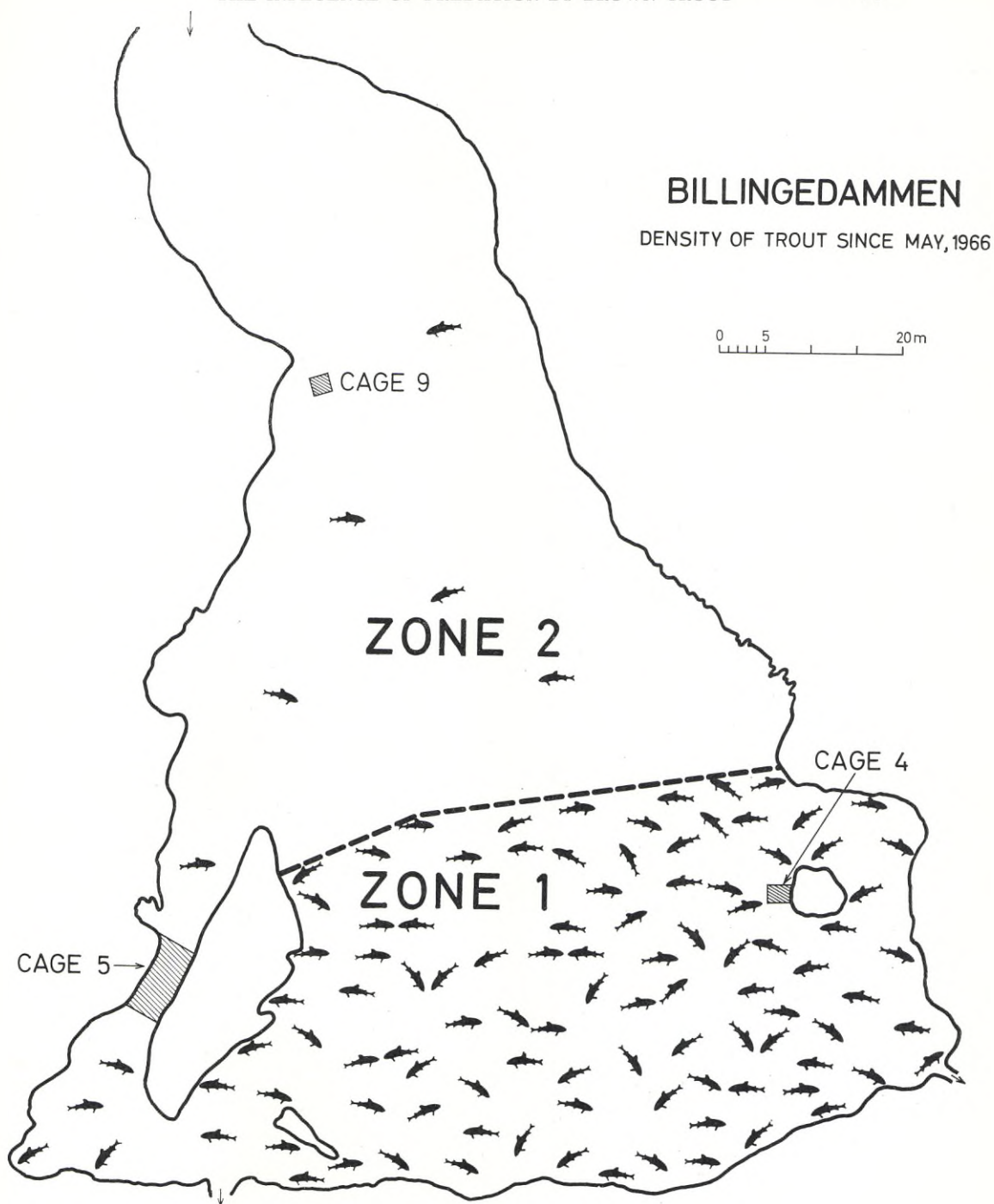
Fig. 1. In the middle of May 1966 the pond was divided into two zones by putting a net across its centre and the trout was transferred to zone 1. Since July 1965, no predation occurred within the cages, where the population dynamics of *Asellus* was studied by sampling with an EKMAN dredge every month. The figure shows the density of trout up to December 1966.
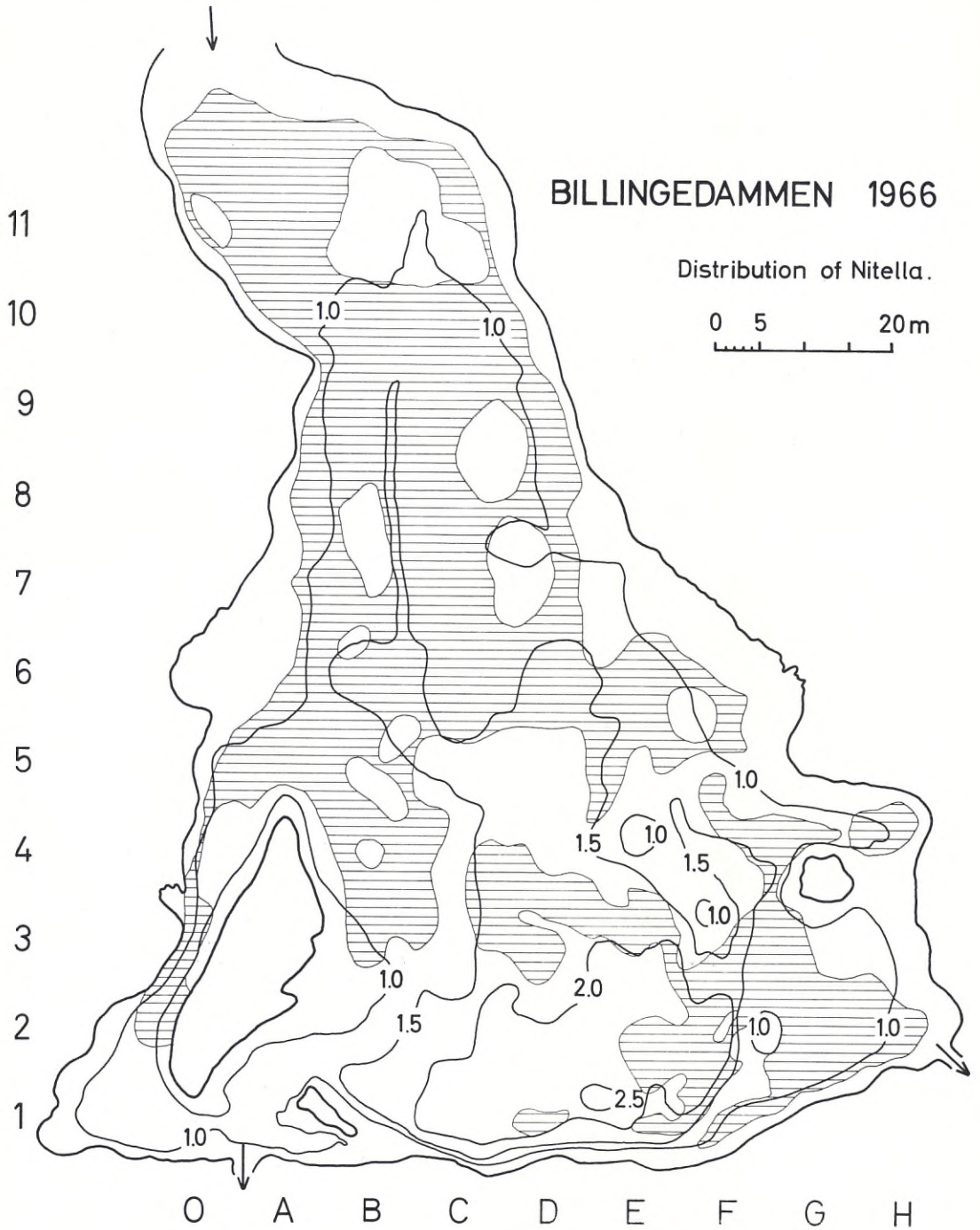
Fig. 2. The charophyte *Nitella* occurs mainly in pure meadows, but suffers from competition with other plants, especially *Potamogeton* and *Equisetum*.
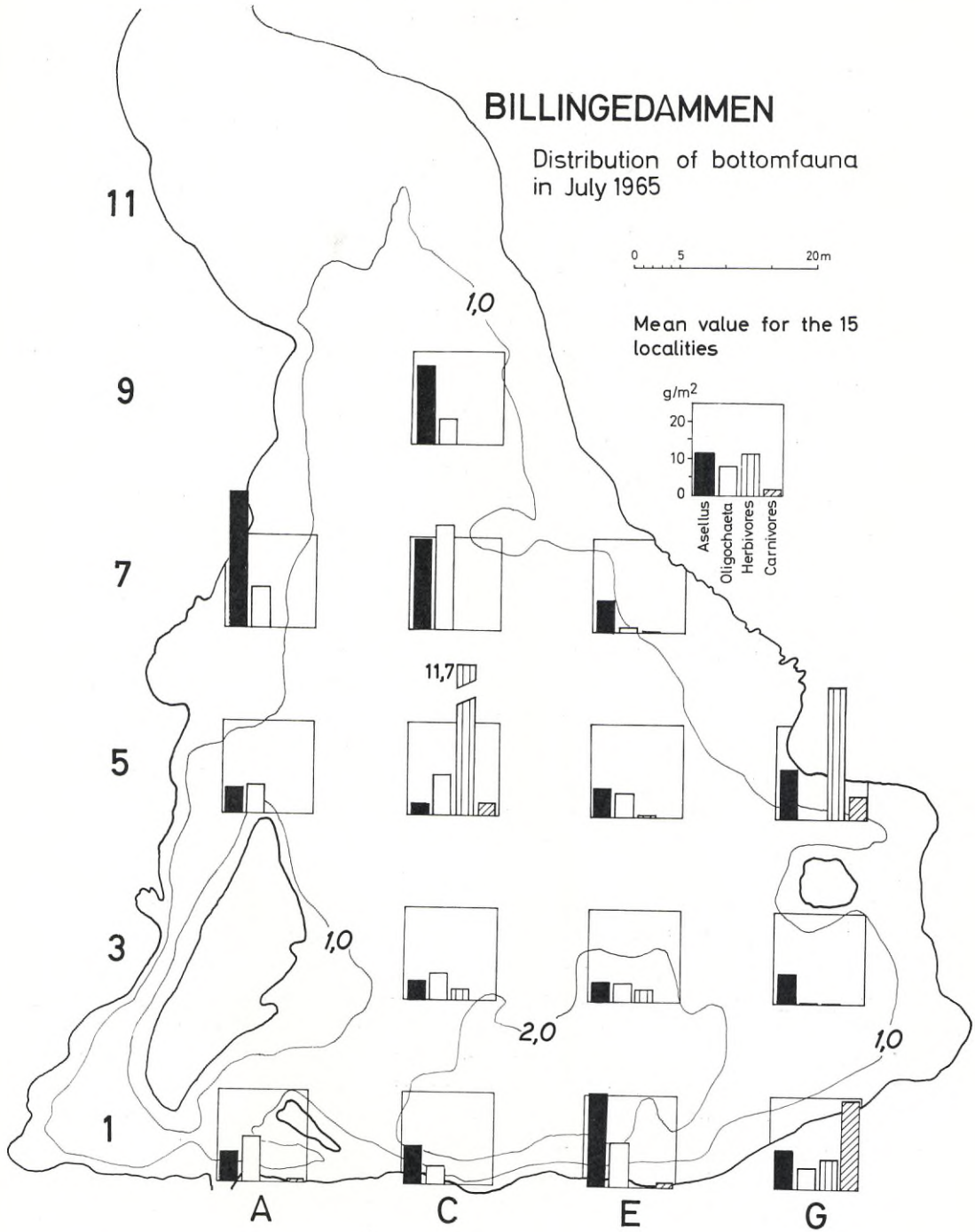
Fig. 3. *Asellus* is the most important species from a quantitative point of view. It is also eagerly utilized by the trout. The total biomass of *Asellus* in the pond was 78 kg in July 1965. Two samples are taken every month within the squares.

Billingedammen

The pond covers about 0.7 hectares (1.7 acres) and has a maximum depth of 2.5 m (Fig. 2). In 1921 the level of the pond was raised considerably through the construction of a concrete dam which, however, collapsed after some years. After that, emigration of trout was possible up to 1965, but not immigration. Trout were indigenous prior to the erection of the concrete dam.

Billingedammen is fed by a brook of spring water and by another carrying humic water. The two unite just before reaching the pond. The spring brook drains a swamp in an esker kettle, where numerous small springs originate. The flow and the physicochemical properties of the spring water are relatively constant throughout the year. The pH varies roughly between 6.7 and 7.0, the specific conductivity is about 70—80 and the water colour 5—10 mg Pt/l. As the humic brook drains an extensive area of swamp and forest which cause great floods during spring, the seasonal variations are very pronounced. Periodically this brook dries up in summer and winter. For this reason the spring water is dominant in the pond at these times, whereas in spring and autumn the humic water preponderates. The pH amplitudes of this brook are higher than that of the spring water, yet the average values are about the same. This applies likewise to the specific conductivity, while the colour of the water is markedly brown, about 80—100 mg Pt/l. In the pond the water colour changes between about 20 and 100. The oxygen conditions are favourable for trout, which never suffer from any lack of it. Because of the intense assimilation of the charophyte meadows at the bottoms, the oxygen content usually reaches maximum values there.

The material of the bottom is in the main fine or coarse detrital gyttja intermingled with half-decayed allochtonous material. Occasionally clay gyttja is found, as are also patches of pure clay covered by a layer of gyttja several millimetres thick. The main part of the bottom is covered with vegetation, especially the charophyte *Nitella opaca,* which harbours by far the greater part of the bottom fauna consumed by the trout. Next to *Nitella, Callitriche* sp. and *Drepanoladus callescens* constitute the most important bottom vegetation. *Potamogeton natans* is the only important plant with floating leaves, while *Equisetum fluviatile* is the dominant helophyte. The biomass of *Equisetum* and *Potamogeton* reaches a maximum in August and September, when these plants cover large parts of the water surface, making net fishing difficult. Along the water's edge *Carex* sp. and *Glyceria fluitans* are dominant. *Nitella* occurs mainly in pure meadows (Fig. 2) and is absent from certain regions. The distribution of *Nitella* depends partly upon the depth of the water. It is absent at the greatest depths, where *Drepanocladus* and *Potamogeton* dominate, but it is also, and especially, rare in shallow waters near the land, where the ice destroys the meadows in winter. Late in autumn *Nitella* forms more scattered assemblages in increasingly shallow

water, causing the appearance of bottom animals there. This is an important factor with regard to the *Asellus* emigrations, discussed below, from shallow cages covered by ice.

It seems from the results given by FORSBERG (1964, 1965) that competition with other plants is the main factor determining the distribution of *Nitella* in this pond, which is regarded as moderately eutrophic. The remarkable abundance of bottom fauna in *Nitella* renders it interesting from the point of view of fishery biology.

In 1966 the biomass of *Nitella* reached its maximum in January. After that it decreased by 25 per cent in February, and by another 15 per cent in March, which together with April and May exhibited the lowest values. Between May and November the biomass in the pond increased by about 40 per cent, the increase being greatest between July and August.

Bottom fauna

The horizontal distribution of the bottom fauna in July is given in Fig. 3. There the fauna has been grouped as follows: (1) *Asellus,* dominant in the environment and in the stomachs of fish; (2) *Oligochaeta,* often a very large group among the herbivores; (3) other herbivores, among them *Trichoptera, Corixa, Gastropoda, Chironomidae, Ephemeroptera, Haliplidae,* and others; and (4) Carnivores, dominated by *Dytiscidae* and *Hirudinea.* In addition *Sialis, Chaoborus,* etc., are found. The subdivision of the herbivores has been made with regard to their availability and degree of utilization as fish food (see pp. 84—86).

Between spring and summer a considerable relative decrease of *Asellus* takes place in the bottom fauna. As an example we can mention that in May 1965 the total biomass of *Asellus* in the pond was 166 kg, that of *Oligochaeta* 57 kg, other herbivores 11 kg, and carnivores 17 kg. In July the values were: *Asellus* 78 kg, *Oligochaeta* 49 kg, other herbivores 71 kg, and carnivores 15 kg.

The seasonal variations of *Asellus* in two localities with average density of vegetation and two with rich vegetation (Fig. 4) show high population maxima in late winter and early spring. Where *Drepanocladus* dominates or is mixed with *Nitella* (A), the winter values of *Asellus* are lower, perhaps because of lower oxygen values, than in localities where *Nitella* occurs in clean meadows (B). The spring maxima are followed by sharp declines with an annual minimum in June–July. Then there generally follows a distinct increase in numbers in August, succeeded by another decline in later autumn.

The egg sac frequency in *Asellus* is at its maximum in March—May (Fig. 13), reaching 15—35 per cent of the adult individuals. The weight at which *Asellus* develops egg sacks is probably dependent upon many factors, e.g. ecotype differentiation, population density affecting growth rate, temperature,

and light conditions, etc.; in Billingedammen egg-sac development occurs
when *Asellus* is reaching a weight of about 9—10 mg, a limit which in this
case has been estimated as an approximate boundary between juveniles and
adults. After May the frequency of egg sacs drops rapidly, reaching zero
value at the end of September.

When the bottom samples are sifted, the newly-hatched specimens pass
through the mesh of 0.6 mm. It is not until August that the small specimens
really make their appearance in the samples, reaching 80 per cent of the
total population. The time of hatching of these individuals is at present not
quite certain, since a large percentage of the egg-carrying individuals in
March—May are devoured by the trout before they have had time to propa-
gate. Laboratory studies will help in solving this problem. In 1966 the fre-
quency of juveniles as a percentage of the total population was as follows
(14,924 specimens counted)

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
30	38	32	26	25	38	28	80	67	48	34	30 %

At the annual minimum in June and July the large specimens, which during
spring attain a length of more than 13 mm, are altogether missing in the
samples.

Plankton

Throughout the year the bottom samples contain semi-bentic *Cyclops*.
Cladoceres, i.e. *Daphnia pulex,* form the greater populations in summer,
especially in the *Equisetum* areas, which are hardly visited by the trout.
MACAN (1966) stresses that with the growing size of the fish an increasing
part of the pond is barred to them on account of the shallow water and thick
vegetation. In Billingedammen there are in addition to plankton great
quantities of ephemerids, hardly touched by trout, in the dense *Equisetum*.
In occasional cases trout have eaten a few cladoceres. Had the population of
trout been dominated by fish of small size, the plankton would probably
assume a different importance for the flow of energy within the ecosystem.

Predation

The problem of the availability and the degree of utilization of bottom
animals as fish food constitutes a very important item in the study of preda-
tion and has been treated by many authors (ALLEN 1942, IVLEV 1961, GRIMÅS
1963, NILSSON 1965, MACAN 1966, and others).

Billingedammen contains on the one hand extremes like *Oligochaeta,*
Chironomidae, Ephemeroptera, Rana larvae, etc., which occasionally attain
very high abundance figures, but are rarely or never consumed by trout.

BILLINGEDAMMEN
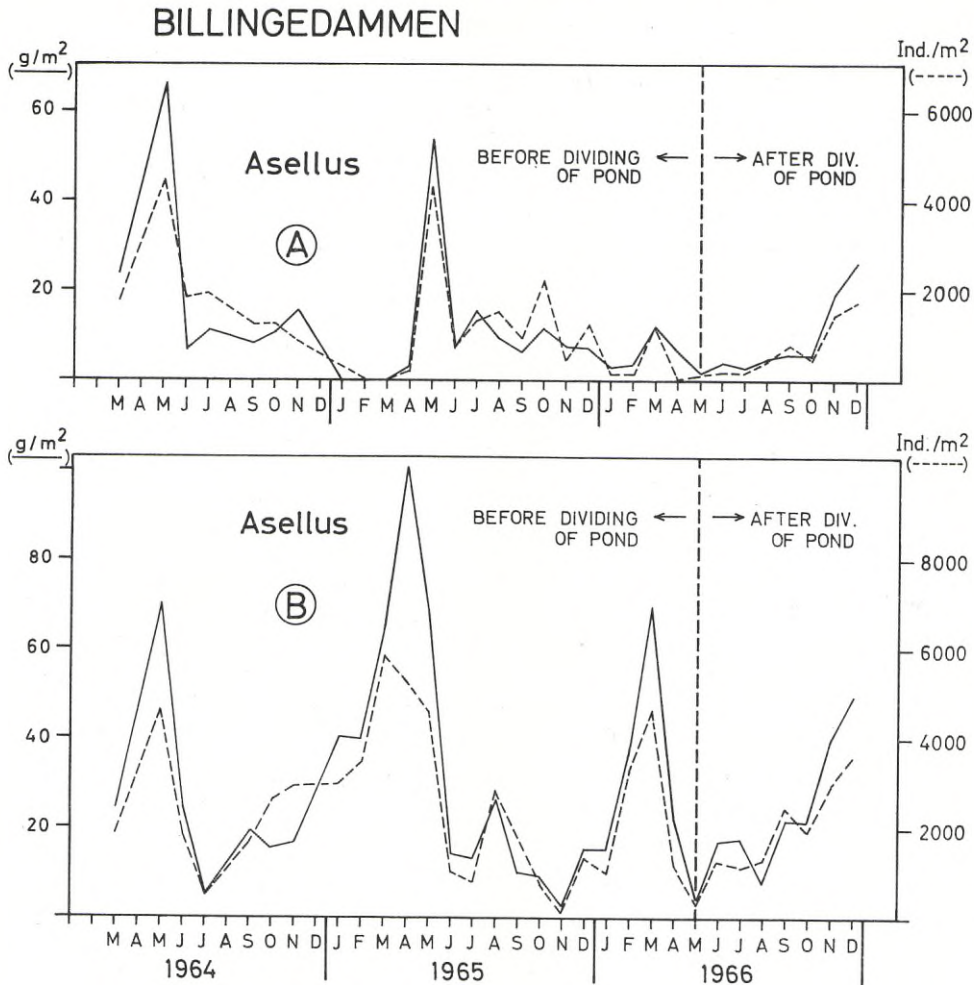
Fig. 4. Where *Drepanocladus* is mixed with *Nitella* (A), the abundance of *Asellus* is lower than where *Nitella* occurs in clean meadows (B). The spring maxima are followed by sharp declines, caused partly by predation, but also to a very high degree by natural mortality of the year-class from the previous year. This reduction is also distinct where trout are absent.

On the other hand very rare groups of animals, e.g. adults of *Dytiscus marginalis, Notonecta, Sialis,* which are hardly ever found in bottom samples, sometimes appear in the stomachs of trout. *Notonecta* was not known to be an inhabitant of the pond until suddenly several were found in some stomachs. The swimming animals exhibit a high selectivity index (IVLEV 1961).

Asellus is intermediate between these extremes. The fact that it occurs in such large quantities as to exceed 90 per cent of the food in the stomachs

Tab. 1. Trout predation July 1965—December 1966.

Year	Month	Mean numbers of animals pro stomach	% Asellus	% empty stomachs
1965	July	47	97.8	59.5
	August	46	93.8	39.3
	September	31	96.1	39.2
	October	1	98.1	86.9
	November	0	—	100.0
1966	March	285	99.5	0
	April	300	99.8	0
	May	139	97.7	14.4
	June	30	97.2	51.9
	July	17	95.8	61.5
	August	11	94.4	49.1
	September	45	98.5	29.8
	October	13	94.0	52.8
	November	43	96.5	37.9
	December	74	98.0	25.9

is partly to be explained by its behaviour. *Asellus* is not so difficult to get at as might be expected. If we may judge from observations in aquaria and in the field, it is fairly mobile and runs about at a surprizing speed, often in the topmost layer of the vegetation. It often climbs in the highest terminal branches of *Nitella* and ought there to be easily discovered by the fish. Since furthermore, *Asellus* forms such a quantitatively important component of the bentic prey fauna, the trout has probably been conditioned to search for it.

In connection with a decrease of the average weight of *Asellus* to a minimum in the course of the summer its utilization degree likewise drops, especially its percentage volume in the stomachs. The volume conditions will be discussed in a later paper. The mean number of animals in trout stomachs, the frequency of *Asellus,* and the frequency of empty stomachs are given in Table 1. The average number in trout stomachs was ten times as great in April as in June, and three times as great in June as in August. In 1966 the ice broke up on May 1. Although the digestion rate must be influenced by temperature (which close to the bottom in Billingedammen is about 5—8°C warmer in summer than in winter), it appears that a great part of the year's predation took place before the breaking up of the ice (Fig. 13).

Growth rate of the trout

The weight increase is greatest in late winter and early spring (Fig. 5), when the days become progressively longer, but temperature is still rather constant, below 4°C. At the same time, the availability of *Asellus,* its abundance and average size, is at its maximum. From July, when the days are

growing shorter and the temperature is rising, and the amount of *Asellus* is at its minimum, the weight increase is often followed by a considerable loss, especially in the case of big trout. The growth rate of smaller trout is more constant throughout the year.

BROWN (1946) found growth rates of trout to be significantly lower with 12 or 18 hours per day of standard light than with only 6 hours per day. SWIFT (1955) has shown correlations between the number of hours of daylight and the activity of the thyroid glands of 3-year-old trout. Experimental evidence from Billingedammen in 1967 seems to indicate that other factors than the amount, quality and availability of food affect the intensity of predation and change of weight.

The cages

The experiments with the cages were originally intended mainly as a preliminary test of the importance of predation in the population dynamics of *Asellus,* which in turn would facilitate the planning of a more exhaustive study of predation. The interpretation of the results has, however, been complicated by the emigrations of *Asellus* from the cages during certain periods. For this reason the sampling in the cages was continued even after the start of the more detailed investigations by means of the division of the pond into two zones. A parallel account of these results is given for the period June—December 1966 (Fig. 9).

The primary data from the cages and from the stations outside them are given in Figs. 6—9. Fig. 10 shows the values from the three cages compared with the mean value for the whole pond.

During the first month of sampling, viz. July 1965, no significant difference seems to exist between the samples from the cages and the other samples. By August, however, a noticeable change was already taking place. At that time the mean value for the pond amounted to only 40 per cent of that in the cages (Fig. 11). In two of the cages the peak in August was followed by a decline in September, and in October a further reduction in the number of *Asellus* occurred in all cages and also, at the same time, in the pond. The ratio between the values for the cages and the pond remained, however, on the whole unaltered until November, when the surface froze and the abundance in the cages was considerably reduced because of the ice.

With the exception of the months December, January and March we find the main tendency that the abundance of *Asellus* in the cages became increasingly great as compared with that in the rest of the pond. During the time prior to the division of the pond in May 1967, the mean values for the cages (92 samples) were more than twice those in the pond (308 samples):
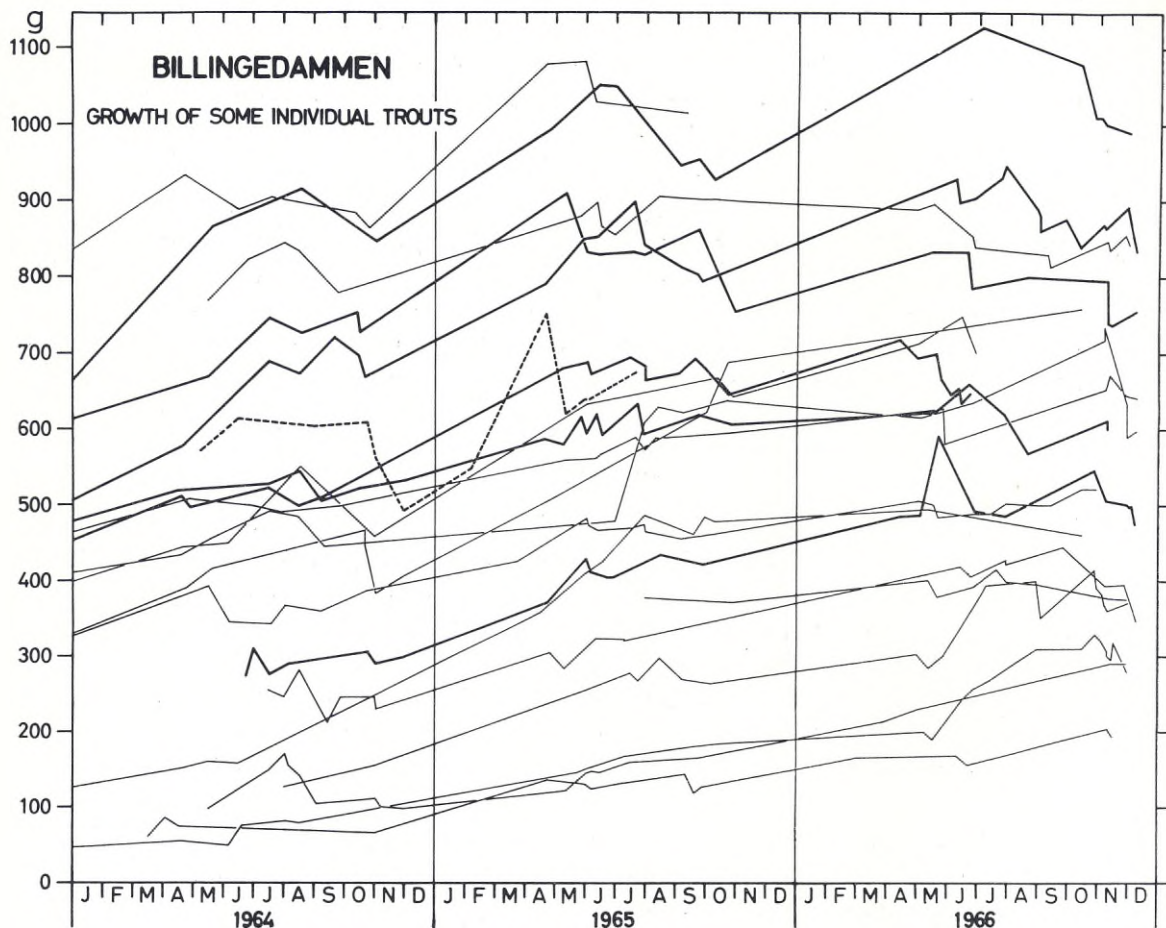
Fig. 5. Every single trout individual has a number placed on its side and can be followed at regular intervals with regard to weight changes. Growth rate is rapid already before the breaking up of the ice, when the temperature is still constant, but the days are growing longer. There is a certain rhythm in the weight changes and the intensity of predation. As a rule, there are distinct peaks every spring, this being most evident in big trout. Small trout grow at a more constant rate throughout the year.

Mean values, July 1965—May 1966

	Cage 4	Cage 5	Cage 9	Entire pond	All cages
g/m²	22.9	26.5	57.0	15.7	35.0
ind/m²	2,545	2,214	2,754	1,288	2,504

In July 1965 the average number in the pond amounted to 106 per cent of the value for the cages, in May 1966 only 18 per cent. The corresponding differences in weight were greater, 144 and 15 per cent (Fig. 11).

From May onwards the pond was divided. In June and July a sharp drop
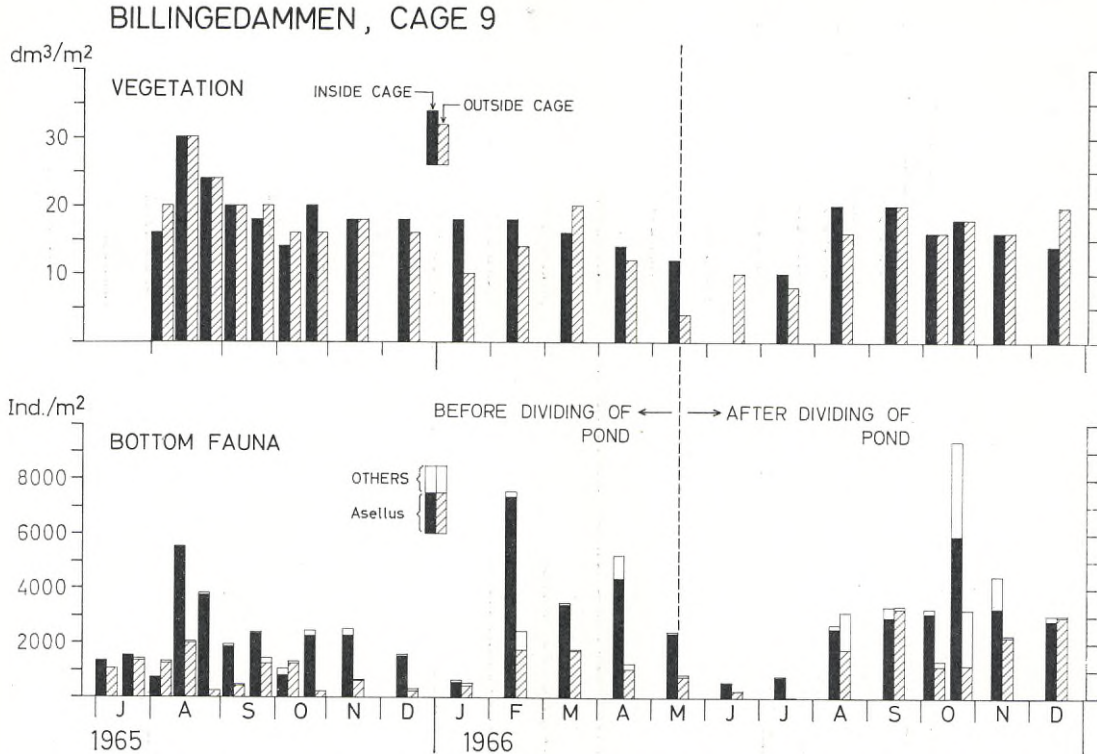
Fig. 6. Development of *Asellus* and other bentic prey animals (*Oligochaeta* and *Rana*, which are not utilized by trout, are excluded here) inside the cage (trout absent) and outside it (trout present), from July 1965 to December 1966. During the first four months, at least two sampling series were taken and thereafter one, inside and outside the cage. Two samples were taken in every series and the values given are mean values for the two samples. In July 1965, there was no significant difference between the abundance of animals inside and outside the cage, but after that an increase, interrupted by emigrations in December and January, took place. There are generally very high population peaks in late winter and early spring, and these peaks are greatest where there is no predation. When the amount of vegetation decreased inside the cage in June and at the same time a heavy mortality of *Asellus* took place, the abundance decreased considerably.

in the population, coinciding with a period of reduced predation, took place. The decrease of *Asellus* was considerable both in the cages and in the zones. Expressed as a percentage it was, however, greatest in the fish-free zone 2. Thus the sharp drop cannot be due to predation.

The tendency of 1965, with an increase in numbers in August followed by a decrease, reappeared in the following year. In cage 5 the difference from the other samples became greater during the autumn, with the exception of October and November, when in this cage the mass of vegetation was very small.

BILLINGEDAMMEN, CAGE 9
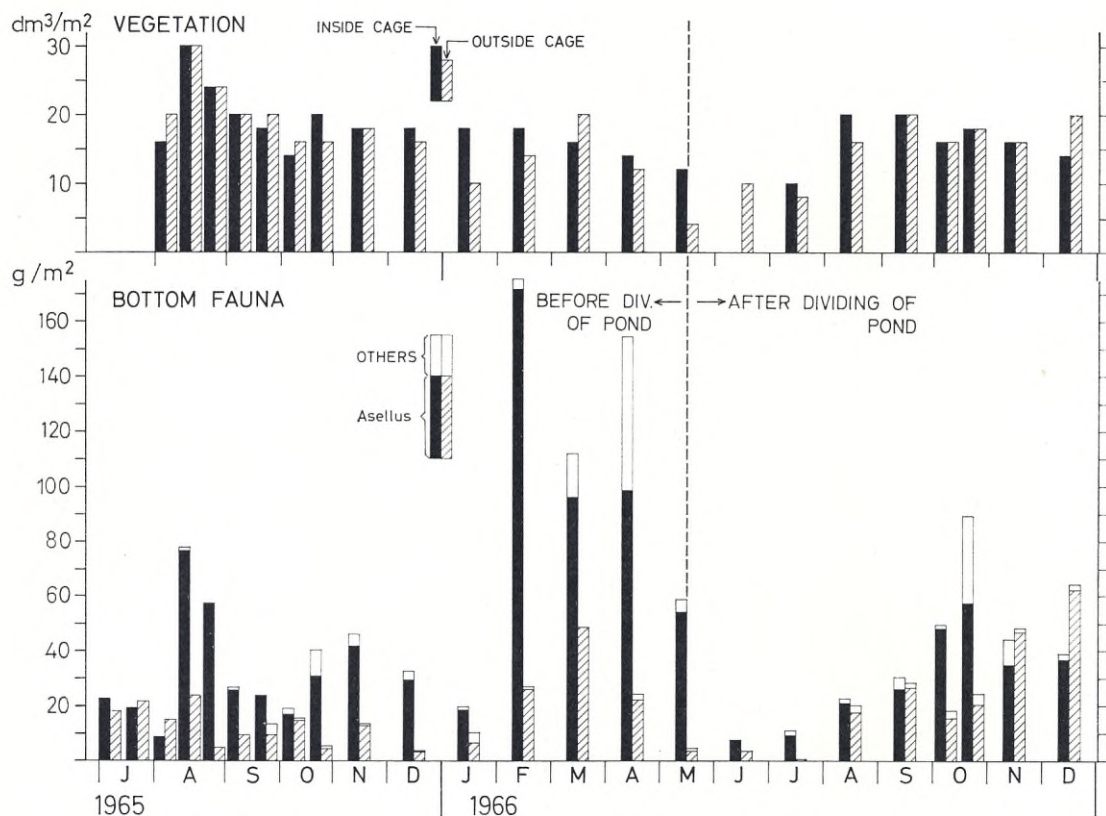
Fig. 7. See Fig. 6 for explanation. The same material as presented in Fig. 6, but bottom fauna expressed as grammes per square metre.

In zone 2, already in October the average number of *Asellus* exceeded the cage values. This is very important in view of the fact that by then zone 2 had been free from fish for just 5 months, while in the cages no fish had been present for 16 months.

Discussion

As a general principle it can be stated that it is only to be expected that any local population peak in a small cage, caused by the prevention of predation, will gradually be followed by a decrease, i.e. an approximation to the average population density in the surrounding environment. This would be due to the haphazard migration that is assumed to occur; as has already been mentioned, *Asellus* is fairly mobile. If the assumption above is correct one would expect the accumulated effect of the absence of trout

BILLINGEDAMMEN, CAGE 4
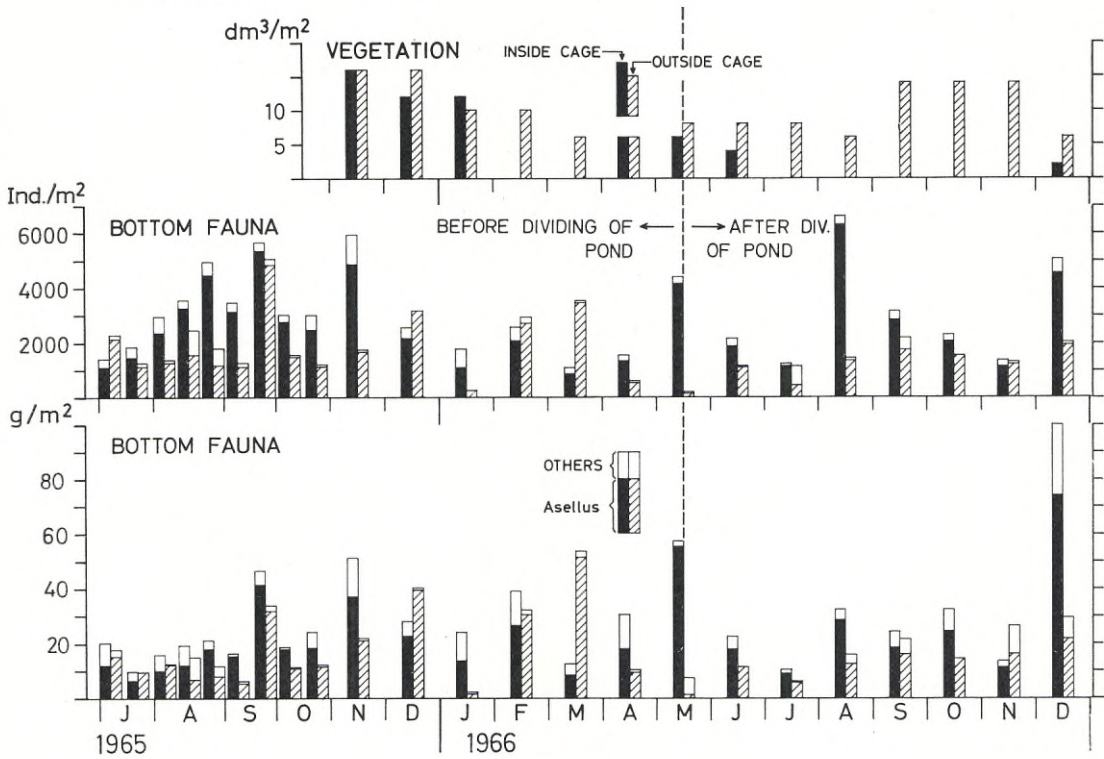
Fig. 8. See Fig. 6 for explanation.

to be most evident in the big cage no. 5, which had natural boundaries along its longer sides. This was indeed, the case, as can be seen when the period July—December 1965 is compared with the same period in the following year:

	Cage 4		Cage 5		Cage 9	
	1965	1966	1965	1966	1965	1966
ind/m²	3,078	2,193	1,833	3,667	2,040	2,731
g/m²	22	29	18	41	31	30

The mean biomass 1966 is more than twice that of previous year in cage 5.

The special conditions for emigration from the cages call for caution in the interpretation of the results. The following are thought to be the main factors influencing these migrations.

(1) *Vegetation conditions*

Overcrowding followed by emigration, diminished growth, or mortality, or perhaps a combination of some or all of these factors, ought to occur more
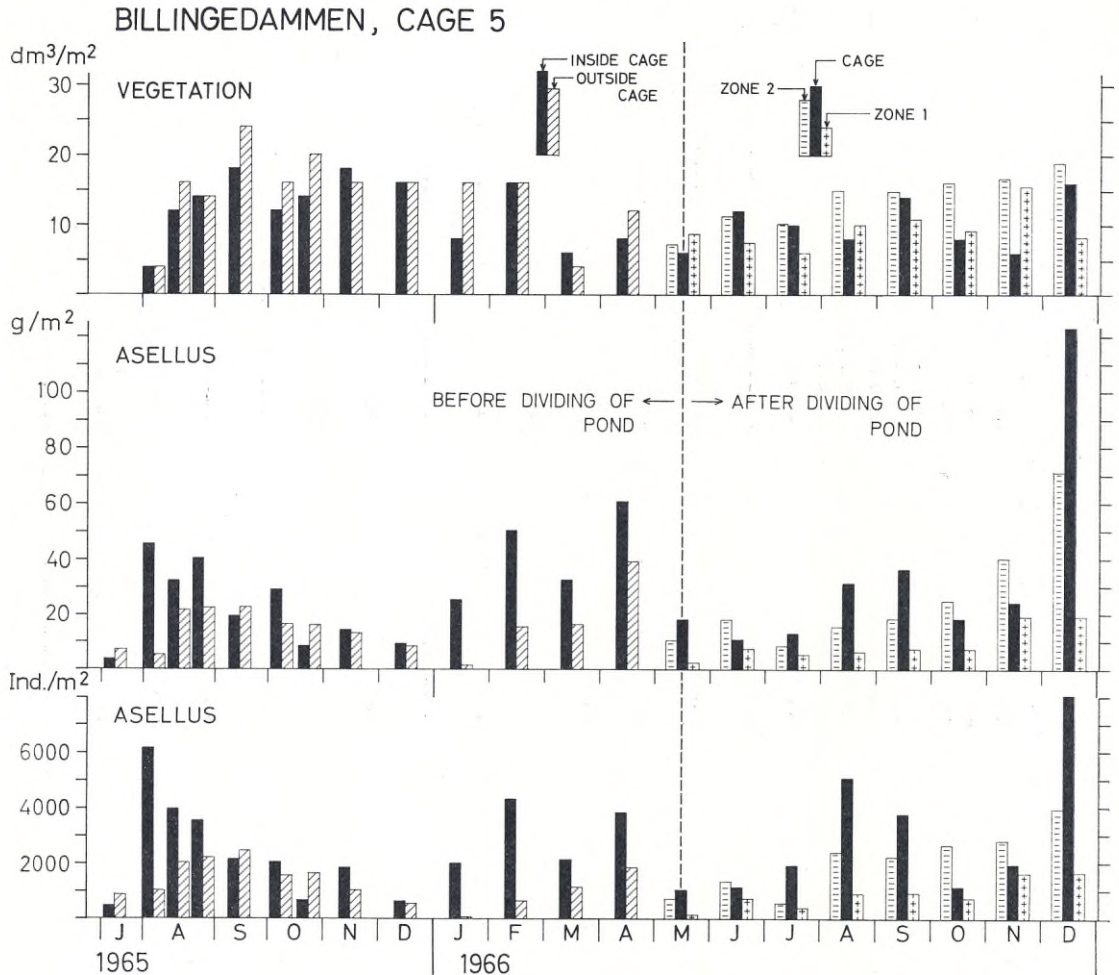
Fig. 9. Development of *Asellus* in the cage (trout absent) is compared with samples taken outside it (trout present) during the time July 1965—April 1966, and after that with mean values for zone 1 (increasing density of trout from May) and mean values for zone 2 (decreasing density of trout, which from May onwards were transferred to zone 1). For other explanations, see Fig. 6 and text.

easily in localities free from predation and with scarce vegetation than in localities with abundant plant life. The "vertical living space" becomes larger and so probably also does the amount of food, e.g. in the form of periphyton and decaying vegetable matter in rich localities. In aquaria, *Asellus* can be seen to form much denser populations in vegetation than on mud, and denser populations in *Nitella* than in other vegetation. On several occasions the abundance of *Asellus* was affected by scarcer vegetation in the bottom samples. Here a few instances only will be mentioned. Cage 9: June 1966 (Fig. 6 and 7).
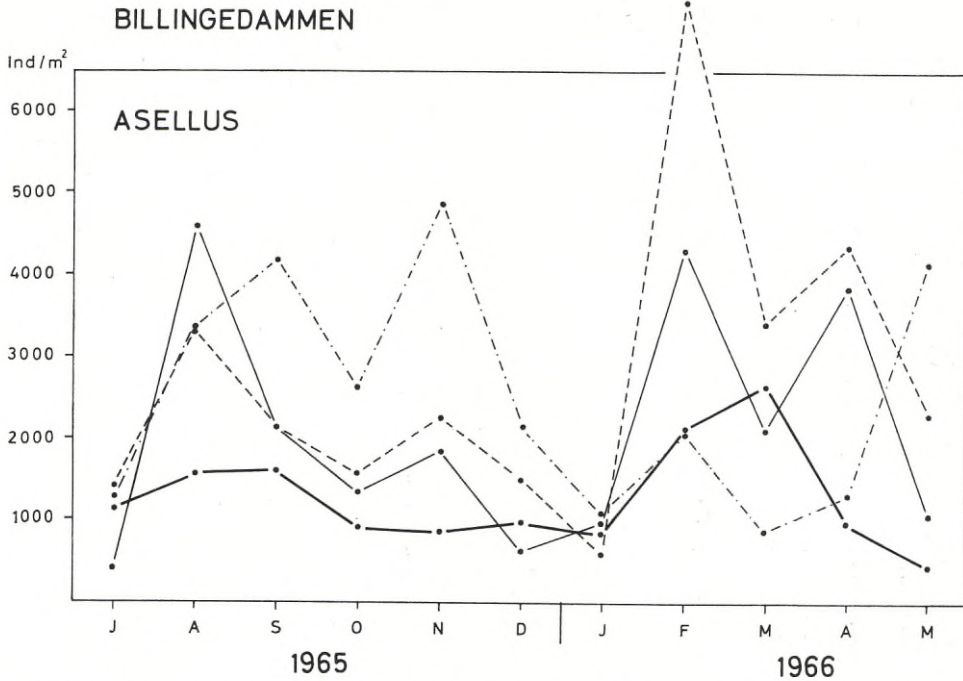
Fig. 10. Development of *Asellus* in the three cages and the pond prior to the dividing of the pond into two zones. —·—·—=cage 4, ———=cage 5, ————=cage 9, ———=pond.

Cage 4: February, March and autumn, especially November 1966 (Fig. 8).
Cage 5: October and November 1966 (Fig. 9).
On a few occasions, e.g. December—February, Cage 9 showed higher vegetation values than outside. The differences in *Asellus* abundance were also pronounced (Fig. 7). It must be stressed here that paucity of vegetation in bottom samples from a cage is indicative of a paucity of vegetation throughout the whole cage. Prior to the sampling the bottom was carefully scrutinized with a water-glass.

The great influence of vegetation upon the abundance of *Asellus* is most evident from Fig. 12. The figures for the biomass of vegetation in the two zones, expressed as percentages of that in the cages, exhibit a striking parallelism with the corresponding figures for the abundance of *Asellus*. This marked parallelism seems highly significant and cannot possibly be the result of chance.

(2) *The effect of ice*

The above-mentioned change in *Asellus* density from June 1965 to May 1966, implying that the values for the cages exhibit a growing relative increase as compared with those of the pond, is interrupted at two distinct

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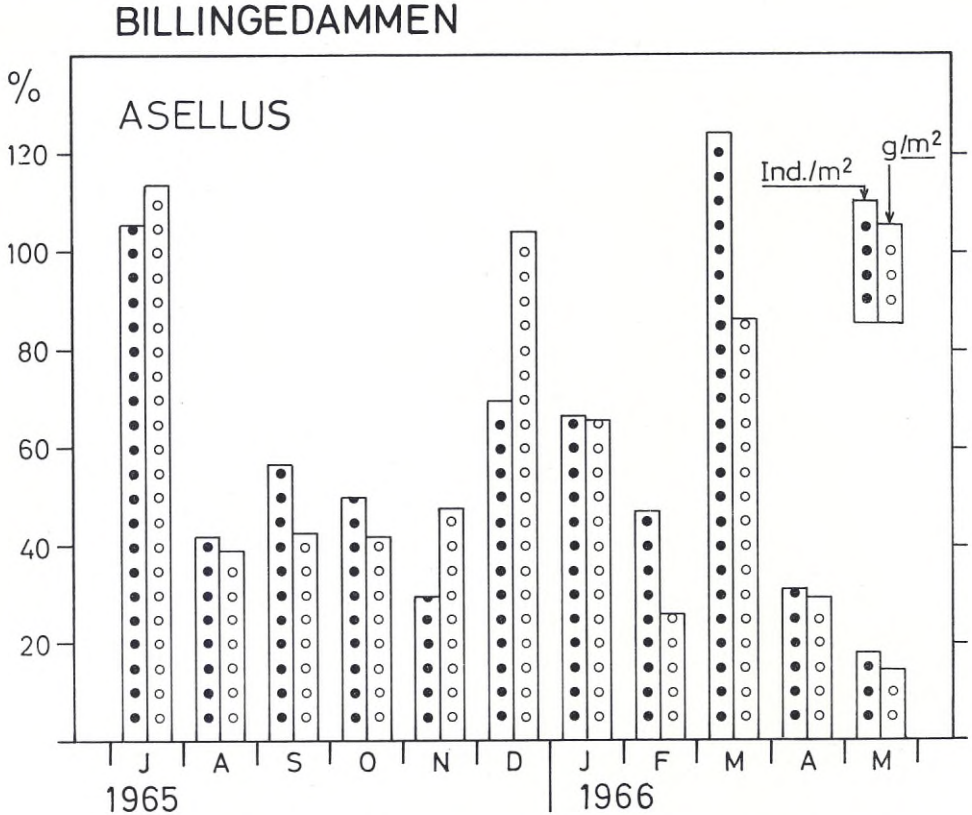
Fig. 11. Abundance of *Asellus* in weight and numbers. The mean values for the entire pond are expressed as a percentage of the mean values for the three cages.

periods. One of these, falling in December—January, has been assumed to be due to the freezing of the water surface which took place already at the beginning of November. The decrease in the number of individuals is greatest in the shallowest localities:

Locality	Mean depth	Change of ind./m²
Cage 4	0.5 m	−3,774
„ 9	1.0 m	−1,687
„ 5	1.2 m	+ 155
Entire pond	>1.2 m	− 72

These data provide a good reason for assuming that the decrease in the shallow cages is ascribable to emigration caused by the ice. Emigration from cage 5 was perhaps unimportant, and the decrease in the rest of the pond might be an effect of predation, which increased in November and December (Fig. 13). Otherwise it remains perhaps within the limits of error of the sampling technique.

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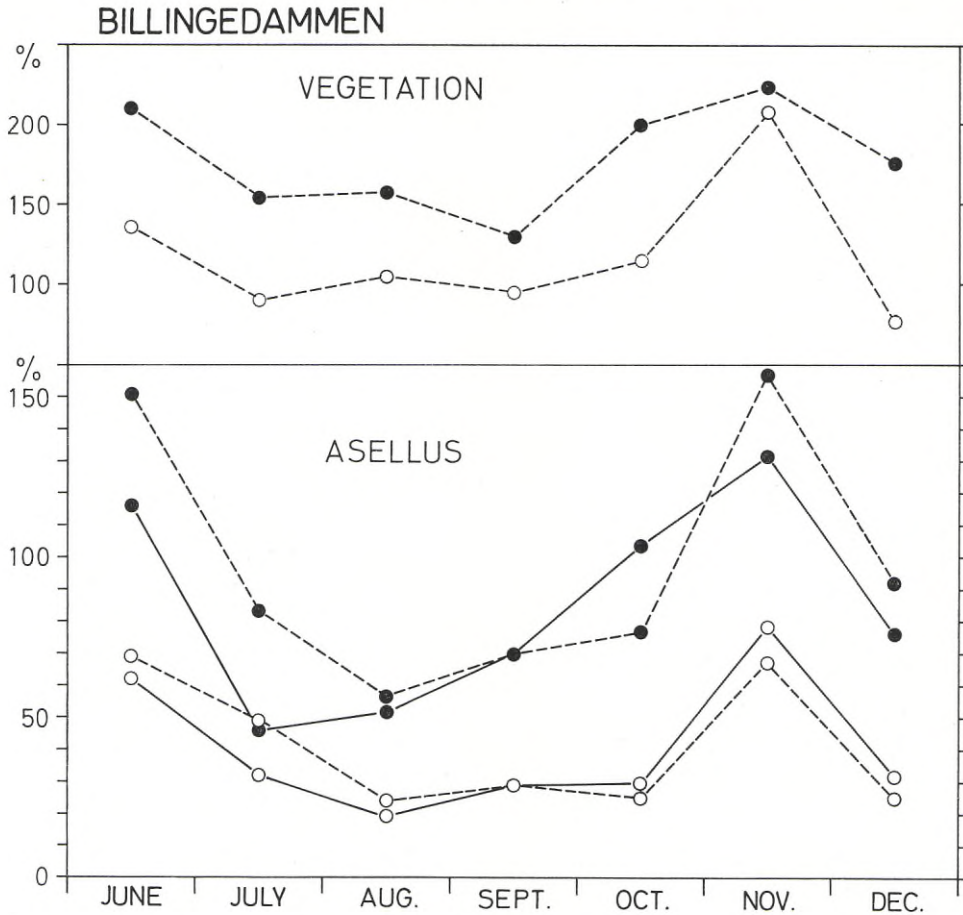
Fig. 12. Mean biomass of Vegetation and *Asellus* under different conditions. A) Vegetation in zone 1 (○) and zone 2 (●) expressed as a percentage of that in the cages. B) Weight (— — —) and numbers (———) of *Asellus* in zone 1 (○) and zone 2 (●) as a percentage of the values in the cages. See text for explanation.

In 1966, the water surface did not freeze until the middle of December, and the *Asellus* abundance in the cages was then rather high.

(3) High density of population in cages

This factor could, for example, explain the second interruption of the main trend mentioned above. The very high numbers in two of the cages in February are considerably diminished in March. The development in the pond at the same time is just the opposite (Fig. 10). It is likely that other cases of emigration due to high population density occurred in the small cages.

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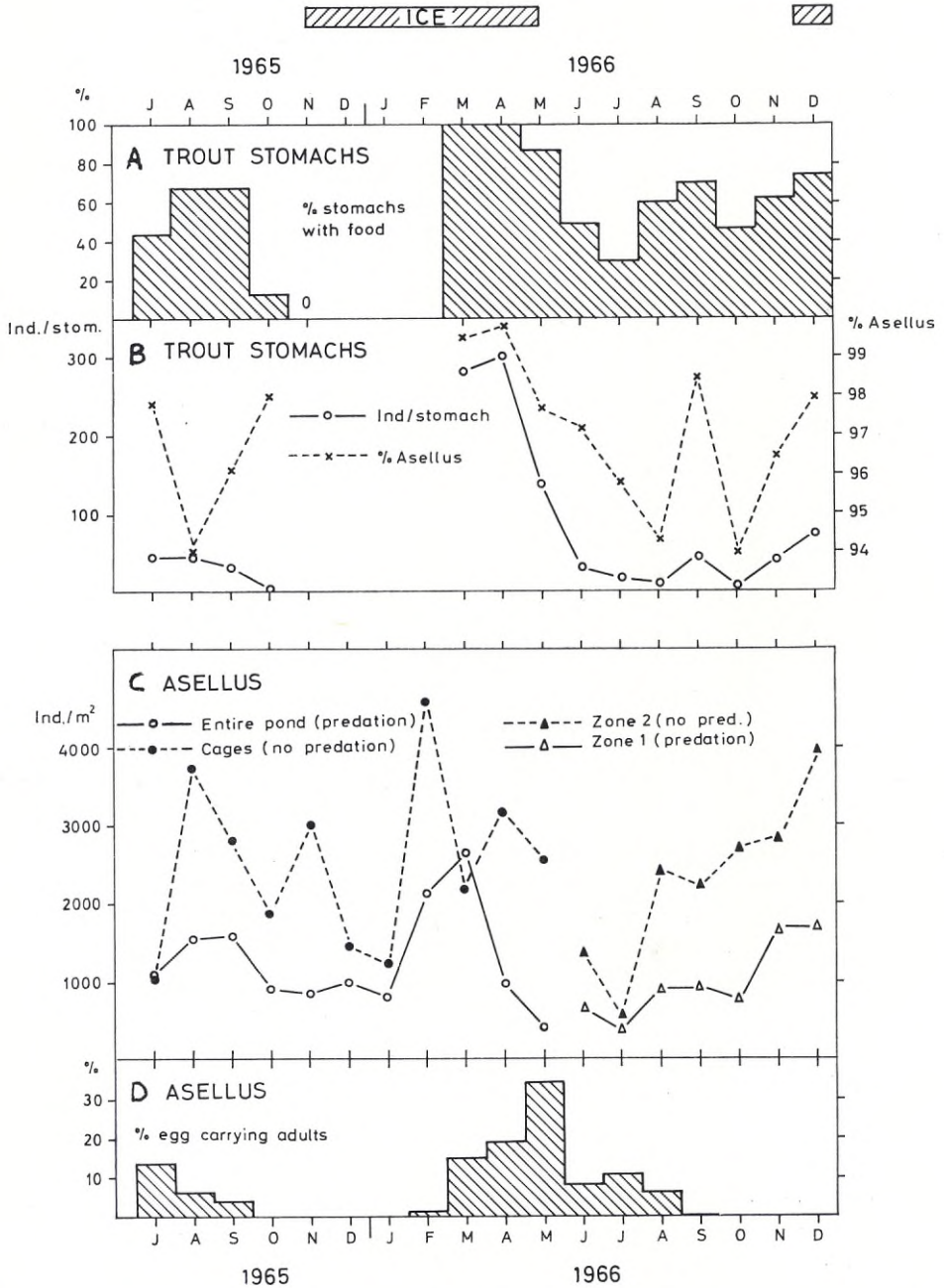
Fig. 13. The average number of animals in the trout stomachs was ten times as great in April as in June and three times as great in June as in August (A, B). Predation severely affects the abundance of *Asellus,* especially during spring (C), when the egg-sac frequency of *Asellus* is at its maximum (D).

The great increase in numbers during February, March and April 1966 cannot be due to hatching of *Asellus* during the same spring, since egg sacs appear only at the end of February and the newly hatched specimens pass through the meshes when sifting is carried out. It is probable that the individuals hatched latest in 1965 (Fig. 13) grew slowly, partly because of the unusually early winter and low temperatures. Consequently they did not appear in the samples until February 1966, when the mean weight of *Asellus* in the pond had diminished from 15.4 to 8.0 mg and in cage 9 from 31.8 to 23.3 mg. The frequency of juveniles increased from 30 per cent in January to 38 per cent in February (cf. p. 84).

The sharp decline of *Asellus* during June and July appears both where fish are present and where they are absent. Since the decline is even more distinct in zone 2 than in zone 1 (Fig. 13), it cannot be an effect of predation, but rather of a heavy mortality of the year-class from the previous year. The hatching period is distributed over a considerable part of the year (Fig. 13), and so probably is the mortality too. The decrease in numbers in September, occurring after a peak in August due to hatching, is probably a result of the continuing mortality of the adult specimens. In aquaria, it has been noticed that mortality is most frequent after hatching.

The combined effect of mortality and the appearance of the new year-class affects the mean weight of *Asellus* during summer (Table 2).

The low value for zone 2 in October suggests that more hatching occurred there than in zone 1. From November, the mean weight increased much faster in the fish-free zone, which again indicates that the trout select specimens of the largest size.

From Denmark, WESENBERG-LUND (1939) reports lengths of 20 mm (males) and 15 mm (females) of *Asellus,* while the maximum size in Billinge-dammen and other places so far north is about 14 mm. It is a well-known rule that many crustaceans attain their largest sizes in colder climates. But the generally smaller sizes of *Asellus* prevailing in northerly latitudes are probably due to the longer winters. Certain evidence from Billingedammen seems to indicate that the growth rate of the small specimens is more restricted by low temperatures than is that of the larger ones. Since the big specimens, however, are selectively caught by the trout, it is difficult to calculate their growth rate where predation is going on.

Within the same area, the size of *Asellus* can vary greatly in different lakes and ponds, and in one place, e.g. Billingedammen, there may exist many micro-habitats, some of which are occupied by large numbers of small specimens and others by a few large ones. MACAN (1965), studying snails and other prey animals, found that when they were numerous some of them were very small and the mean size was less than when numbers were lower. He discussed the possibility that adults might secrete substances inhibiting the growth of small specimens. In the case of *Asellus,* however,

7

Table 2. Mean weight of *Asellus* where trout are present (Zone 1)
and absent (Zone 2).

Month	Zone 1	Zone 2	Month	Zone 1	Zone 2
May	12.3 mg	14.4 mg	September	8.5 mg	8.5 mg
June	11.4 ,,	13.2 ,,	October	10.8 ,,	9.3 ,,
July	12.7 ,,	14.9 ,,	November	10.5 ,,	14.5 ,,
August	7.1 ,,	6.4 ,,	December	11.6 ,,	18.3 ,,

the adults are much more mobile than the juveniles, which seem to stay a long time where they are hatched and therefore can be found in large amounts together. The possibility for big specimens to aggregate within small areas is probably inhibited by the presence of a predator, which tends to prey most where it finds the densest populations of the biggest specimens. In Billingedammen, patchiness of adults was more marked in the cages than outside them. *Asellus* shows no aggressive behaviour or territorial defence, as does e.g. dytiscids, so where there are no predators the factor controlling growth may be temperature and the quality and supply of food. In aquaria, *Asellus* and *Gammarus* grow faster in *Nitella* than in other vegetation, e.g. *Callitriche* or *Cladophora*.

The production rate of *Asellus* will be discussed in a later paper. Since the mean biomass of *Asellus* in the pond is not so very much greater than that of the trout, the growth of the *Asellus* population must be rather rapid. This can be seen from the change in biomass in zone 2 from July (8.6 g/m^2) to December (71.8 g/m^2), an increase of 63.2 g/m^2. During the same period, the increase in zone 1 was only 15.5 g/m^2.

BALL and HAYNE (1952) showed the effectiveness of sunfish in reducing a bottom fauna, mainly consisting of insect larvae, and estimated the average production of bottom food to be about 17 times that of the standing crop during a growing season, when large amounts of fish were present. The relationship between bottom fauna and fish predators must, however, be to a very high degree dependent on the kinds and amounts of prey-objects and predators within the ecosystem (GRIMÅS 1965, NILSSON 1965). MACAN (1965, 1966) has studied the effect of predation by *Salmo trutta* in a pond which is just a little smaller than Billingedammen. The bentic fauna consisted mainly of insect larvae, upon which the trout preyed. In addition there were large amounts of *Rana* and *Bufo* larvae, *Limnaea, Gammarus,* and other animals. After the introduction of 1,000 trout, some species were greatly reduced, possibly eliminated. Some common species were not much affected by the predation, others were restricted to a much smaller area than they had inhabited before. Among the species greatly reduced were *Odonata, Coleoptera* and *Notonecta.* The elimination of *Rana* and *Bufo* was also

thought to be due to predation, but that of *Gammarus* was not. *Limnaea* was not reduced until four years after the introduction of trout.

In Billingedammen, the population level of e.g. dytiscids, *Notonecta, Hirudinea* and *Odonata* (imagines are seen every year, but not nymphs) is most probably affected by the presence of trout, but that of *Rana* is not. Very large amounts of *Rana* larvae are seen in the pond every year, but no such larvae have ever been found in any stomach of trout. The only important predators of *Rana* in Billingedammen seems to be the big larvae of *Dytiscus marginalis,* which in turn are utilized by the trout.

In 1967, more than 2 million *Gammarus pulex* were introduced to Billingedammen. They hatch in the pond, especially in *Nitella,* and swim about everywhere in the open water. Results obtained just before this was written indicate that the trout now prey relatively more on *Gammarus* than on *Asellus.*

An animal's sensitiveness to predation, is of course, dependent not only on the way it moves and exposes itself but also to a high degree on the number of eggs it may produce. *Asellus* carries just over 50 eggs. The reaction of *Asellus* to predation is in part to be explained by its availability. With regard to Billingedammen, however, it is of greater importance that the trout predation is most intense at the time when the frequency of egg sacs in *Asellus* is at its maximum (Fig. 13). The majority of the egg-carriers probably never propagate, because of predation. Since, according to the discussion above, emigrations from the cages ought to have influenced the changes of the populations to a much higher degree than possible immigrations to them, we can assume that the differences in percentage given for the elucidation of the importance of predation are rather too low than too high.

Summary

In the studied ecosystem in Billingedammen, *Nitella* is the dominating vegetation, reaching maximum biomass during winter. The crustacean isopod *Asellus* dominates the bottom fauna, its maximum biomass during late winter and early spring being followed by a considerable decrease. The main predator and the only fish in the pond is the brown trout. It has a very rapid growth rate in early spring, before the ice breaks up and the temperature rises. This increase in weight is often followed by a decrease during summer and autumn.

Every trout specimen in the pond has a number branded on its side, and the specimens are individually checked at regular intervals with regard to stomach contents (by means of stomach evacuation of the live fish) and growth rate. Predation is heaviest when the early spring maximum of *Asellus* occurs. The parallelism of food supply and intensity of predation

is the object of continued investigations. The effect of predation on *Asellus* is studied by means of the placing in the pond of cages preventing predation and by division of the pond into two zones, one with, the other without trout.

The interpretation of the result has been complicated by emigrations of *Asellus* from the cages. However, from July 1965 to May 1966 the mean value of *Asellus* for the whole pond declined from more than 100 per cent to less than 20 per cent of that of the cages. From July to December 1966, when little hatching of *Asellus* took place, the mean production rate of *Asellus* was about 10 grammes per m² per month in the fish-free zone. Where fish were present, the increase during the same period was less than 3 grammes per m² per month.

The decrease of *Asellus* caused by predation is in part to be explained by its availability. The most important fact is, however, that the main part of the year's predation occurs during the few months when the frequency of egg sacs in *Asellus* is at its maximum.

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Report on Current Field Investigations Concerning the Mercury Content in Fish, Bottom Sediment, and Water

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I. Introduction

At the Swedish National Water Protection Service (nowadays National Nature Conservancy Board) there has been used since 1961 a method by which fish are exposed in net cages in watercourses and lakes in order to follow the extent of the toxicological and taste-impairing effects of certain wastes, and to trace unknown sources of pollution (Hasselrot 1964, 1965, 1966). Particularly topical in this respect has been pollution from sulphate cellulose mills, from mining, from factories releasing wastes containing phenol, and plants releasing substances that have proved to have a previously so far unknown, biologically active effect even in very small concentrations. As an example of the latter can be mentioned the great fish anaemia in 1962 in the River Dalälven, downstream from the town of Avesta. This disease, which was noticeable to the mouth of the river about 60 miles downstream from Avesta, was caused by a factory discharge of yellow phosphorus that seemed quantitatively negligible in relation to the water flow.

These trials in cages have often been complemented by bio-assay studies in the factories, using fish in containers that are directly connected with different types of waste liquids, in varying degrees of solution.

The technique of investigation mentioned has been judged suitable in some respects also in solving the problems of mercury pollution, primarily in order to trace in reliable manner a suspected source of pollution in a watercourse or lake, secondly in order to obtain, in conjunction with analytical data from fish caught in their natural state, and other material, a foundation for calculating the geographical extent of the area of risk below a localized release of mercury. A third object has been to check the effects of the measures taken for water protection.

II. Procedure

Over 5,000 young salmon, predominantly one-summer or one-year-old material from the Kvistforsen salmon hatchery on the River Skellefteälven, have since January 1966 been exposed in net cages upstream and downstream of factories with mercury-containing wastes, in the outlets of lakes
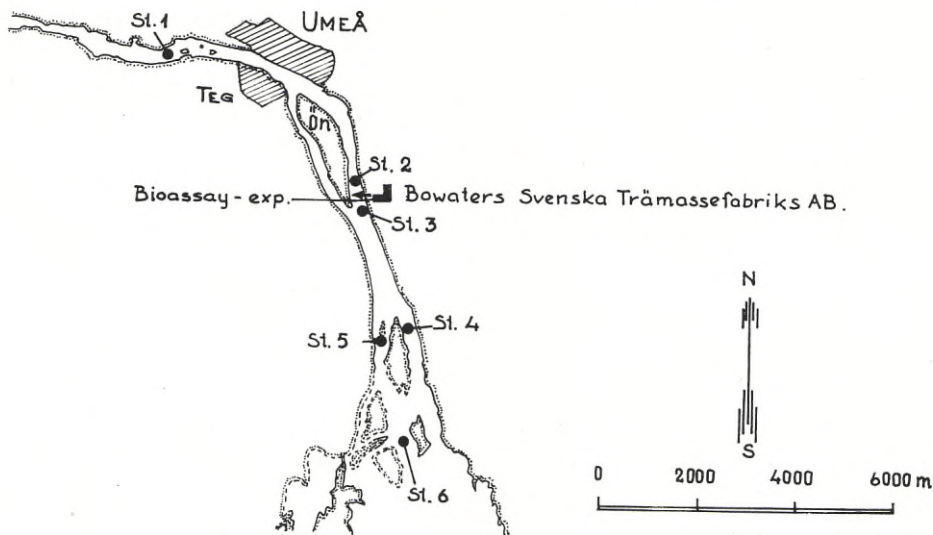
Fig. 1. Mercury content of caged one-summer or one-year-old salmon, *Salmo salar* L., exposed in the River Umeälven 1966. Water flow during the winter and summer exposures 132—350 and 296—516 cu.m./sec. respectively. For further explanations, see text.

Key.

1 mon.w., 1 mon.s.=one month's exposure in winter and summer conditions respectively.
K=homogenized sample from muscle tissue.
L=homogenized sample from liver.
B=sample of blood corpuscle material.
r=relation of analysis value of original of material exposed. Content of mercury given in nanogram per g (ng/g) of the sample.

St. 1.

1 mon.w	r.	2 mon.w.	r.
K 140	1.0	140	1.0
L 175	0.9	170	0.9
B 385	0.9	580	1.3

St. 2.

1 mon.w.	r.	2 mon.w.	r.	1 mon.s.	r.
K 153	1.1	190	1.3	118	1.1
L 200	1.0	200	1.0	110	0.8
B 460	1.1	500	1.2	340	0.7

Bio-assay exp.

River-water	r.	Waste water/river water 1 : 100	
K 160	1.1	220	1.5
L 230	1.2	460	2.4
B 510	1.2	560	1.3

St. 3.

1 mon.w.	r.	1 mon.s.	r.
K 180	1.1	250	2.3
L 700	3.9	2,900	20.4
B 900	1.6	1,040	2.2

St. 4.

1 mon.w.	r.	2 mon.w.	r.	2 mon.s.	r.
K 170	1.2	195	1.4	120	1.1
L 350	1.8	590	3.0	180	1.3
B 570	1.3	760	1.8	—	—

St. 5.

1 mon.w.	r.	2 mon.w.	r.	1 mon.s.	r.
K 146	1.0	210	1.5	125	1.1
L 250	1.3	430	2.2	132	0.9
B 570	1.3	660	1.5	370	0.8

St. 6.

1 mon.w.	r.	2 mon.w.	r.
K 160	1.1	167	1.2
L 220	1.1	160	0.8
B 450	1.0	540	1.3

situated in predominantly industrial areas, in markedly agricultural and mountain areas, and adjoining the raw water intakes for our three largest cities, Stockholm, Göteborg, and Malmö.

The net cages were covered with nylon netting without knots and fitted with stay rings 35 cm in diameter.

During 1966, a bio-assay facility was erected adjoining the out-going waste water from the Bowaters wood-pulp mill on the River Umeälven. Similar facilities have been set up this year at the EKA chlorine alkali plant on the River Göta älv, and, to investigate the effects of filtration in bringing down e.g. the mercury content, in the raw water at the Stockholm and Göteborg water-works.

In each cage and bio-assay container there have been placed as a rule at least 40 young salmon, of which 20 have been used for the production of homogenized samples from the muscular tissue and liver, and 10 for blood tests.

In connection with the areas covered by the cages, fish have been collected in their natural state to determine their mercury content. This work has been performed under Professor Alf Johnels, Museum of Natural History, Stockholm, in accordance with methods worked out by him and Professor

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Fig. 2. Mercury content of caged one-summer or one-year-old salmon, *Salmo salar* L., exposed in Lake Vänern and the River Göta älv 1966. Water flow of the river during the winter and summer exposures 273—921 and 51—916 cu.m./sec. respectively. For further explanations, see text.

St. 1.

1 mon.w.	r.	2 mon.w.	r.	1 mon.s.	r.
K 148	1.0	175	1.2	145	1.3
L 180	0.9	310	1.6	170	1.2
B 560	1.3	560	1.3	—	—

St. 2.   *St. 3.*   *St. 4.*

1 mon.w.	r.	1 mon.s.	r.	1 mon.s.	r.
K 200	1.4	K 200	1.8	K 135	1.2
L 190	1.0	L 1,050	7.4	L 255	1.8
B 435	1.0	B 1,020	2.1	B 375	0.8

St. 5.   1 mon..s.

A	r.	B	r.	C	r.
K 110	1.0	105	1.0	120	1.1
L 480	3.4	800	5.6	740	5.2
B 670	1.4	760	1.6	700	1.5

St. 6.

1 mon.	w.	r.	r.	1 mon.s.	r.
K 151	160	1.1	1.1	131	1.2
L 240	340	1.2	2.5	280	2.0
B 420	—	1.0	—	730	1.5

St. 7.

1 mon.	w.	r.	r.	1 mon.s.	r.
K 190	200	1.3	1.4	147	1.3
L 290	380	1.5	1.9	290	2.0
B 470	820	1.1	1.9	620	1.3

Fig. 2.

Table 1. Mercury content (in ng/g wet weight) of caged young salmon, *Salmo salar* L., exposed above and below industrial plants discharging mercury-containing wastes, in lakes in industrial areas, in agricultural and mountain areas, and at the raw water intakes to Sweden's three largest cities. For further explanations, see Fig. 1.

Exposure stations	One-summer (one-year) salmon								Two-summer (two-year) salmon					
	1 mon. w.	r.	2 mon. w.	r.	1 mon. s.	r.	2 mon. s.	r.	2 mon. w.	r.	1 mon. s.	r.	2 mon. s.	r.
Industrial plants:														
Rottneros, upstream (wood-pulp) mill (River Rottnan) K	165	1.2	165[3]	1.2	148	1.3	140	1.3	100[2]	1.1	—	—	125[3]	1.4
L	190	1.0	200[3]	1.0	145	1.0	104	0.8	115[2]	1.1	—	—	135[3]	1.0
B	520	1.2	—	—	560	2.2	490	2.2	—	—	—	—	365[3]	1.3
Rottneros, downstream mill (River Rottnan) K	230	1.6	360[3]	1.8	860	7.8	160[1]	1.5	165[3]	1.9	630[2]	1.5	132[1,3]	7.2
L	780	4.0	950[3]	4.9	—	—	1,050[1]	7.8	1,030[3]	9.6	15,200[2]	8.3	1,160[3]	8.3
B	1,280	3.0	1,250[3]	2.9	—	—	—	—	—	—	—	—	—	—
Mellan-Fryken (Fölsvik) K	—	—	170	1.2	150	1.4	135	1.2	—	—	—	—	120[3]	1.4
L	—	—	240	1.2	210	1.5	145	1.1	—	—	—	—	175[3]	1.3
B	—	—	680	1.6	410	2.3	510	2.3	—	—	—	—	420[3]	1.5
Rockhammar, upstream (wood-pulp) mill (River Sverkestaån) K	170	1.0	—	—	120	1.1	128	1.2	—	—	—	—	—	—
L	225	1.3	—	—	118	0.8	112	0.8	—	—	—	—	—	—
B	600	1.1	—	—	410	0.9	420	0.9	—	—	—	—	—	—
Rockhammar, downstream mill (Lake Hammarsjön) K	118	0.7	—	—	203[4]	1.8	118	1.1	—	—	—	—	—	—
L	102[3]	0.6	—	—	950[4]	6.7	138	1.0	—	—	—	—	—	—
B	640[3]	1.1	—	—	630	2.9	630	2.9	—	—	—	—	—	—
Ringaby (River Sverkestaån) K	106	0.6	—	—	—	—	—	—	—	—	—	—	—	—
L	45	0.3	—	—	—	—	—	—	—	—	—	—	—	—
B	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lake in industrial area: Roxen, outlet K	155	1.1	150	1.1	84	0.8	—	—	—	—	—	—	—	—
L	165	0.8	200	1.0	95	0.7	—	—	—	—	—	—	—	—
B	460	1.1	600	1.4	430	0.9	—	—	—	—	—	—	—	—
Lake in agricultural area: Tåkern, outlet K	155	1.1	—	—	—	—	—	—	—	—	—	—	—	—
L	165	0.8	—	—	—	—	—	—	—	—	—	—	—	—
B	380	0.9	—	—	—	—	—	—	—	—	—	—	—	—

Exposure stations	One-summer (one-year) salmon						Two-summer (two-year) salmon					
	1 mon. w.	r.	2 mon. w.	r.	1 mon. s.	r.	2 mon. w.	r.	1 mon. s.	r.	2 mon. s.	r.
Lakes in mountain area: K	170	1.0	190	1.1	91 [3]	0.8	—	—	—	—	—	—
(Långfjället) L	210	1.2	160	0.9	155 [3]	1.1	—	—	—	—	—	—
Grötvallsjön B	580	1.0	520	0.9	—	—	—	—	—	—	—	—
Hävlingen K	160	1.0	175	1.0	110	1.0	—	—	—	—	—	—
L	220	1.2	150	0.8	71	0.5	—	—	—	—	—	—
B	550	1.0	570	1.0	480	1.0	—	—	—	—	—	—
Övre Fosksjön K	123	0.7	—	—	137	1.2	—	—	—	—	—	—
L	185	1.0	—	—	125	0.9	—	—	—	—	—	—
B	510	0.9	—	—	—	—	—	—	—	—	—	—
Raw-water intakes: K	165	1.0	260	1.5	122	1.1	—	—	—	—	—	—
Stockholm, Norsborg L	270	1.5	200	1.1	96	0.7	—	—	—	—	—	—
(Lake Mälaren) B	560	1.0	630	1.1	380	0.8	—	—	—	—	—	—
Lovö K	155	0.9	180	1.1	110	1.0	—	—	—	—	—	—
L	250	1.4	240	1.3	137	1.0	—	—	—	—	—	—
B	580	1.0	720	1.3	340	0.7	—	—	—	—	—	—
(Göteborg reported in Fig. 2)												
Malmö K	220	1.3	160	1.0	—	—	—	—	—	—	—	—
(Lake Vombsjön) L	200	1.1	220	1.2	113	0.8	—	—	—	—	—	—
B	530	0.9	720	1.3	270	0.6	—	—	—	—	—	—
Stockholm inner archipelago:												
Tenösund K	180	1.1	140	0.8	105	1.0	—	—	—	—	—	—
L	250	1.4	121	0.7	145	1.0	—	—	—	—	—	—
B	490	0.9	—	—	395	0.8	—	—	—	—	—	—

[1] 7 days
[2] 10 fish
[3] <10 fish
[4] Fish dead in bottom sediment

Table 2. Mercury content in pike, *Esox lucius* L., caught in the water system of the River Delångersån during May 1966. For further explanations, see Fig. 1 and text.

Place of catch Type of sample	Weight of pike Mean weight in brackets (g)	Content in ng/g wet weight	
		K	L
Lake Södra Dellen. 1.5 km upstream Forså Bruk.			
Homogenized samples from 20 individuals	163—835 (426.7)	360	195
Samples from individuals	146	154	48
	955	625	315
	2,850	1,340	180
Lake Kyrksjön. 5 km downstream Forså Bruk.			
Homogenized samples from 20 individuals	370—951 (549.2)	6,600	11,500
Samples from individuals	353	4,400	7,800
	397	7,500	[1]
	851	6,000	9,000
	918	6,900	9,800
	940	5,400	[1]

[1] Sample lost in radiation.

Torbjörn Westermark, Royal College of Technology, Stockholm (WESTERMARK 1965, JOHNELS et al 1967).

Only one collection of fish in their natural state was made by the National Water Protection Service under its own auspices in 1966, namely upstream and downstream of Forså Bruk, a cellulose mill manufacturing paperboard and cardboard, situated on the River Delångersån in central Sweden. A barrier to migration by the fish exists here in the form of a dam above the mill.

Samples were prepared and homogenized in the biological laboratory of the Water Protection Service, after which they were sent, codified, to the Isotope Techniques Laboratory in Stockholm.

The weight, length and haematocrite value (measure of the condition of the fish) were recorded when the experimental fish were exposed and collected.

Physico-chemical data were obtained from the water environment of the cages by repeated sampling. Water samples and samples of bottom sediment were also taken at each station for subsequent mercury analysis. A similar sampling programme was used in the bio-assay experiments.

III. Results and conclusions

The analysis values obtained so far have been collected in Figs. 1 and 2 and Tables 1, 2 and 3.

Fig. 1 shows the mercury content of young salmon exposed below the plant on the River Umeälven of AB Bowaters Svenska Trämassefabriker,

Table 3. Mercury content in sediment and water samples. Sampling in water system of the River Delångersån and in the River Göta älv, during March—April 1967. For further explanations, see Fig. 1 and text.

Station	Sediment samples. Content in ng/g dry weight							Water samples. Content in ng/g				
	Distance under bottom (cm)							Distance above bottom (m)				
	0—1	1—2	2—3	3—4	4—5	4—6	6—7	0.01—0.1	0—0.4	1	5	Surface
River Delångersån:												
Lake Södra Dellen. 1.5 km upstream Forså Bruk	71	41	—	—	—	—	—	—	—	—	—	—
River 1.6 km downstream Forså Bruk	—	—	—	18,400[1]	—	—	—	—	0.36	0.03	0.04	0.04
Lake Kyrksjön. 5 km downstream Forså Bruk	4,300	10,100	—	1,600	—	—	97	0.26	—	0.06	0.09	0.04
Lake Kyrksjön. 7 km downstream Forså Bruk	8,000	3,500	1,200	—	—	250	—	—	—	—	—	—
River Göta älv:												
150 m upstream EKA	164	34	—	—	38	—	—	0.08	—	—	—	0.04
A. 550 m downstream EKA	11,600	22,200	—	26,500	—	—	—	0.56	—	—	—	0.51
B. 650 m » »	3,200	590	—	61	—	—	—	0.26	—	—	—	0.40
C. 750 m » »	1,200	63	400	—	—	—	—	0.31	—	—	—	0.27
Agnesberg, 7 km downstream EKA	440	47	270	—	—	—	—	0.20	—	—	—	0.11
Alelyckan, 10 km » »	140	16	—	41	—	—	—	0.09	—	—	—	0.26

[1] Loose fibrous bottom slime. Sampling with 2-litre BÜTTNER sampler.

Sweden's largest mechanical pulp mill. This mill uses phenylmercuric acetate as an additive in the pulp. The annual loss of mercury into the water has been estimated at approx. 525 kg.

Fig. 2 shows the mercury content of young salmon exposed in a study area from Lurö in Lake Vänern to the intake at the Göteborg water-works on the River Göta älv. On this stretch there are above all two major industrial discharges of mercury-containing wastes, namely from the mechanical pulp mill on the River Göta älv with an estimated annual loss of approx. 80 kg of mercury, and from the EKA chlorine alkali plant at Bohus, with an estimated annual loss of mercury into the water of approx. 1,400 kg.

The mercury contents of caged young salmon from the other areas investigated are given in Table 1.

Table 2 gives the analysis values obtained from fish collected in their natural state upstream and downstream of the Forså cellulose mill. The mill's annual consumption of phenylmercuric acetate amounted in 1964 to 1,200 kg, and in 1965 to 600 kg. With a view to combating slime, the mill used mercuric additives up to the end of 1965.

Table 3, finally, gives the figures on mercury content obtained from water and sediment samples collected in the Rivers Delångersån and Göta älv.

The results obtained so far can be summed up as follows.
1. Cage experiments with fish have shown themselves a practical means of safely localizing, causally and quantitatively in figures, a suspected current source of mercury pollution.
2. Clearly increased mercury contents in the fish exposed below both wood-pulp mills releasing organic mercury and below a chlorine alkali plant releasing unorganic mercury have been established.
3. Recorded figures in the cages below the mechanical pulp mills have in the summer investigations been considerably higher than in the corresponding exposure times in the winter at the stations nearest the discharge (20.4 and 3.9 times the base value for liver samples from below the Bowaters mill).
4. The mercury contents from fish exposed in the various types of control lakes mentioned suggest that no increase has occurred in these, by and large, during the period of exposure.
5. When an increase did occur, it was primarily the mercury content of the blood corpuscle material that rose to maximally something over 1,000 ng/g, even with strong contamination, after which the content in the liver rose to considerably higher values. The increase of mercury in the muscular tissue progressed considerably more slowly.
6. The investigation of fish (pike) caught in their natural state shows that great differences in mercury content can exist in fish caught upstream and downstream of a cellulose mill, even several months after the mill

has ceased to use the organic mercuric preparation concerned, namely phenylmercuric acetate.

7. The mercury content of sediment samples taken below the same cellulose mill more than a year after the mill had ceased to use organic mercury, shows a marked difference as between the upstream and downstream values. The same picture is presented by the analysis figures from sediment and water samples taken above and below a chlorine alkali plant with a current discharge of unorganic mercury.

8. The analysis values so far obtained from water samples indicate a higher content of mercury in water strata close to the bed, above the sediment contaminated by a previous discharge of organic mercury. It has hitherto been impossible to demonstrate any similar tendency to an excretion of mercury from the bottom sediment downstream of a plant releasing unorganic mercury.

IV. Acknowledgements

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The Rôle of Feeding Habits in the Accumulation of Fall Out ^{137}Cs in Fish

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The accumulation of radionuclides in organisms is the result of two simultaneous processes, namely uptake and elimination. In a steady-state condition these two processes balance each other. Both the uptake and the elimination are known to be influenced by several factors, such as temperature, species, type of food, etc. The uptake in a water organism may be either of a direct type by diffusion from the surrounding water through the outer epithelia or indirect, by absorption from the food.

Several investigators have demonstrated the inverse relationship between the potassium concentration of the water and the accumulation factor for ^{137}Cs in fish and other water organisms (Hannerz 1966, Häsänen et al 1966, Kolehmainen et al 1966, Nelson 1960, Rice 1963, Williams 1958 and 1960). The accumulation factor, however, is quite different in different species of fish (Hannerz 1966) usually being highest in predacious fish and in some plankton feeders. Häsänen, Kolehmainen and Miettinen (1967) have found that the differences between fish species can be explained by differences in the elimination rates for ^{137}Cs.

The importance of the food consumed as a medium for the transport of ^{137}Cs from the water to the fish has been stressed by several authors. Kolehmainen, Häsänen and Miettinen (1966) were able to show that the direct uptake of radiocesium from the water by the gill absorption was of minor importance for the accumulation.

In order to elucidate the effect of these various factors on the accumulation of "fall out" ^{137}Cs in fish, pike and whitefish were collected during the autumn of 1966 and the spring of 1967 from a large number of lakes in different parts of the country and from the Baltic coast.

In whitefish there were found variations which could not be explained by variations in the potassium concentration of the water. The causes of these variations have been the object of a separate investigation.

Methods

The ^{137}Cs concentration of the fish muscles was measured with a multi-channel gamma analyser with a $4'' \times 4''$ NaI crystal. The weight of the meat

samples varied from 300 to 700 grammes. The samples were measured in so-called "Marinelli" beakers so constructed as to surround the free mantle surfaces of the crystal. To achieve the same geometry and thus the same volume of the sample in the beaker, the sample was mixed with wet sawdust to a volume of 1 litre. The multichannel analytic equipment was calibrated with a ^{137}Cs source contained in the same type of beaker, which was borrowed from the Research Institute of National Defence.

The muscle samples were separated from the skeleton after brief heating in a pressure cooker, in a manner described earlier (HANNERZ 1966).

The ^{137}Cs concentrations are expressed in pCi per kg (wet weight) and the standard deviation in pCi at the 95 per cent confidence level.

The speciation in whitefish

Whitefish can be divided into a number of species, of which five have been recognized in Sweden (SVÄRDSON 1957). These five species are very similar morphologically and can mostly be recognized only by their number of so-called gill rakers, which are small processes on the gill arches, a racial criterion which is very conservative. Several whitefish species may be found in one and the same lake and this is true of a number of lakes dealt with in this paper.

Where whitefish species are found together there usually exists a segregation in their feeding habits. This segregation is most pronounced in lakes or seasons where there is a shortage of food for the fish and least pronounced when a surplus of food exists. In situations with keen food competition the whitefish species *Coregonus peled* has a tendency to specialize in catching food objects of terrestrial origion which has been trapped on the water surface, whereas *Coregonus lavaretus* has a tendency to specialize on a plankton diet (NILSSON 1960, LINDSTRÖM and NILSSON 1962). Other species are more inclined to feed on bottom organisms, such as insect larvae. The feeding habits of the different whitefish species vary, however, from lake to lake.

^{137}Cs in whitefish

Whitefish from a number of lakes were analysed as to their gillraker count (Table 1) and separated into species according to the definitions by Svärdson. In some cases only a few fish were obtained. As the taxonomic characteristics are of the meristic type the determinations as to species are in these cases uncertain. Water was taken for determination of its potassium concentration at the same time as the sample of fish.

From Lake Langas two samples were analysed for ^{137}Cs. The fish of both samples presumably belonged all to the species *Coregonus lavaretus*. A con-

Table 1. Whitefish.

| Date of sampling | Lake and River system | No of fish | Length cm | Gilrakers count | | ^{137}Cs pCi/kg of meat w. w. | Probable species | Swedish name | K-conc. of water mg/l |
				No of Gill-rakers	No of fish				
Oct. 66	Lake Langas Stora Lule River	6	26.2—31.5	28	4	2,630±49			0.42
		—	—	29	2	—			
		—	—	30	2	—			
				32	1	—			
		5	29.7—32.5	34	1	3,910±60	*Coregonus lavaretus*	Blåsik	
Sept. 66	Lake Parkijaure Lilla Lule River	5	25.0—30.5	20	1	5,170±60	*Coregonus pidschian*	Storsik	0.26
		—	—	21	2	—			
		—	—	22	1	—			
				23	1	—			
		5	26.0—33.6	22	1	4,030±38	*Coregonus nasus*	Älvsik	
		—	—	23	1	—			
				24	1	—			
				25	1	—			
				26	1	—			
		8	20.5—32.6	29	1	3,400±46	*Coregonus lavaretus*	Blåsik	
		—	—	30	2	—			
				31	1	—			
				33	1	—			
				34	2	—			
		3	20.0—38.4	34	1	1,960±48	*Coregonus oxyrhynchus*	Planktonsik	
		—	—	36	2	—			
		2	30.0—34.5	47	1	1,320±54	*Coregonus peled*	Aspsik	
		—	—	54	1	—			
Oct. 66	Lake Uddjaur Skellefte River	8	—	—	—	3,250±43	*Coregonus peled* + *C. pidschian*	Storsik+ Aspsik	0.48
		29	—	—	—	6,600±28	*Coregonus lavaretus*	Blåsik	
	Lake Storavan Skellefte River	8	—	18	2	4,410±49	*Coregonus peled* + *C. pidschian*	Storsik+ Aspsik	0.36
		—	—	23	1	—			
		—	—	34	1	—			
				39	1	—			
				47	1	—			
				48	1	—			
				49	1	—			

Date of sampling	Lake and River system	No of fish	Length cm	Gillrakers count		^{137}Cs pCi/kg of meat w. w.	Probable species	Swedish name	K-conc. of water mg/l
				No of Gill-rakers	No of fish				
		22	—	26	1	8,250 ±64	*Coregonus lavaretus*	Blåsik	
			—	31	3	—			
			—	32	1	—			
			—	33	3	—			
			—	34	5	—			
			—	35	4	—			
			—	36	3	—			
			—	39	1	—			
May 67	Lake Rasjön River Nissan	18	—	20	1	6,520 ±65	*Coregonus lavaretus*	Blåsik	0.51
			—	25	2	—			
			—	26	2	—			
			—	27	2	—			
			—	28	5	—			
			—	29	1	—			
			—	30	4	—			
			—	31	1	—			
		37	—	18	1	4,650 ±69	Probable mixture of *C. lavaretus* and *C. pidschian*		
			—	19	2	—			
			—	20	1	—			
			—	21	2	—			
			—	22	0	—			
			—	23	3	—			
			—	24	3	—			
			—	25	1	—			
			—	26	3	—			
			—	27	4	—			
			—	28	1	—			
			—	29	2	—			
			—	30	2	—			
Oct. 66	Lake Vänern	9	31.0—43.5	32	1	1,560 ±50	*C. oxyrhynchus*	Planktonsik	0.99
			—	33	2	—			
			—	34	2	—			
			—	35	1	—			
			—	36	2	—			
			—	38	1	—			

siderable difference between the samples indicates a variation within the species as to the food selection. A similar intraspecific variation has been demonstrated for perch (HANNERZ 1966).

In Parkijaure all the whitefish species recognized in Sweden exist together. It is found that there is almost a fourfold difference between the lowest (*Coregonus peled*) and the highest (*Coregonus nasus*) concentration of ^{137}Cs. Unfortunately the feeding habits of the whitefish species in this lake have not been studied. It is likely that *Coregonus peled* feeds on organisms floating on the water surface and *C. nasus* and *C. pidschian* on bottom invertebrates. *C. oxyrhynchus* is called "planktonsik" in Swedish. However, this species is not obligatorily bound to a plankton diet, as is known from other lakes than Langas. The radiocesium concentration in *Coregonus lavaretus* is of the same order of magnitude in both Lake Langas and Lake Parkijaure despite the fact that the potassium concentration in Parkijaure is only about half that in Langas.

Lake Uddjaur and Lake Storavan have *Coregonus lavaretus* populations with dwarfed fish. In these lakes *Coregonus peled* and *Coregonus pidschian* also are present. An analysis of the feeding habits of the whitefish in the lakes has been carried out by NILSSON (1960) and LINDSTRÖM and NILSSON (1962). *C. pidschian* is mainly a bottom feeder living on insect larvae and molluscs, while *C. peled* feeds on insects. *C. lavaretus* seems in these lakes to feed entirely on plankton organisms. Unfortunately, not enough material was available to make possible a separate radiocesium analyses of the *C. pidschian* and *peled*.

As will be found from Table 1, the plankton-feeding *C. lavaretus* has radiocesium concentrations that are almost twice as great as those of the other two species. This is in good agreement with the findings from Lake Mälaren, where the cisco, which is also a plankton-feeding *Coregonus* species (*C. albula*), was found to have radiocesium concentrations only slightly lower than those of the predacious fish species. *C. lavaretus* in Lake Storavan has a radiocesium concentration more than twice as great as the same species in Lake Parkijaure; yet the potassium concentrations of the water, are only slightly different. *C. lavaretus* from Rasjön, a small lake in southern Sweden with approximately the same potassium concentration as Lake Udd- jaur, has radiocesium concentrations of the same order of magnitude as those from the last-mentioned lake. Another sample from Lake Rasjön consists of a mixture of at least two species. The radiocesium concentra- tion of this sample was lower.

It is interesting to note that *C. oxyrhynchus* from Lake Vänern has a radiocesium concentration only slightly lower than that found in the same species in Lake Parkijaure.

Table 2. Char.

Date	Lake and River system	No of fish	Lenght cm	Habital	pCi/kg meat w. w.
5 Sept. 1966	Lake Övre Björkvattnet	16	15.0—23.0	pelagic	1,950 ± 48
	„	8	23.5—28.6	„	2,170 ± 36
	„	21	13.9—35.0	littoral	5,640 ± 55
	„	10	16.0—22.0	„	5,480 ± 87

^{137}Cs in char from Lake Övre Björkvattnet

In a recent paper (1967) FILIPSSON has demonstrated probable sibling species of char with corresponding food segregation and differences in their habits.

Two types of char can be obtained in a small lake called Övre Björkvattnet in the Ume River system. One of the types is obtained by fishing with pelagic nets, the other by fishing with nets close to the shore.

FILIPSSON found differences in the morphology of the ear stones (otoliths) from the two char types. Otherwise it was not possible to distinguish one from the other by comparing morphological characteristics.

A difference in the growth rates could be demonstrated; the pelagic char growing faster than the bentic. All analyses of the stomach contents of the two char types revealed that the fast-growing pelagic char had fed on terrestrial insects trapped on the water surface while the slow-growing bentic type mostly fed on bottom organisms (N.-A. NILSSON: personal communication).

Mr Filipsson generously supplied me with char of the both types for radiocesium analyses.

It can be seen from Table 2 that the different feeding habits have resulted in differences of the radiocesium concentrations.

The fish feeding on surface food had the lowest radiocesium concentration. This is in good agreement with the findings in Lake Parkijaure, where *C. peled,* which is known to be a surface feeder, also has a low radiocesium concentration.

Discussion

A considerable variation in the radiocesium concentration of a number of closely related species of whitefish and char living together in the same lake has been found. Such an interspecific variation can not of course be explained as an effect of differences in the potassium concentration of the water.

It seems to me unlikely that the variations are caused by differences in

the relation between the uptake and elimination rates. Species so closely related as are those described here must be supposed to have a similar type of metabolism. Furthermore, it is found that one and the same species, as e.g. *C. lavaretus,* may have very different concentration levels in different lakes.

All this argues in favour of a hypothesis that the variations are caused by differences in the way of living of the fish, including their feeding habits.

It may be, however, that the radiocesium concentration of the food is not the only explanation of the variations found. In Lake Mälaren it has been found that ciscos have a radiocesium concentration that is close to that found in predacious species in spite of the fact that their food, crustacean plankton, has a low radiocesium concentration as compared with the food of the predacious species.

A possible explanation is that the metabolic rate (not necessarily the metabolic type) is different in fish with different habits.

The potassium concentration of the water plays an important rôle for the radiocesium accumulation in fish. Whitefish from the Baltic with potassium concentrations around 45—66 mg/l have been found to hold only 60—380 pCi ^{137}Cs/kg of meat, which should be compared with 1,000—8,000 pCi/kg in whitefish caught at the same time in lakes with 0.25—0.99 mg K/l.

In the majority of Swedish lakes, however, the variations of the potassium concentration of the water are responsible for only a minor part of the variations in the radiocesium concentrations of the fish. Here, instead, the ecology of the fish must be of decisive importance. In secondary consumers, such as whitefish, differences in this respect may cause 3—4 fold differences in the radiocesium concentration.

The findings of KOLEHMAINEN *et al* (1966) that the direct uptake of radiocesium from the water plays only a minor rôle for the radiocesium accumulation in fish are borne out by this investigation. This circumstance in turn is explicable if the radiocesium in natural freshwater is presumed to be largely bound to particles.

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Experimental Investigations on the Accumulation of Mercury in Water Organisms

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Introduction

During the last few decades alcyle and alcoxyalcyle mercury compounds have come into an increased use in agriculture as seed desinfectants. In the pulp industry, phenylmercuric acetate has become an important means of slime control and the predominating conservant for wet ground pulp.*

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* The use of methylmercury in agriculture and phenylmercury in industry has now been prohibited.

Mercury has been carried to streams, lakes and the sea in increasing amounts with waste waters from the pulp industry and run-off from the fields. Investigations by JOHNELS and WESTERMARK (1967) and WESTERMARK (1965), using the neutron activation analytical method (CHRISTELL et al 1965), have revealed high mercury concentrations in fish from many lakes and streams in the southern and central parts of Sweden. Values as high as 8,000 ng Hg/g have been reported, as compared with the 30—180 ng Hg/g that can be regarded as a normal background concentration for fresh-water fish (RAEDER and SNEKVIK 1942, 1949 a 1949 b). There are many indications that the high mercury concentrations found in fish and other water organisms are direct consequences of the use of mercury in agriculture and industry. Fish from certain lakes have actually been judged unfit for human consumption (BERGLUND and WRETLIND 1967).

This alarming situation emphasized the need for a better knowledge of the accumulation, retention and elimination of the mercury compounds concerned in fish and other water organisms and the experimental studies reported here were therefore started in 1965. They have been financially supported by the Swedish Agricultural Research Council.

Methods

Analysis

The use of labelled compounds in the experiments permitted studies of mercury uptake from the water with mercury concentrations so low that they approached those actually found in streams where industrial wastes containing mercury were released.

All the compounds studied have been labelled with ^{203}Hg, which has a gamma ray with an energy of 0.279 Mev and a half-life of 47 days.

All analyses have been carried out with a single-channel gamma spectrometer equipped with a $3'' \cdot 3''$ well NaI crystal and sample changer.

Ponds, tanks and aquaria

The experiments have been made in ponds, tanks and aquaria. The ponds, which are dug out in the ground, have the dimensions 82 by 35 by 4 feet. They were lined with polyethylene sheets, welded together to ensure that no leakage could take place to the surrounding soil. Before experiments were started, gravel, earth and water plants of various kinds from Lake Mälaren were put in and water added to a depth of about 1 foot in the shallow ends and about 2 feet in the deeper ends of the ponds. The water volume was then about 110 m³.

The ponds were thereafter supplied with a continous through-flow of untreated water from Lake Mälaren for a few weeks before the start of the

experiment. During this time an invertebrate population was obtained from natural sources. Shortly before the start, small pike received from a fish hatchery and — as food objects for these — a large number of perch fry and roach fry caught with a scap net in Lake Mälaren or young pike-perch obtained from a hatchery were introduced. Two pond experiments were run simultanously at each time. In three of the pond experiments, namely those with methylmercuric hydroxide, methoxyethylmercuric hydroxide and mercuric chloride the compound was dosed continuously into the inflowing water by means of a dosing pump. In the experiment with phenylmercuric acetate, it proved difficult to dissolve the necessary amount of the compound to a stock solution of reasonable volume and it was thus impossible to introduce this in the same manner as the other three compounds. It was therefore added to the water in a weak alcoholic solution as a single dose, by means of a pump. The volume of the pond water was sufficient to dissolve the amount of phenylmercuric acetate used, i.e. 1,155 mg.

Water was sampled every day at the inlets and the outlets of the ponds. Vegetation and fish were sampled once a week. For the tank experiments, glassfibre reinforced plastic tanks with the dimensions $2 \text{ m} \cdot 2 \text{ m} \cdot 0.8 \text{ m}$ were used. These tanks are equipped with bottom outlets and an adjustable waterlevel maintenance gauge, which makes possible a continuous throughflow of water.

The mercury compounds were introduced in the tank water either as single doses or continuously with the help of dosing pumps.

The aquaria used are of an ordinary 65 litre type.

Sampling and sample preparation

Vegetation, invertebrates and sediments from the pond experiments

Representative parts of plants of different species were regularly collected. The emergent and submersed parts were separated, if possible, into different samples.

Invertebrates were collected with finely meshed nets and sorted into species.

Sediments were scooped up from the bottom or scraped with a spoon from the plastic lining of the pond. This latter material, which had entirely sedimented during the experiment, was a light ooze.

The samples were homogenized and 4 g aliquots carried over to plastic test tubes, weighed, preserved with alcohol and analysed.

Fish

The following organs and organic complexes were regularly analysed, namely: blood, heart muscle, spleen, liver, kidneys, stomach wall, gonads,

eyes, brain, gills, dorsal fins, scales, muscles and bone. Sampling was performed as follows.

The tail fin was cut off, after which the fish was placed in a vertical position to allow the drainage of blood through the wound. Part of the blood sample was taken for analysis. The heart sample included also the bulbus arteriosus. Liver samples were taken from the caudal part of the left lobus. The entire spleen could usually be analysed. In cod, only the cranial parts of the kidneys were sampled. In pike, however, as much as possible of the kidneys was taken. A suitable piece of the stomach wall was cut out and carefully rinsed from stomach contents before analysis. The eyes were cut out after removal of the conjunctivae. The brain samples contained also the medulla and parts of the cranial nerves. The gill arches of the left side was used for analysis. Muscle samples were taken from the longitudinal dorsal muscles beneath the first dorsal fin and bone samples from the spine between the caudal end of the coelomic cavity and the tail.

After weighing, the samples were preserved with alcohol. The test tubes were never filled with the sample over a certain level, to ensure approximately the same "geometry" in measurements in the gamma spectrometer.

Calculation of Hg concentrations

From the labelled stock solution, which always had a very precisely known concentration of mercury, "standard samples" were taken and weighed to a high degree of precision. These samples, which thus had known contents of mercury, were always analysed together with the samples from the experiments.

After correction for background, the gamma spectrometer readings were recalculated to impulses per gram of wet weight per minute. With the help of the "standard" readings, the impulse readings were then used to calculate ng/Hg per gram. The method used made corrections for radioactive decay unnecessary.

Brief description of the experiments

Pond experiments

1. Phenylmercuric acetate

Dates of the experiment: 31 Aug.—5 Oct. 1965.

Type and amount of mercury compound used: 1,153 mg phenylmercuric acetate dissolved in 10 litres of 15 per cent alcohol.

Mode of introduction of the mercury compound: Single dose, injected into the pond water by means of a pump and a hose which was pulled through the water.

Mercury concentration in the water: 10 ng/g at the start and 6 ng/g at the end of the experiment.

^{203}Hg activity concentration of the water: $1.2 \cdot 10^{-4} \mu$Ci/ml.

Fish: Pike: 93.7 ± 4.3 mm, Pike-perch: 78.0 ± 3.6 mm.

Perch: 31.0 ± 1.3 mm, Roach: fry.

Special remarks: 10 ng Hg/g water proved to be too high a concentration. About half of the fish died within 24 hours after the start. Also the invertebrates, especially the snails, died in large numbers. The pike-perch were introduced on 15 Sept. when the bottom invertebrate fauna had recovered and no additional death of fish had been observed for about 2 weeks.

2. Methylmercuric hydroxide

Dates of the experiment: 13 Sept.—15 Oct. 1965.

Type and amount of mercury compound used: 1,729 mg methylmercuric hydroxide in water solution.

Mode of introduction of the mercury compound: Continuous dosing during 24 days.

Concentration of mercury in the pond water: 3.0 ng Hg/g as a mean for the whole experiment.

^{203}Hg activity concentration of the water: $1.4 \cdot 10^{-4} \mu$ Ci/g at the start of the experiment.

Fish: Pike: 93.7 ± 4.3 mm, Pike-perch: 78.0 ± 3.6 mm.

Perch: 31.0 ± 1.3 mm, Roach: fry.

Special remarks: The pike-perch were introduced on 15 Sept.

3. Methoxyethylmercuric hydroxide

Dates of the experiment: 15 July—10 Oct. 1966.

Type and amount of mercury compound used: 900 mg methoxyethyl-mercuric hydroxide in water solution.

Mode of introduction of the mercury compound: Continuous dosing during 25 days.

Mercury concentration in the water: Varied. A peak concentration of 1.4 ng Hg/g was reached 18 days after the start, decreasing thereafter to about 0.3 ng Hg/g by the end of the experiment. The mean concentration for the whole experiment was 0.58 ng Hg/g.

^{203}Hg activity concentration in the water: $8 \cdot 10^{-5} \mu$ Ci/ml at the peak concentration.

Fish: Pike: 185.5 mm, Perch: 36.0 mm, Roach: 29.3 mm.

Mean temperature (readings at 9—9.30 AM): 16.5°C.

Special remarks: Owing to clogging of the lake-water feeding pipe, the water throughflow in the pond was interrupted from 10 Aug. to 1 Sept. During this time there was no addition of mercury to the pond. Owing to evaporation, the water level sank to about half of the original depth during this period.

4. Mercuric chloride

Dates of the experiment: 29 July—5 Oct. 1966.

Type and amount of mercury compound used: 72.6 mg mercuric chloride in weak hydrochloric acid.

Mode of introduction of the mercury compound: Continuous during 25 days by means of a dosing pump.

Mercury concentration in the pond water: The concentration varied during the experiment with a peak of 0.16 ng Hg/g 14 days after the start, decreasing thereafter to 0.035 ng Hg/g by the end of the experiment. The mean for the whole experiment was 0.05 ng Hg/g.

^{203}Hg activity concentration in the water: 10^{-4} μ Ci/ml at the peak concentration 14 days after the start.

Fish: Identical with experiment No. 3.

Mean temperature (readings at 9—9.30 AM): 15.2°C.

Special remarks: The water throughflow was interrupted from 10 Aug. to 1 Sept. for the same reasons as in experiment No. 3.

Tank experiments

5. Phenylmercuric acetate

Intention of the experiment: Studies of the elimination rate of phenyl mercury in fish.

Dates of the experiment: 5 Oct.—22 Nov. 1965.

Concentration of mercury in the water: Untreated water from Lake Mälaren was run through the tank throughout the experiment.

Fish: Pike-perch which had accumulated phenyl mercury in experiment No. 1.

Temperature of the water: Gradually decreasing from about +10°C to about freezing point. At the end of the experiment, the tank was covered with ice.

Special remarks: The pike-perch were carried over from the pond to the tank on 5 Oct. Samples of bone, muscles and viscera from 20 to 24 fish were analysed after 2, 34, 42 and 48 days.

6. Methylmercuric hydroxide

Intention of the experiment: Studies of the elimination rate of methyl mercury in fish.

Date of the experiment: 15 Oct. 1965.

Special remarks: Pike-perch which had accumulated mercury in experiment No. 2 were carried over to a tank with running untreated lake water (cf. exp. No. 6). The fish, however, were much less vital and could not withstand the stresses of the transport and the new environment. Almost all the fish died within a few days.

7. Methoxyethylmercuric hydroxide

Intention of the experiment: Uptake of methoxyethyl mercury directly from the water.

Dates of the experiment: 4 July—12 July 1966.

Type and amount of mercury compound used: 21.6 mg Hg as methoxyethylmercuric hydroxide with a total initial activity of 0.49 mCi was dissolved in distilled water to a stock solution of 20 litres volume.

Mercury concentration of the tank water: 0.6 ng Hg/g.

Activity concentration of the water: 10^{-6} μ Ci/ml.

Mode of introduction: Continuous, by means of a dosing pump.

Water: Throughrunning. Salinity: 33.7 per mille.

Mean temperature: $+13.8°$C.

Fish: Cod with a mean length of 28.8 cm obtained with bow nets in Gullmar Fjord.

Special remarks: Five cod with a representative length distribution were sampled and analysed every day.

8. Methoxyethylmercuric hydroxide

Intention of the experiment: Uptake of methoxyethyl mercury from the food.

Dates: 13 July—15 July 1966.

Mercury concentration in the water: 0.

Water: Salinity and temperature as in experiment No. 7.

Fish: Cod (10) obtained as above with a mean length of 28.4 cm.

Remarks: The fish were kept in an aquarium with running sea water. Meat of mussels which had accumulated methoxyethyl mercury to a concentration of 3,914 ng/g was given to the fish. The cod were killed and analysed after 2 days.

9. Methylmercuric hydroxide

Intention of the experiment: Uptake of methyl mercury from the water.

Dates: 5 July—13 July 1966.

Type and amount of mercury compound used: 40.5 mg Hg as methylmercuric hydroxide which was dissolved in distilled water to a stock solution with a volume of 10 litres.

Mercury concentration of the water: 1.1 ng Hg/g.

Mode of introduction: Continuous, by means of a dosing pump.

Water: Running. Salinity and temperature as in experiment No. 7.

Fish: 35 cod obtained as above, with a mean length of 28.4 cm.

Remarks: Sampling and analysis as in experiment No. 7.

10. Methylmercuric hydroxide

Intention of the experiment: Uptake of methyl mercury from the food.

Dates: 12 July—14 July 1966.

Duration of the experiment: 2 days.

Mercury concentration of the water: 0.

Water: Running. Salinity and temperature as in experiment No. 7.

Fish: Cod obtained as above (exp. No. 7), with a mean length of 26.6 cm.

Remarks: The fish were kept as in experiment No. 8. Meat of mussels obtained in the same way as in experiment No. 8 and with a mercury concentration of 5,250 ng/g was given as food to the cod. The fish were killed and analysed after 2 days.

11. Methoxyethylmercuric hydroxide

Intention of the experiment: Uptake of methoxyethyl mercury directly from the water.

Dates: 26 July—4 Aug. 1966.

Mode of introduction: Continuous.

Mercury concentration of the water: 1.4 ng/g.

Water: Mean salinity 5.8 per mille. Mean temperature 15.0°C.

Fish: 40 pike with a mean length of 14.4 cm.

Remarks: The pike were obtained from a fish hatchery and had been kept in running brackish water for acclimatization for about 14 days before the start of the experiment.

The water throughflow was only 1,000 l per 24 hours and the tank was therefore aerated.

12. Methoxyethylmercuric hydroxide

Intention of the experiment: Uptake of methoxyethyl mercury from the food.

Dates: 12 Aug.—15 Aug. 1966.

Mercury concentration in the water: 0.

Water: Running. Mean salinity: 6.2 per mille. Mean temperature: 14.1°C.

Fish: 6 pike with a mean length of 19.1 cm.

Remarks: Fry of roach and perch obtained with scap nets in the Baltic were kept in a tank with brackish water and a mercury concentration of 1.4 ng Hg/g (as methoxyethylmercuric hydroxide) for three days, after which the tanks were carefully rinsed with running sea water from the Baltic during 24 hours. The pike, which had been kept in starvation in net cages in the Baltic, were carried over to the tanks. They preyed immediately on the fry.

13. Methylmercuric hydroxide

Intention of the experiment: Uptake of methyl mercury directly from the water.

Dates: 26 July—4 Aug. 1966.

Mode of introduction: Continuous.

Mercury concentration in the water: 1.0 ng Hg/g.

Water: Salinity and temperature as in experiment No. 11.

Fish: 40 pike with a mean length of 14.5 cm.

Remarks: The experiment was carried out in the same way as experiment No. 11.

14. Methylmercuric hydroxide

Intention of the experiment: Uptake of methyl mercury from the food.

Dates: 12 Aug.—15 Aug. 1966.

Mercury concentration of the water: 0.

Water: Running water with a salinity and temperature as in experiment No. 12.

Fish: 6 pike with a mean length of 18.6 cm.

Remarks: The experiment was carried out in the same way as experiment No. 12.

15. Methoxyethylmercuric hydroxide

Intention of the experiment: Studies of the uptake directly from the water.

Dates: 23 Aug.—1 Sept. 1966.

Mode of introduction: Single dose at the beginning of the experiment.

Mercury concentration of the water: Mean concentration: 0.24 ng Hg/g.

Water: Mean salinity: 6.38 per mille. Mean temperature: 12.6°C.

The tank was aerated.

Fish: 55 cod with a mean length of 32.7 cm.

Remarks: The fish were obtained from fishermen's pond nets off the Baltic coast, from where they were transported in tanks with running sea water to the place of the experiment. The water of the experimental tanks was aerated, but no water throughflow was arranged. 28 of the fish died within 24 hours after the start of the experiment, presumably as a result of the stresses of transportation. The remaining fish, however, were in good condition.

16. Methylmercuric hydroxide

Intention for the experiment: Studies of the uptake directly from the water.

Dates: 23 Aug.—1 Sept. 1966.

Mode of introduction: Single dose at the beginning of the experiment.

Mercury concentration of the water: 0.45 ng Hg/g.

Water: Mean salinity as in experiment No. 15. Mean temperature: 12.3°C.

17. Mercuric chloride

Intention of the experiment: Studies of the uptake directly from the water.

Dates: 19 Sept.—28 Sept. 1966.
Mode of introduction: Single dose at the beginning of the experiment.
Mercury concentration in the water: 0.30 ng Hg/g.
Water: Fresh water from Lake Mälaren, not aerated. Mean temperature: 8.6°C.
Fish: 12 pike with a mean length of 17.7 cm.
Remarks: The pike were delivered from a fish hatchery.

18. Mercuric chloride

Intention of the experiment: Studies of the uptake from the food.
Dates: 28 Sept.—12 Oct. 1966.
Mercury concentration of the water: 0.
Water: Untreated water from Lake Mälaren.
Fish: 11 pike with a mean length of 22.3 cm, which had been kept in starvation in net cages in Lake Mälaren, were carried over to a tank with running lake water. In another tank, fry of perch (mean length 5.75 cm) and roach (mean length 3.58 cm) had been kept for 9 days in a solution of mercuric chloride with a mean concentration of 0.32 ng Hg/g. The fry was then throroughly washed with lake water and given to the pike. Its mercury concentration was then 231 ng Hg/g. Predation on the fry started immediately.

19. Methoxyethylmercuric hydroxide

Intention of the experiment: Studies of the uptake directly from the water.
Dates: 9 Aug.—19 Aug. 1966.
Mercury concentration of the water: 0.4 ng Hg/g.
Mode of introduction: Single dose at the beginning of the experiment.
Water: Untreated water from Lake Mälaren with a mean temperature of 17.2°C.
Fish: 21 pike with a mean length of 13.9 cm, obtained from a fish hatchery.

20. Methylmercuric hydroxide

Intention of the experiment: Studies of the uptake directly from the water.
Dates: 9 Aug.—19 Aug. 1966.
Mercury concentration of the water: 0.3 ng Hg/g.
Mode of introduction: Single dose at the beginning of the experiment.
Fish: 20 pike with a mean length of 13.7 cm.

21. Mercuric nitrate

Intention of the experiment: Studies of the uptake directly from the water.

9

Dates: 9 Feb.—16 Feb. 1967.

Mercury concentration of the water: 0.06 ng Hg/g.

Mode of introduction: Continous, by means of a dosing pump.

Water: Sea water with a mean salinity of 33.5 per mille and a mean temperature of 2.9°C.

Fish: 65 cod with a mean length of 30.1 cm, obtained from Gullmar Fjord.

22. Mercuric nitrate

Intention of the experiment: Studies of the uptake of mercury from the food.

Dates: 14 Feb.—16 Feb. 1967.

Mercury concentration of the water: 0.

Water: Running sea water with a mean salinity of 33.5 per mille and a mean temperature of 2.7°C.

Fish: 10 cod with a mean length of 23.3 cm, obtained as above.

Remarks: Mussels (*Mytilus edulis*) were kept in running sea water with a mercury concentration of 0.06 ng Hg/g for 4 days, after which the meat was removed from the shells. The mean concentration of the mussel meat was 14.2 ng Hg/g. The meat was used to feed the cod, which had been kept in starvation in running sea water for about one week.

The relative uptake of mercury in fresh water biota when given as methylmercuric hydroxide, methoxyethylmercuric hydroxide, phenylmercuric acetate and mercuric chloride (experiments 1—4)

Experiments Nos. 1 to 4 offer an opportunity to compare the relative uptake in water biota of the four different mercury compounds studied. Two of the experiments were carried out during the summer of 1965 (1 and 2) and two during the summer of 1966 (3 and 4). The two ponds used were identical. The temperature conditions, and the composition of the water vegetation and water fauna, were very similar. In three of the experiments, however, the isotopes were gradually dosed into the water by means of a dosing pump over a couple of weeks (experiments Nos. 2—4), while in the experiment with phenylmercuric acetate the compound was introduced as a single dose at the beginning of the experiment. The comparability is thus less for experiment No. 1.

The ability of an organism to concentrate an element or a compound from the water is characterized by a concentration factor. The term concentration factor is defined as:

$$\frac{\text{the concentration in the organism}}{\text{the concentration in water}}$$

In the experiments reported here, the concentrations in the water varied during the work.

In the calculation of concentration factors, there have been used the mean concentrations of the water from the beginning of the experiment up to the date of sampling. As will be shown later (p. 138) there are great differences between the various groups of organisms as regards the time required to reach an equilibrium in the exchange between the mercury in the organism and that in the surrounding water. The process is much more rapid in plants, for instance, than in fish. It is thus not relevant to compare the concentration factors, as calculated here, between organism groups in order to elucidate the differences in their ability to concentrate the compound at a steady state condition. These concentration factors, however, may be used for comparisons of the accumulation rates within organism groups, and between experiments with different mercury compounds.

Inter- and intra-specific variations (Tables 1—4)

Vegetation

Considerable differences are found in the mercury concentrations of emergent and submersed parts of the water plants. In the experiments with phenyl and methyl mercury, the submersed parts of reed had concentrations 10—20 times higher than those in the emergent parts. The explanation of this difference is presumably that there is a considerable adsorption of mercury on the submersed surfaces of the plants.

The uptake in the plant tissues seldom gives a concentration factor exceeding 100 and is of very much the same order of magnitude in different species. The assimilation of Hg in plants is thus comparably small. A much greater variation is found when comparing the concentrations of the sub-surface parts of the plants. The yellow iris always has a low concentration, no matter what the type of mercury compound. This applies also for bull-rush, in most of the experiments. High concentrations of the submersed parts are found in *Lysimachia nummularia,* sedge, moss and reed.

This intraspecific variation seems to depend to a certain degree on the relation between the surface area and the weight of the plant, which confirms the importance of the surface adsorption for the mercury accumulation in the submersed parts of the plants. The larger the area, the greater the possibilities for surface adsorption.

Colonies of the blue-green algae *Nostoc pruniformes* consequently have low concentrations, and the filamentous algae (*Oedogonium*) have high concentrations.

The accumulation to the submersed surfaces of a plant can be of different types. A purely physico-chemical adsorption is possible, in which the molecules are bound to the cell walls of the plant. The submersed parts of a

Table 1. Experiment no 1.

Days after start	Phenylmercuric acetate Concentration factors	
	28	35
V e g e t a t i o n		
Reed, *Phragmites communis*, emergent parts	7	9
submersed parts	530	850
Bulrush, *Scirpus lacustris,* emergent parts	230	90
submersed parts	400	790
Yellow iris, *Iris pseudacorus*, emergent parts	55	20
submersed parts	170	40
Polygonum amphibium, stem and leaves	1,000	1,250
Carex sp., stem and leaves	1,100	1,900
Scirpus palustris, leaves	650	1,050
Lysimachia nummularia, submersed leaves	—	2,350
Ranunculus sp., submersed leaves	—	4,200
»Moss», submersed	—	3,900
Filamentous algae, (*Oedogonium* sp.)	—	1,200
Nostoc sp.	—	86
Annelids:		
Haemopis sanguisuga	—	2,030
Snails:		
Planorbis sp...	—	1,280
Lymnaea stagnalis	—	1,800
Insects:		
Mayfly naiads (*Ephemeridae*)	—	900
Bloodworms (*Chironomidae*)	—	12,700
Corixa sp. (*Hemiptera*)	—	4,200
Crustaceans:		
Daphnia sp..	—	3,570
S e d i m e n t		
Sludge from the wall of the pond. Sedimented during the experiment	—	6,800

plant, however, very often have an attached microscopical fauna and flora. These organisms can act as concentrators of the mercury from the water. It is also possible for the brushlike surface of a plant to act as a strainer on particles in the water, and thus concentrate the activity mechanically.

Invertebrates

The molluscs offer a good material for comparisons of concentration factors. The latter are relatively similar for the two snails *Lymnaea* and *Planorbis,* of which, however, *Planorbis* usually exhibits a somewhat higher concentration (with an exception for phenylmercuric acetate). In two of the experiments, *Physa fontinalis* was found in the ponds. This species had a much higher concentration factor than the two previously mentioned.

The predacious insect larvae, e.g. those of dragon flies and *Sialis,* water beetles (especially *Hydrophilidae*), all have high concentration factors, while species living on detritus and decaying plant material mostly have lower factors. The chironomids were found to vary in this respect.

Table 2. Experiment no 2.

Days after start	Methylmercuric hydroxide Concentration factors	
	14	32
Vegetation		
Alder, *Alnus glutinosa*, leaves	7	4
Reed, *Phragmites communis*, emergent parts	7	25
submersed parts	76	530
Bulrush, *Scirpus lacustris*, emergent parts	4	8
submersed parts	350	1,250
Yellow iris, *Iris pseudacorus*, emergent parts	6	18
submersed parts	—	34
Polygonum amphibium, stem and leaves	600	1,010
Carex sp., submersed parts	1,800	1,870
»Grass», submersed parts	—	2,340
Scirpus palustris, submersed parts	59	1,800
Duckweed, *Lemna minor*	1,520	2,950
Lysimachia nummularia, submersed leaves	—	3,200
Ranunculus sp., submersed leaves	—	2,360
»Moss», submersed	—	5,900
Annelids:		
Haemophis sanguisuga	—	450
Glossosiphonia complanata	—	110
Sludge worms (*Oligochaeta*)	—	1,780
Snails:		
Planorbis sp.	—	3,570
Lymnaea stagnalis	—	3,480
Insects:		
Mayfly nymphs (*Ephemeridae*)	—	3,290
Bloodworms (*Chironomidae*)	—	3,070
Corixa sp. (*Hemiptera*)	—	8,470
Notonecta glauca (*Hemiptera*)	—	2,160
Sediment		
Sludge from the wall of the pond. Sedimented during the experiment	—	6,100

The leach *Hæmopis sanguisuga,* which is believed to prey on insect larvae. had high concentrations in experiment Nos. 1 and 3, but relatively low concentrations in exp. No. 2 (missing in exp. No. 4).

The leach *Glossosiphonia complanata* seems to concentrate mercury to a lesser degree. This species is believed to feed mainly on small mollusca.

The hemipterans *Notonecta* and *Corixa* had in two of the experiments similar, medium-high concentrations. Experiment No. 2, with methylmercuric hydroxide, offers an exception. *Corixa* had in this experiment a much higher concentration factor than *Notonecta*.

Corixa and *Notonecta* are both pelagic, but are feeding on different trophical levels. *Corixa* is a filter feeder but *Notonecta* is predacious and feeds mainly on small insect larvae. The high figure for *Corixa* in experiment No. 2 is presumably explained by a larger supply of mercury in the particles of the water in this experiment. When trying to explain the difference

Table 3. Experiment no 3.

Days after start	Methoxyethylmercury. Concentration factors							
	11	18	24	31	65	69	76	89
Vegetation:								
Reed, *Phragmites communis*,								
emergent parts	25	49	74	4	6	9	10	8
submersed parts	48	93	139	68	77	32	70	—
Bulrush, *Scirpus lacustris*,								
emergent parts	14	69	39	53	—	—	—	56
submersed parts	83	77	190	120	150	160	—	—
Scirpus palustris, submersed parts	—	—	438	206	113	—	—	—
Yellow iris, *Iris pseudacorus*,								
emergent parts	3	31	10	13	38	48	26	—
submersed parts	14	90	40	98	77	54	—	—
Polygonum amphibium,								
stem and leaves	100	149	175	140	77	59	48	—
Carex sp., submersed parts	243	568	244	216	72	—	132	—
Duck weed, *Lemna minor*	97	250	480	226	471	260	—	—
Lysimachia nummularia,								
submersed leaves	423	871	1,300	771	1,031	—	3,488	—
Alisma plantago aquatica,								
emergent parts	75	129	155	254	—	218	226	—
submersed parts	173	120	470	380	200	—	80	—
Butomus umbellatus, emergent parts	40	40	130	490	—	—	—	—
submerced parts	170	150	210	350	300	—	—	—
Filamentous algae, *Oedogonium* ..	840	2,640	990	920	250	460	260	230
Nostoc	—	—	—	—	170	—	42	13
Sediments								
Sludge from the wall of the pond.								
Sedimented during the experiment	363	551	843	743	924	1,649	1,642	1,320
Annelids:								
Haemopis sanguisuga	—	—	—	—	—	—	—	1,148
Glossosiphonia complanata	—	—	—	—	—	—	—	640
Sludge worms (*Oligochaeta*)	—	—	—	—	690	—	—	626
Snails:								
Planorbis sp.	1,065	1,518	1,698	1,970	—	1,203	956	846
Lymnaea stagnalis	875	728	1,051	1,178	—	1,190	636	792
Physa fontinalis	3,365	—	4,266	2,705	—	—	—	2,650
Insects:								
Mayfly naiads (*Ephemeridae*)	—	589	680	508	—	—	—	636
Caddisfly larvae (*Trichoptera*) ...	—	—	—	—	909	—	—	740
Sialis lutaria, larvae	—	—	—	—	—	—	—	1,270
Tipula sp., larvae	—	625	—	—	—	—	—	—
Bloodworms (*Chironomidae*)	—	—	—	—	—	—	450	988
Dragonfly nymphs (*Odonata*)	—	—	—	—	—	—	—	1,296
Damselfly nymphs (*Odonata*)	—	—	—	—	—	—	—	1,186
Dytiscus marginalis (*Coleoptera*)								
imag.	—	—	—	—	—	—	—	800
Hydrophilidae (*Coleoptera*) larvae	—	—	—	—	—	—	—	3,134
Corixa sp. (*Hemiptera*)	—	—	—	—	—	—	—	740
Notonecta glauca (*Hemiptera*)	—	—	—	—	—	—	—	674
Gerris najas (*Hemiptera*)	—	—	—	—	—	—	—	754
Crustaceans:								
Eurycerus (*Cladocera*)	—	—	—	—	—	—	—	286
Aquatic saw bug, *Asellus aquaticus*	—	—	—	—	—	—	—	954
Acarina:								
Hydracnidae sp.	—	—	—	—	—	—	—	624
Mean concentration in the water up								
to the date of sampling ng/g	0.64	0.84	0.80	0.79	—	0.56	0.50	0.50
Mean concentration in the water								
between the dates of sampling ng/g	0.64	1.40	0.67	0.67	—	0.30	0.36	0.30

Table 4. Experiment no 4.

Days after start	Mercuric chloride. Concentration factors								
	6	14	21	34	41	49	54	49	65
Vegetation:									
Reed, *Phragmites communis,*									
emergent parts	—	33	14	19	56	23	—	—	—
submersed parts	71	149	127	—	85	122	—	—	—
Bulrush, *Scirpus lacustris,*									
emergent parts	—	40	77	2	2	3	—	18	—
submersed parts	—	37	48	—	70	—	68	—	—
Scirpus palustris, submersed parts	15	73	—	—	72	252	763	—	—
Yellow iris, *Iris pseudacorus,*									
emergent parts	3	12	3	4	9	13	12	18	6
submersed parts	3	10	4	3	6	23	16	—	—
Polygonum amphibium,									
stem and leaves	14	41	26	9	31	79	138	195	—
Carex sp., submersed parts	33	63	252	60	55	—	—	—	—
Duck weed, *Lemna* sp.	—	—	—	—	70	—	—	—	—
Lysimachia nummularia,									
submersed parts	70	131	184	264	418	486	531	257	—
Alisma plantago aquatica,									
emergent parts	0	9	—	43	40	67	27	158	—
submersed parts	30	74	5 7	30	79	280	245	—	—
Butomus umbellatus, emergent parts	7	12	42	—	—	20	—	—	—
submerced parts	49	58	43	—	—	—	172	—	—
Filamentous algae (*Oedogonium*) ..	530	538	290	252	185	—	871	912	—
»Moss», submersed	—	263	307	—	393	—	400	—	1,502
Nostoc	—	10	4	6	6	9	6	6	6
Sediments:									
Sludge from the wall of the pond sedimented during the experiment	85	178	359	—	532	—	546	962	550
Annelids:									
Glossosiphonia complanata	—	—	—	—	—	—	—	—	670
Herpobdella octoculata	—	—	—	—	—	—	—	—	534
Sludge worms (*Oligochaeta*)	—	234	281	—	—	—	—	—	517
Snails:									
Planorbis sp.	109	241	337	—	560	—	793	795	414
Lymnaea stagnalis	195	297	234	205	247	—	—	—	293
Physa fontinalis	—	637	—	—	—	—	—	—	—
Ephemeroptera, larvae	—	28	—	—	—	—	—	—	138
Trichoptera, larvae	—	—	—	—	—	—	—	513	259
Tipula sp., larvae	—	—	—	—	840	—	—	517	—
Chironomidae, larvae	—	—	—	277	—	—	—	175	362
Damselfly nymphs (*Odonata*)	—	—	—	—	—	—	—	—	655
Hydrophilidae, larvae (*Coleoptera*)	—	—	—	—	—	—	—	—	603
,, , imagines (*Coleoptera*)	—	—	—	—	—	—	—	—	862
Corixa sp (*Hemiptera*)	—	—	—	—	—	—	—	—	414
Notonecta glauca (*Hemiptera*)	—	—	—	—	—	—	—	—	483
Gerris (*Hemiptera*)	—	—	—	—	—	—	—	—	431
Mean concentration in the water up to the date of sampling .... ng/g	0.073	0.124	0.107	0.083	0.075	0.69	—	0.58	0.056
Mean concentration in the water between the dates of sampling ng/g	0.073	0.162	0.073	0.044	0.029	0.038	—	0.036	0.030

found in concentration factors, it is necessary to take into account that the measurements have been taken on homogenates of whole animals, including their stomach contents. The percentage share of this material in relation to the total weight may vary considerably between species. It is possible that much of the mercury of the stomach contents though not available for resorption in the gastrointestinal tract may have a decisive importance on the concentration figure for the total animal analysed. This may apply especially to the detritus feeders. Even if this is taken into account, it is impossible to find any general connection between the trophic level of the organism and its concentration factor. The snails all feed on the same trophic level, but *Physa fontinalis* differs from the other two by its much higher mercury concentration.

The hemipterans, which are both pelagic, have in spite of different feeding habits very similiar concentration factors, in two of the experiments. The water saw bug, *Asellus aquaticus,* which feeds mainly on decaying plant material, has in experiment No. 3 a higher concentration factor than other organisms feeding on the same type of material e.g. the caddis fly nymphs.

The often heard hypothesis of a successive accumulation in the food chain can thus not alone explain the differences in concentration factors between the water organisms. Nor does this hypothesis agree with what is known of the importance of the direct uptake of mercury from the water (p. 163).

When comparing the habits of the snails analysed, it is found that *Physa fontinalis* is the most actively moving of the species. The predacious insect larvae are all more actively moving than the scavengers and filter feeders. *Haemophis* is more often seen swimming than *Glossosiphonia*. It seems thus likely that the muscular activity, and as a function of this the metabolic rate, of the animal should play an important role for its ability to concentrate mercury. The differences in concentrations between different organisms are thus presumably the result of several parameters, in which both feeding habits and metabolic rate, as well as stomach contents (see above), are of importance.

Sediments

During the experiment, an ooze made up of a mixture of minerogenic and organogenic particles settled on the sloping walls of the pond, which were covered with plastic sheets. This material was regularly sampled and analysed. As can be seen from the tables, this material contained relatively high concentrations of mercury in all of the experiments. This indicates that the suspended solids of the water act as scavengers carrying the adsorbed mercury to the bottom. It was observed that the snails at least did ingest this material, which may act as an important link in the transport of mercury from the water to the bottom fauna.

Table 5. Concentration factors after about one month. Pond experiments. Days after start within brackets (Mercuric chloride).

	Methoxy-ethyl mercury	Methyl mercury	Phenyl mercury	Mercuric Chloride
Days after start	31	32	35	21—41
Water plants:				
Lysimachia nummularia	771	3,200	2,350	264 (34)
Polygonum amphibium	140	1,010	1,250	26 (21)
Iris pseudacorus, emergent parts	13	18	20	3 (21)
submersed parts:	98	34	40	4 (21)
Lemna minor	226	2,950	—	70 (41)
Phragmites c., emergent parts	4	25	9	56 (41)
submersed parts:	68	530	850	85 (41)
Scirpus lacustris, emergent parts	53	8	90	77 (21)
submersed parts	120	1,250	790	48 (21)
Carex	216	1,870	1,900	60 (34)
Algae *(Oedogonium)*	920	—	1,220	252 (34)
Moss	560	5,900	3,900	393 (41)
Sediments:				
Ooze from plastic surface	743	6,100	6,800	359
Invertebrates:				
Planorbis sp.	1,990	3,570	2,280	560 (41)
Lymnaea stagnalis	1,180	3,480	1,800	247 (41)
Mayfly — larvae	510	3,290	900	—
Corixa sp.	740 (89)	8,470	4,200	431 (65)

Variations in the accumulation of different mercury compounds

It has already been mentioned that there are only moderate differences in the concentration factors of the emergent parts of the plants for the different mercury compounds studied (Tab. 5). The mean value for *Iris, Phragmites* and *Scirpus* is for methoxyethyl mercury 23, for methyl mercury 17, for phenyl mercury 39 and for mercuric chloride 34. These differences are not significant. There are significant differences, however, in the concentration factors for the submersed parts of the plants, those for methyl mercury and phenyl mercury being much higher than for the other two compounds. This means that the surface adsorption was much stronger for phenylmercuric acetate and methylmercuric hydroxide than for the other two mercury compounds studied, presumably as a result of a greater tendency to form particles or to be adsorbed to other particles in the water. This hypothesis is supported by the fact that the accumulation factors for the sediments were ten or more times higher for these two compounds than for methoxyethyl mercury and mercuric chloride.

The differences for the invertebrates are smaller. When comparing the concentrations of the invertebrates in the different experiments, it must again be remembered that the analysis included the stomach contents of the ani-

mals. This may play an important role in the detritus feeders, as the concentration of the sediments differed considerably from experiment to experiment (Tab. 5). The difference in the activity of the stomach contents may not necessarily mean corresponding differences in the concentrations of the body tissues.

The exchange of mercury between the water and the biota

There is a considerable practical interest in studies of the exchange rate of mercury between the water and the biota. On the exchange rate depends namely the rate of "recovery" after the discontinuation of the contamination of the lake water.

In two of the pond experiments, namely Nos. 3 and 4, the mercury concentration changed during the experiments. The biota were sampled and analyzed throughout the experiment, and the concentrations in the organisms regularly established.

Fig. 1 shows the variations in mercury concentration in water, algae (*Oedogonium*), sediments and *Polygonum amphibium* in the pond experiment with methoxyethylmercuric hydroxide. The concentration peak for the filamentous algae coincides in time very well with that of the water, indicating that the exchange of this mercury compound between the water and the algae is fairly rapid. *Polygonum amphibium* reacts more slowly to changes in the mercury concentration in the water.

The measurements on the sediments are less reliable than those of the plants, owing to the difficulties involved in taking representative sediment samples. However, there is no doubt a great difference in exchangeability between the mercury bound to the sediments and that bound to the plants, exchangeability in the former being much less.

In the snails *Planorbis* and *Lymnaea*, the mercury concentrations follow that of the water with a certain time lag (Fig. 2). Again, the complicating effect of the mercury of the stomach contents must be remembered. It may very well be so that the concentrations of the tissues followed the water concentration more closely than is found from the concentration values for whole animals including their stomach contents.

Also in the experiment with mercuric chloride, the maximum concentration peak for algae coincides very well with that of the water. After the 40th day, however, there is a rapid increase in the concentration of the algae, which has only an insignificant counterpart in the water. The reason for this is obscure. Owing, however, to a clogging of the water supply tube the pond was partly emptied between the 11th and the 36th day of the experiment. A large release of mercury from the sediments at the refilling of the pond would have been observed in the water samples. One possible explanation for the rapid increase in the mercury concentrations of the plants may be
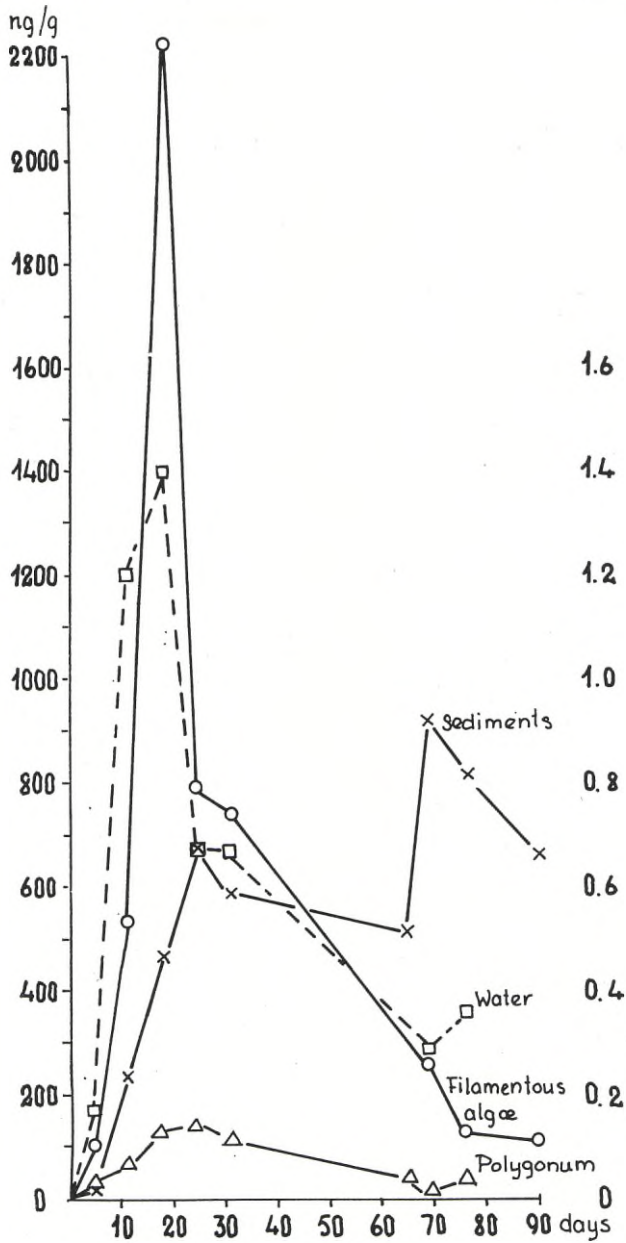
Fig. 1. Mercury concentrations in the pond experiment with methoxyethyle mercury.
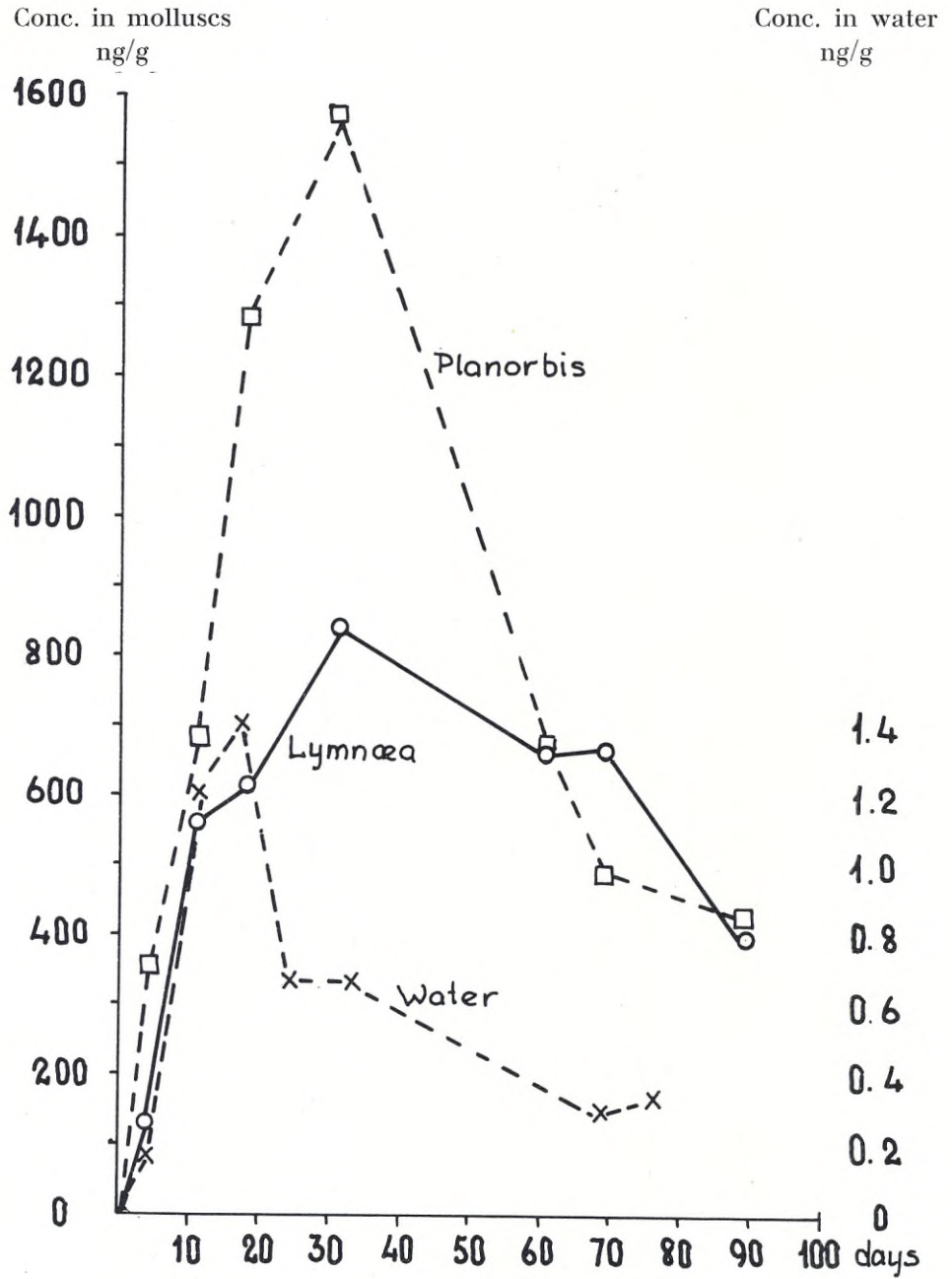
Fig. 2. Mercury concentrations in the pond experiment with methoxyethyle mercury.
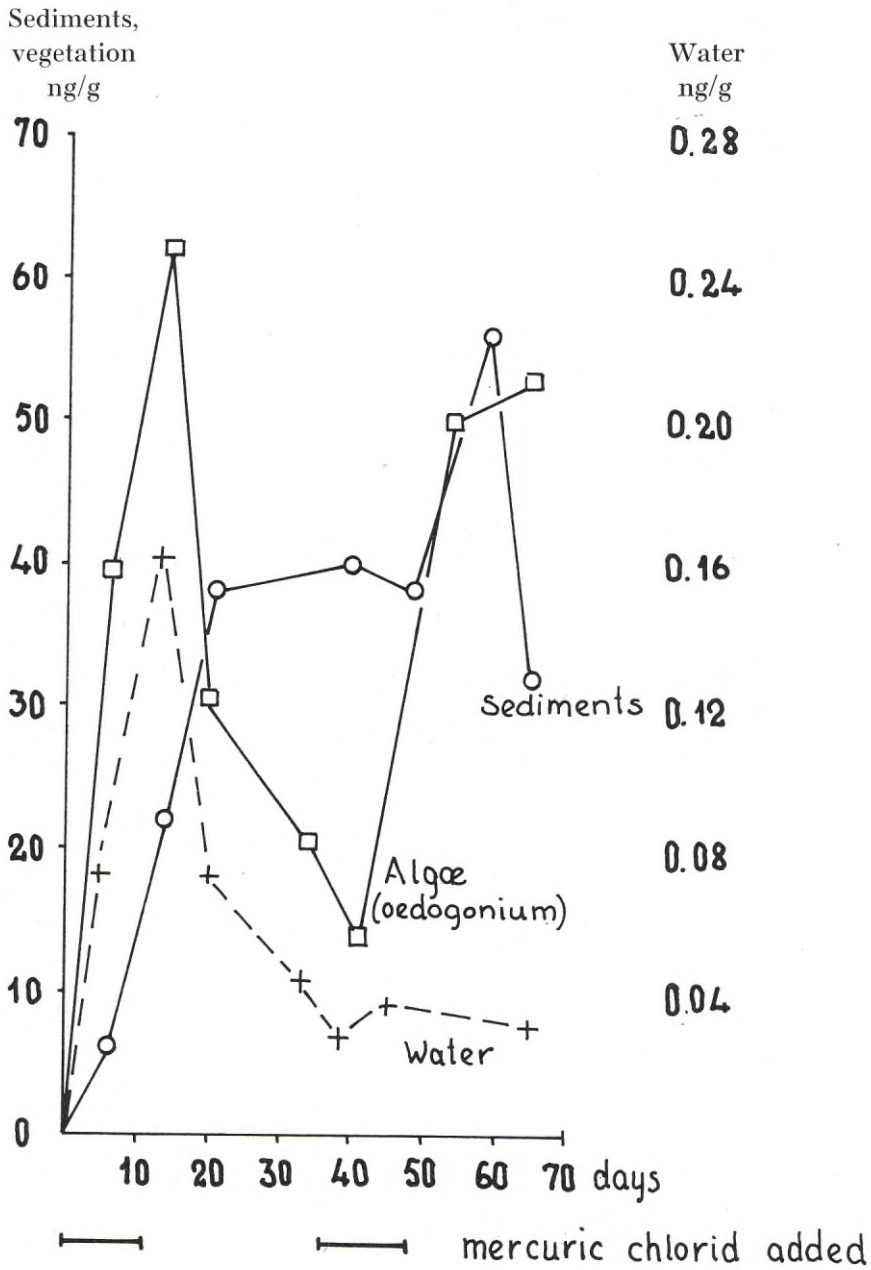
Fig. 3. Mercury concentrations in the pond experiment with mercuric chloride.
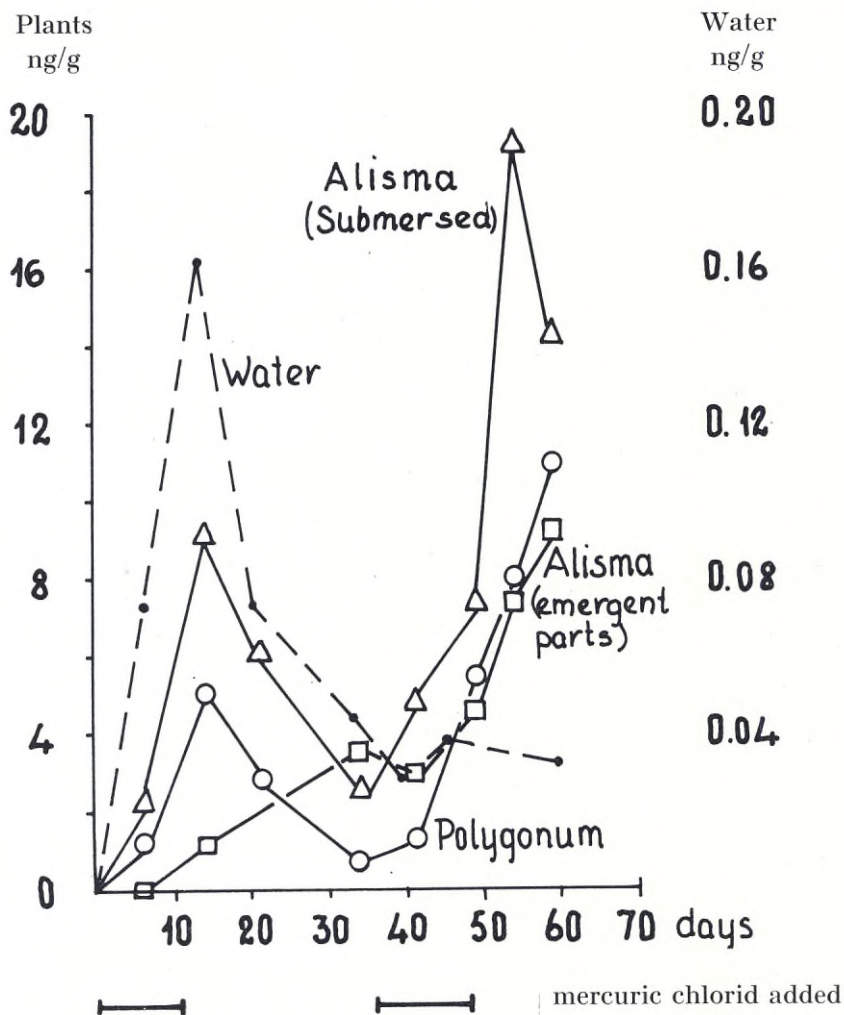
Fig. 4. Mercury concentrations in the pond experiment with mercuric chloride.

that mercury from the sediments was released in a chemical form that was more available for uptake in the algae than mercury in the chloride form.

It is found also from Fig. 3 that the mercury concentration of the sediments, in agreement with what was found in the experiment with methoxy-ethyl mercury, did not follow the water concentration very closely. Again there is an indication that part of the mercury bound to the sediments is very little exchangeable with that of the water.

Great differences are found in a comparison of the concentration curves for the submersed and emergent parts of *Alisma plantago aquatica*. The
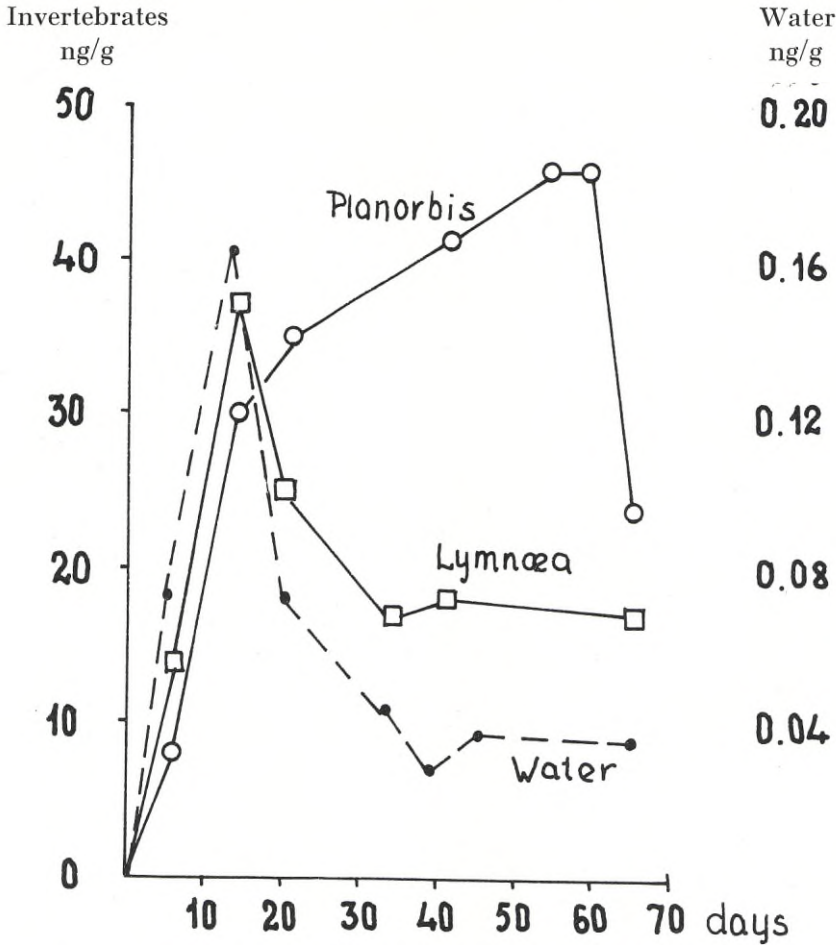
Fig. 5. Mercury concentrations in the pond experiment with mercuric chloride.

emergent parts continued to accumulate mercury from the water throughout the experiment. The peak concentration of the submersed parts coincides in time very well with that of the water, which indicates a rapid exchange of adsorbed mercury. From the 33rd day of the experiment, the concentration increased more rapidly than can be explained from the water concentration; this is in good agreement with what was found for *Polygonum*.

The accumulation of mercury in fish

The accumulation of mercury is the result of two simultaneous processes, namely uptake and elimination, the rate of uptake being higher than the rate of elimination. As the uptake rate decreases and the elimination rate in-
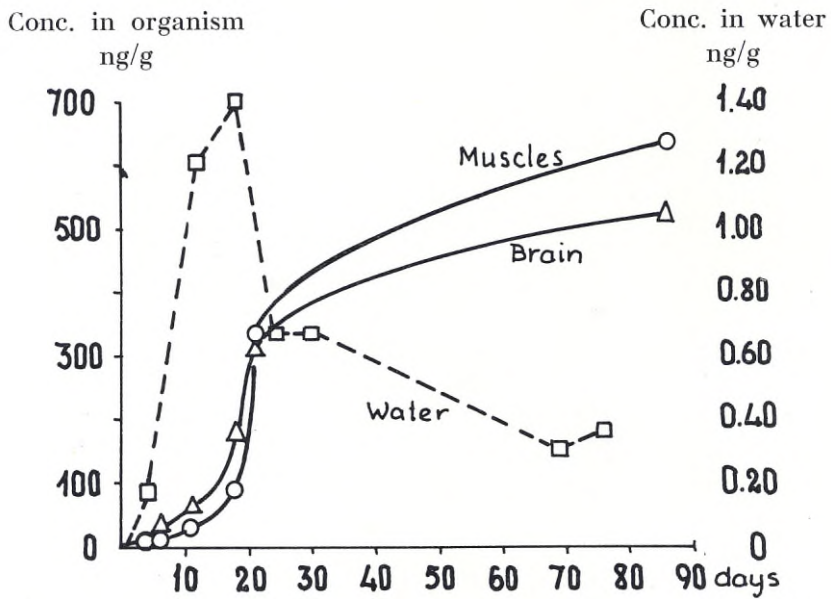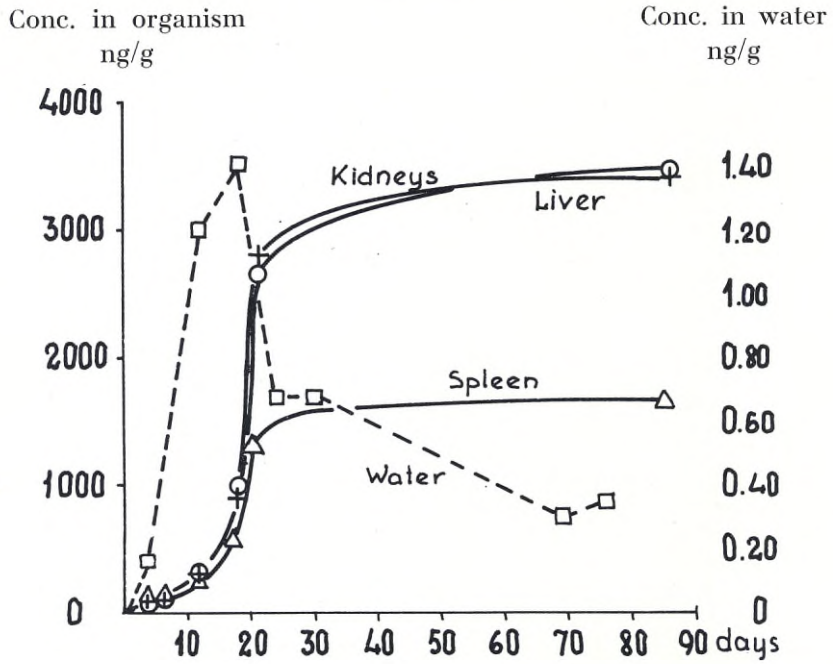
Fig. 6. Mercury concentrations in the tissues of pike and the water from the pond experiment with methoxyethylmercuric hydroxide.
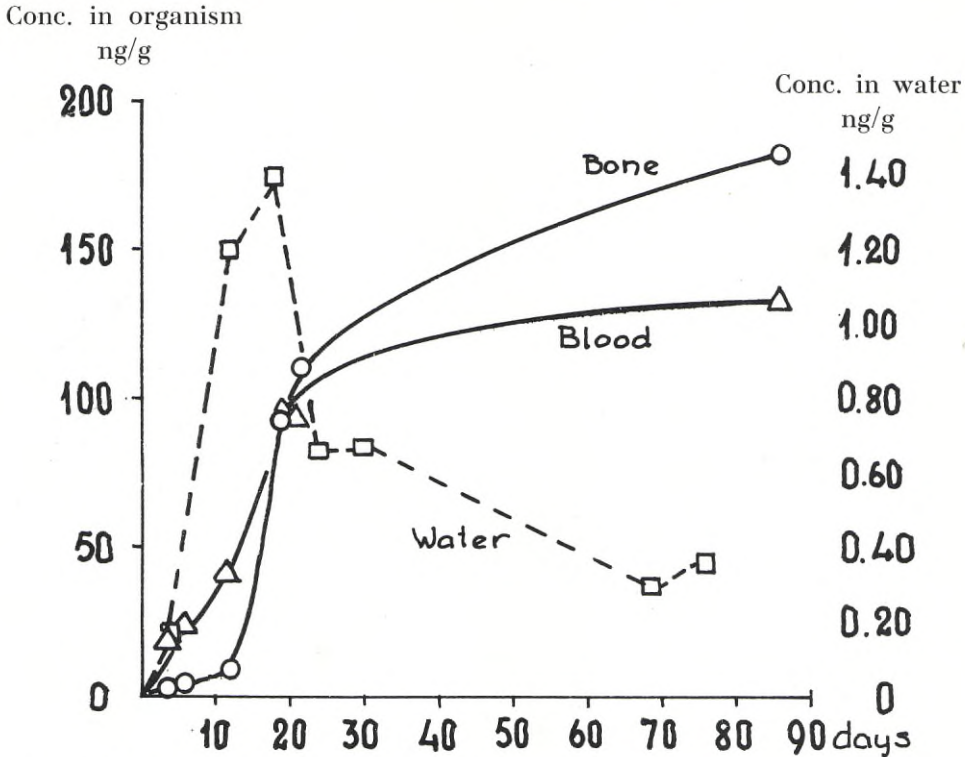
Fig. 7. Mercury concentrations in the tissues of pike and the water from the pond experiment with methoxyethylmercuric hydroxide.

creases with accumulated amount of mercury sooner or later a steady state is reached, in which the uptake is balanced by the elimination. The concept of concentration factor is often defined as the quotient $\dfrac{\text{conc. in organism}}{\text{conc. in water}}$ at this steady stage. In this paper, however, the concentration factor has been used in a slightly different sense (p. 130).

The accumulation of different mercury compounds in fish has been studied both in pond experiments and in tank and aquaria experiments.

Figs. 6 and 7 illustrate the uptake of mercury in pike from the pond experiment with methoxyethylmercuric hydroxide. The rates of accumulation differ considerably between different organs. The highest accumulation rates in this case are found in the liver and kidneys, the concentration curves of which follow each other closely. The curve for the spleen is fairly similar in type to those of the kidneys and the liver, but it levels off earlier. The curve for the concentrations in the blood levels off at a relatively low concentration (note differences in the scale between the figures). The curves of brain muscles and bone have slopes that are less steep than those mentioned above.

10

The accumulation rate was with other words still relatively high at the end of the experiment.

When comparing the curves for blood and bone it is found that the blood concentration, as could be expected, increases initially much more rapidly than that of the bone. Later on, however, the concentration of the blood approaches an equilibrium with the environment, while there is still an accumulation in the bone. The curves of blood and bone crossed each other on about the 20th day. The exchangeability of the mercury in fish is much less than that in invertebrates and plants. From the figure, it is seen that the curves of the fish tissues do not follow that of the water. A continuous accumulation is found, in spite of a radically lowered water concentration.

More or less the same type of curves were obtained in the pond experiment with mercuric chloride as with methoxyethylmercuric hydroxide.

In experiment No. 22, the uptake of mercury in cod from a solution of mercuric nitrate was studied in a rather large material (Figs. 8—11 and Tab. 6). Owing to a low temperature, the cod could be supposed to have a low metabolic rate. The slow uptake rate obtained was presumably a result of this.

Uptake during the first days was very slow, after which the rate increased rapidly. The concentration in blood increased fastest, which is in good agreement with the findings from the methoxyethylmercury experiment. The uptake curve for the brain deviates from that found in the methoxy ethyl mercury experiment. It levels off at a very low concentration. The concentration of bone increased more rapidly than that of muscles. The curve for the heart concentrations is of the same form as that for liver, kidneys, etc.

The curve for the concentrations of the fins exhibits a peculiar form, with a hump 3 to 4 days after the start of the experiment. This is presumably the result of an accumulation of mercury to the organs in two different ways, at different rates. One of these is an ordinary uptake in the tissues from the blood; but there is also a surface adsorption. This adsorbed mercury component reaches equilibrium sooner than the component adsorbed from the blood. A double uptake of this kind would lead to curves of the type observed. The gills had concentrations of mercury which were 50—100 times those of other organs. The gills are in marine fish important for the salt excretion. The concentration of the mercury in the blood, however, is so low that it is highly unlikely that the excretion alone could be responsible for the high gill concentrations. The explanation of the phenomenon must rather be a very heavy surface accumulation, which cannot be explained otherwise than that a considerable part of the mercury in the water was in particulate form and that the particles were adsorbed on the gills.

Table 6. Uptake of mercuric nitrate from the water in cod.

Days	1		2		3		4		5		6		7	
No. of fish	10		10		5		10		10		10		10	
Mean length	27.3 cm		28.2 cm		29.2 cm		28.3 cm		33.5 cm		31.2 cm		32.5 cm	
	ng/g	c.f.	ng/g	c.f.	ng/g	c.f.	ng/g	c.f.	ng/g	c.f.	ng/g	c.f.	ng/g	c.f.
Blood	0.125	1.95	0.293	4.56	0.467	7.30	0.784	12.25	1.262	19.72	1.699	26.55	2.511	39.2
Heart	0.061	0.95	0.577	9.02	0.465	7.27	1.004	15.69	1.711	26.73	2.783	43.48	4.574	71.47
Liver	0.067	1.05	0.079	1.23	0.150	2.34	0.241	3.77	0.365	5.70	0.664	10.38	0.876	13.69
Spleen	0.113	1.77	0.350	5.47	0.661	10.33	0.623	9.73	0.913	14.27	1.276	19.94	1.998	31.22
Gonades	0.169	2.64	0.526	8.22	0.850	13.28	1.091	17.05	0.487	7.61	0.524	8.19	0.4412	6.89
Kidneys	0.096	1.50	0.207	3.23	0.422	6.59	0.585	9.14	0.798	12.47	0.936	14.63	1.529	23.89
Stomach	0.034	0.53	0.198	3.09	0.301	4.70	0.465	7.27	0.670	10.47	0.822	12.84	1.248	19.50
Brain	0.035	0.55	0.149	2.33	0.131	2.05	0.199	3.11	0.193	3.02	0.133	2.08	0.190	2.97
Eyes	0.012	0.19	0.054	0.84	0.081	1.27	0.168	2.63	0.153	2.39	0.164	2.56	0.270	4.22
Gills	16.6	259.50	47.800	746.80	947.500	1480.50	1083.800	1693.40	147.818	2309.70	355.984	5562.30	234.784	3668.20
Fins	0.405	6.33	1.463	22.86	2.154	33.66	3.020	47.19	3.443	53.79	4.623	72.23	7.173	112.08
Scales	0.464	7.25	2.993	46.77	2.606	40.72	2.937	45.89	3.865	60.39	3.547	55.42	5.620	87.81
Muscles	0.011	0.17	0.027	0.42	0.044	0.69	0.076	1.19	0.105	1.64	0.096	1.50	0.2162	3.38
Bone	0.027	0.42	0.072	1.13	0.123	1.92	0.280	4.38	0.250	3.91	0.773	12.08	0.675	10.55

c.f. = concentration factor.
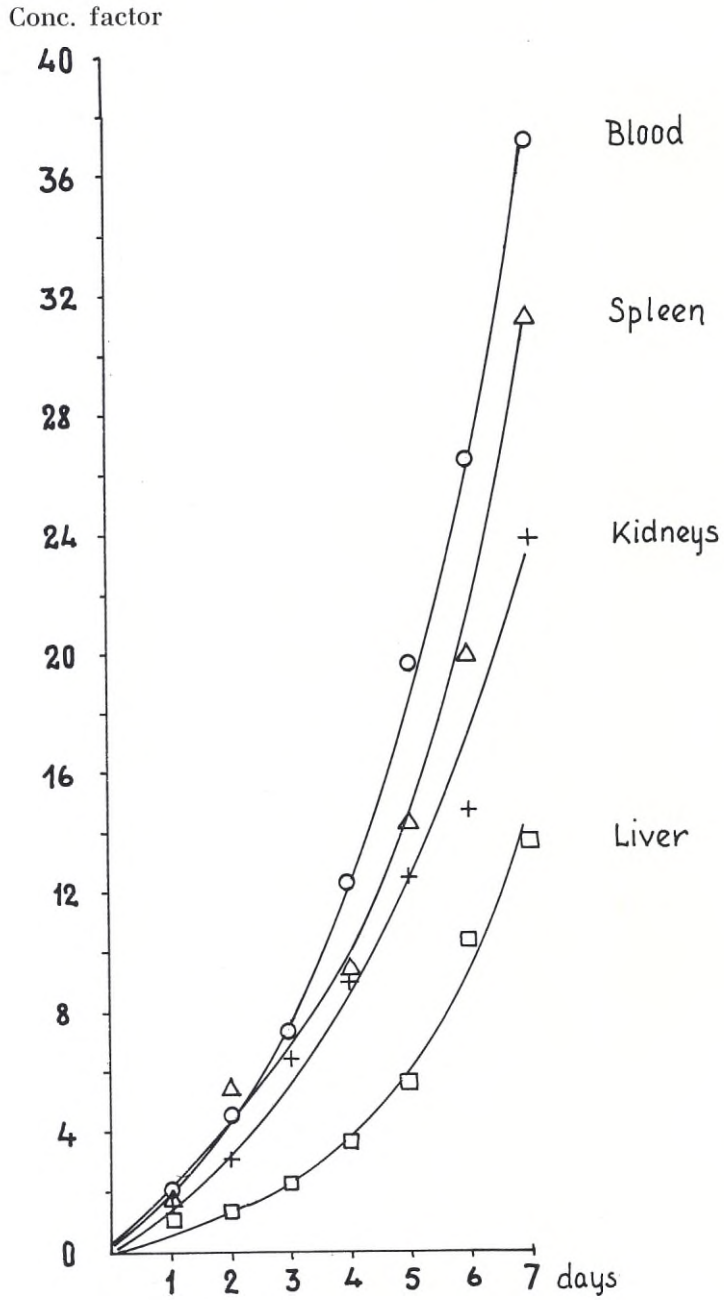
Fig. 8. Tank experiment with mercuric nitrate. Uptake in cod directly from the water.

Conc. factor
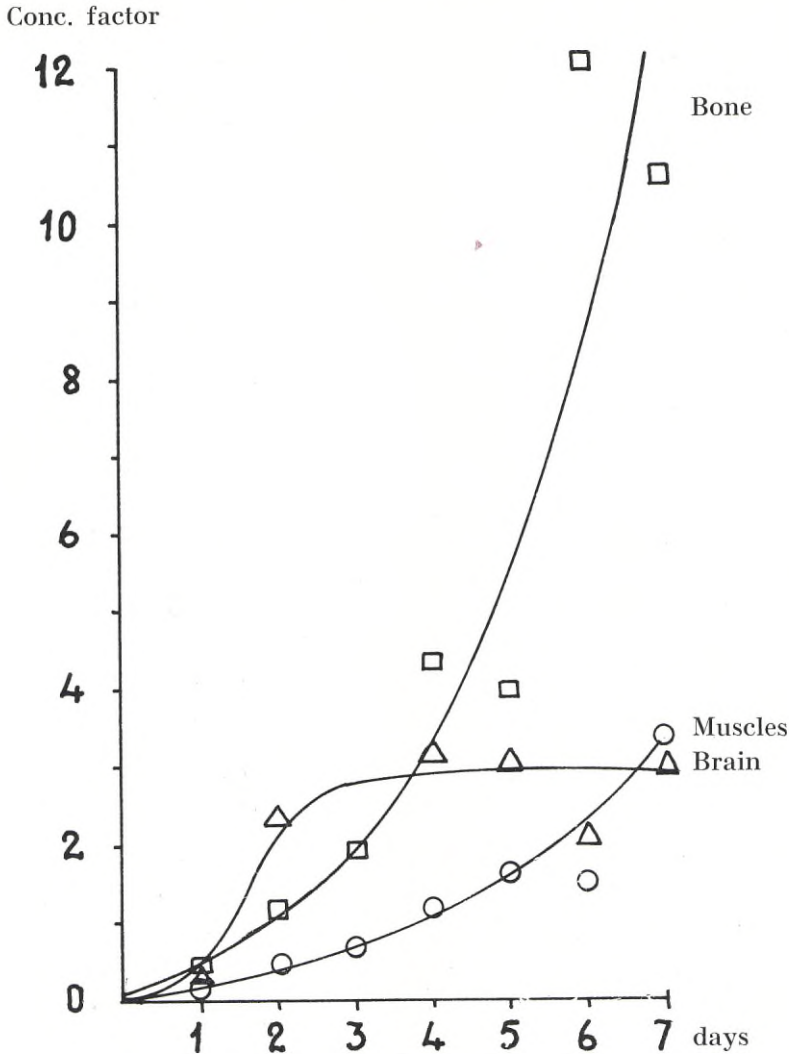
Fig. 9. Tank experiment with mercuric nitrate. Uptake in cod directly from the water.

The relative concentrations of mercury in different organs

The highest concentrations are usually found in the kidneys and the liver (Figs. 12—14). High concentrations are also found in heart, spleen and gills. The brain, too, accumulates considerable amounts of mercury. The concentrations of the blood, the gonads, the eyes and bone are relatively low.

The relatively high concentration in the gills is found irrespectively of whether the mercury is given by the food or by the water, which indicates
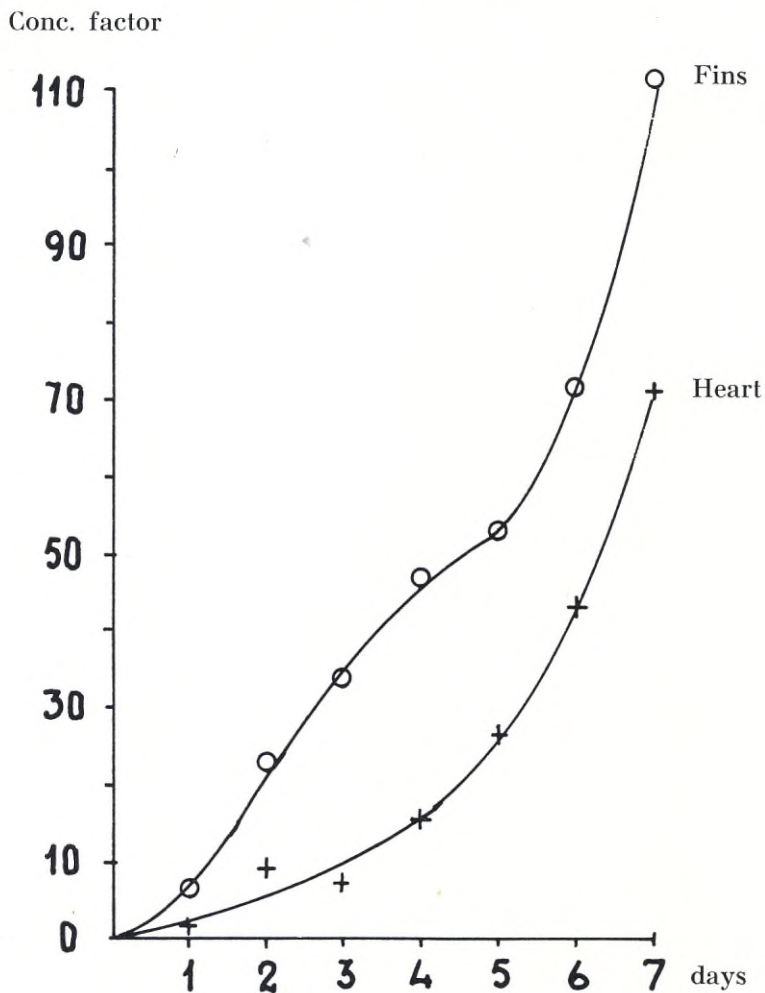
Fig. 10. Tank experiment with mercuric nitrate. Uptake in cod directly from the water.

that the gills are important for the mercury exchange between the fish and the water.

The differences of mercuric chloride, methoxymethylmercuric hydroxide and methylmercuric hydroxide as to their relative distribution among different organs are illustrated in Table 7.

The relative uptake in the muscles is very similar for the different compounds studied. Methyl mercury seems to be more readily taken up in the heart muscles and the brain than the other two compounds. Both methoxyethyl mercury and methyl mercury show relatively high figures for the kidneys. On the whole, the differences in relative distribution are less than

Conc. factor
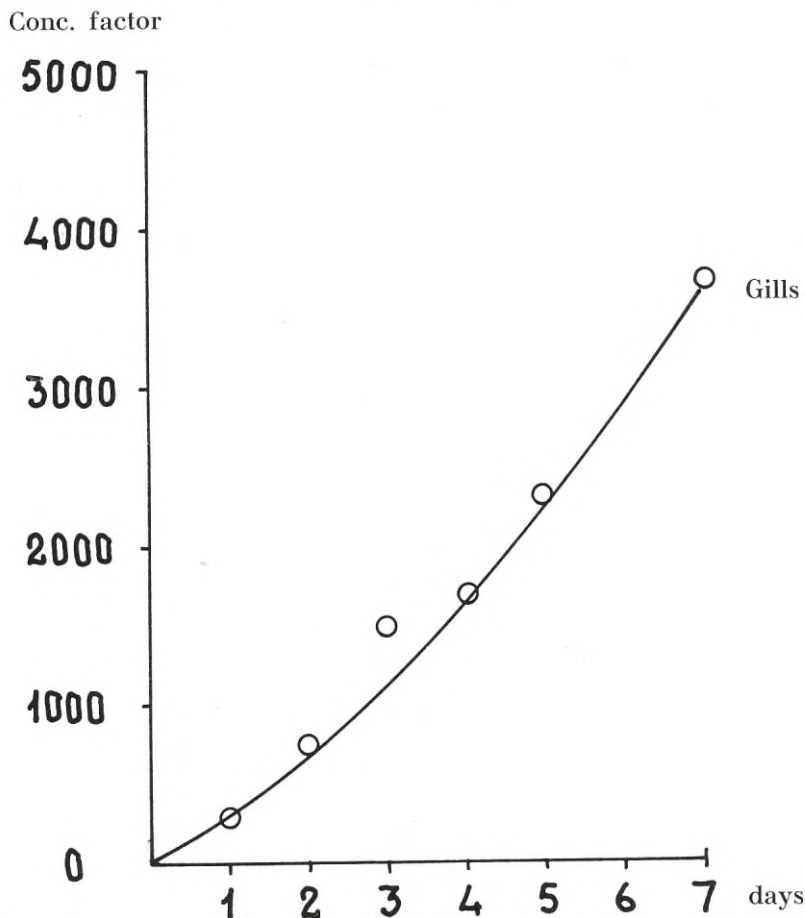
Fig. 11. Tank experiment with mercuric nitrate. Uptake in cod directly from the water.

could have been expected in view of the results reported by BERLIN and ULL-BERG (1963) from their experiments with mice.

The differences are larger when the concentration factors are compared. Methyl mercury is most readily taken up by all of the compounds studied (Fig. 12).

The mean concentration factor for all organs analysed in the pond experiments (with the exception of blood, for which no data are available from the methyl mercury experiment) is for methyl mercury 4.2 times higher than for inorganic mercury, and 1.7 times higher than for methoxyethyl mercury.

The differences in concentration factors between methyl mercury and methoxyethyl mercury in the tank experiments (Tab. 8) are larger than those from the pond experiments (above).
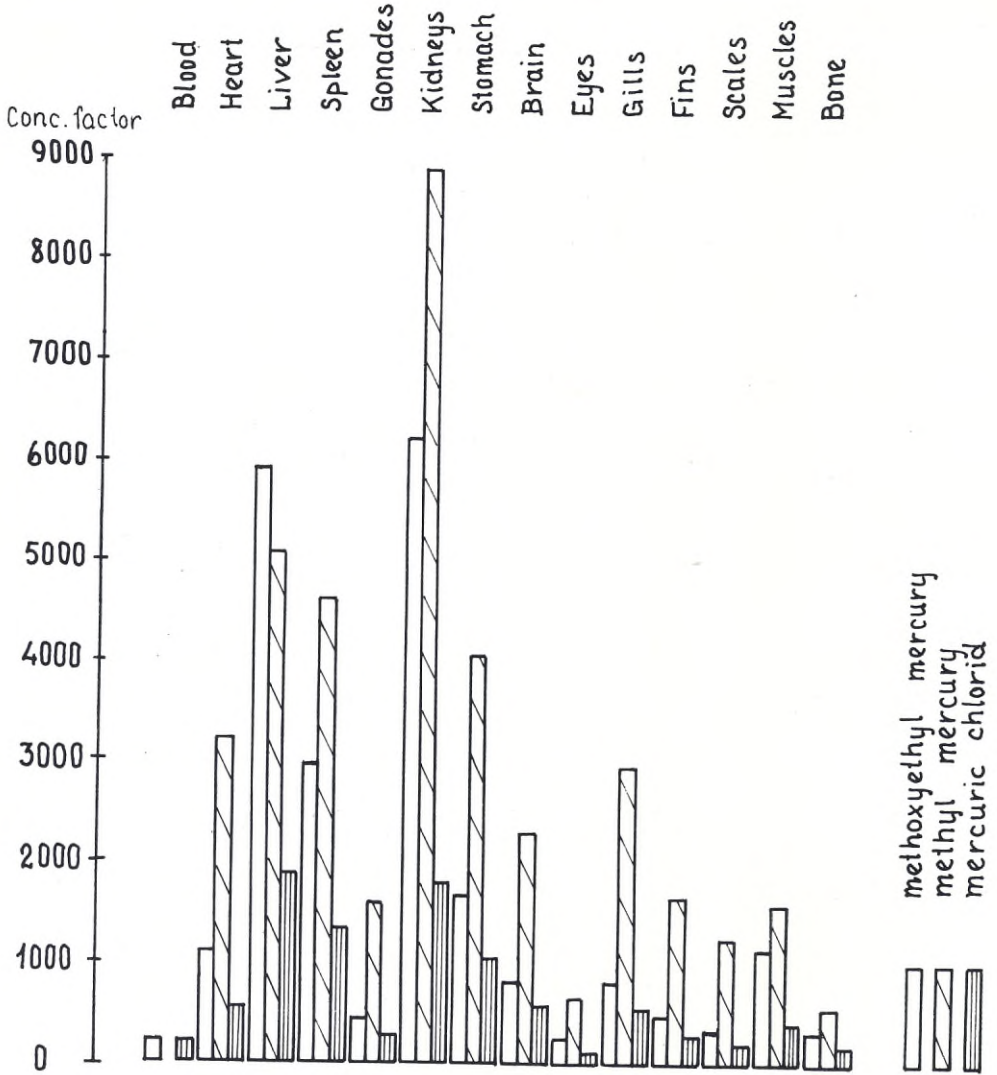
Fig. 12. Pond experiments. Concentration factors for pike.

Especially noticeable is the difference in uptake in the muscles. The explanation of the discrepancy between the pond and tank experiments may be the difference in the duration of the experiments (i.e. 10 days in the tank experiments and 70—90 days in the pond experiments) and the differences in the shape of the accumulation curves. Methyl mercury reaches an equilibrium sooner than methoxyethyl mercury. Another explanation, however, cannot be excluded, namely that the mercury in the pond experiments is partly transformed in one way or other to the same chemical form (c.f. page 173).
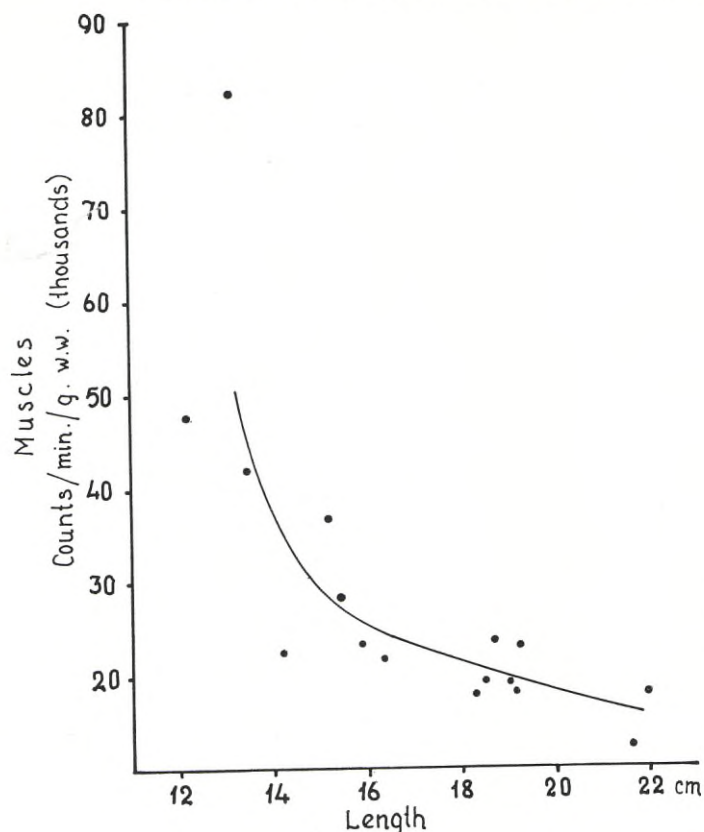
Fig. 13. The relation between the length of fish and the mercury concentration in muscles (Exp. No. 1 Pikeperch).

Individual variations in accumulation rate

58 pike-perch of approximately the same size from the pond experiment with phenylmercuric acetate (experiment No. 1) were analysed individually. A considerable individual variation was found (Tab. 9). There was a more than ten-fold difference between the highest and the lowest value for muscles, in spite of the fact that all of the fish had been subjected to the same concentration of phenylmercuric acetate in the water.

A tendency to a groupage of the concentration figures can be traced in the material. One group is centered around the concentration class 750—1,000 ng/g and another and much smaller around the 2,751—3,250 ng/g class.

In the same fish, the mercury concentrations of viscera and bone were also established, and similar distribution patterns were found.

The cause of this groupage of the concentrations is not known. It may be supposed that differences in habits of living play an important role in this connection. The observed pattern for the distribution of concentrations makes it clear that large samples are necessary when establishing concentration criteria for a population.

Table 7. Distribution of concentrations among different organs
(Concentration in bone=1) Pond experiments.

	Mercuric chloride [1]	Methoxyethyle mercury [1]	Methyl mercury [2]
Blood	1.0	0.7	—
Heart	3.1	3.1	5.8
Liver	11.1	19.1	9.1
Spleen	7.9	9.0	8.3
Stomach	6.1	5.1	7.2
Kidneys	10.6	19.1	15.9
Gonades	1.6	1.5	2.8
Eyes	0.7	0.6	1.2
Brain	3.2	2.9	4.1
Gills	3.2	2.5	5.3
Scales	1.2	1.0	2.3
Fins	1.7	1.4	2.9
Muscles	2.3	3.5	2.8
Bone	1.0	1.0	1.0

[1] Pike
[2] Pike-perch

The influence on accumulation of the size of the fish

Sixteen pike from the pond experiment with methylmercuric hydroxide (exp. No. 22) were analysed individually as to the ^{203}Hg concentrations in different organs. A variation which could be negatively correlated with the length of the fish was found (Tab. 10).

This correlation is stronger for muscles, brain, gills, eyes and fins than for liver, kidneys and bone. The relations between the length of the fish and the mercury concentrations of different organs have been expressed graphically in Figures 13 and 14.

Table 8. Relations between the concentration factors in experiments nos 19 and 20. Uptake in pike directly from the water.

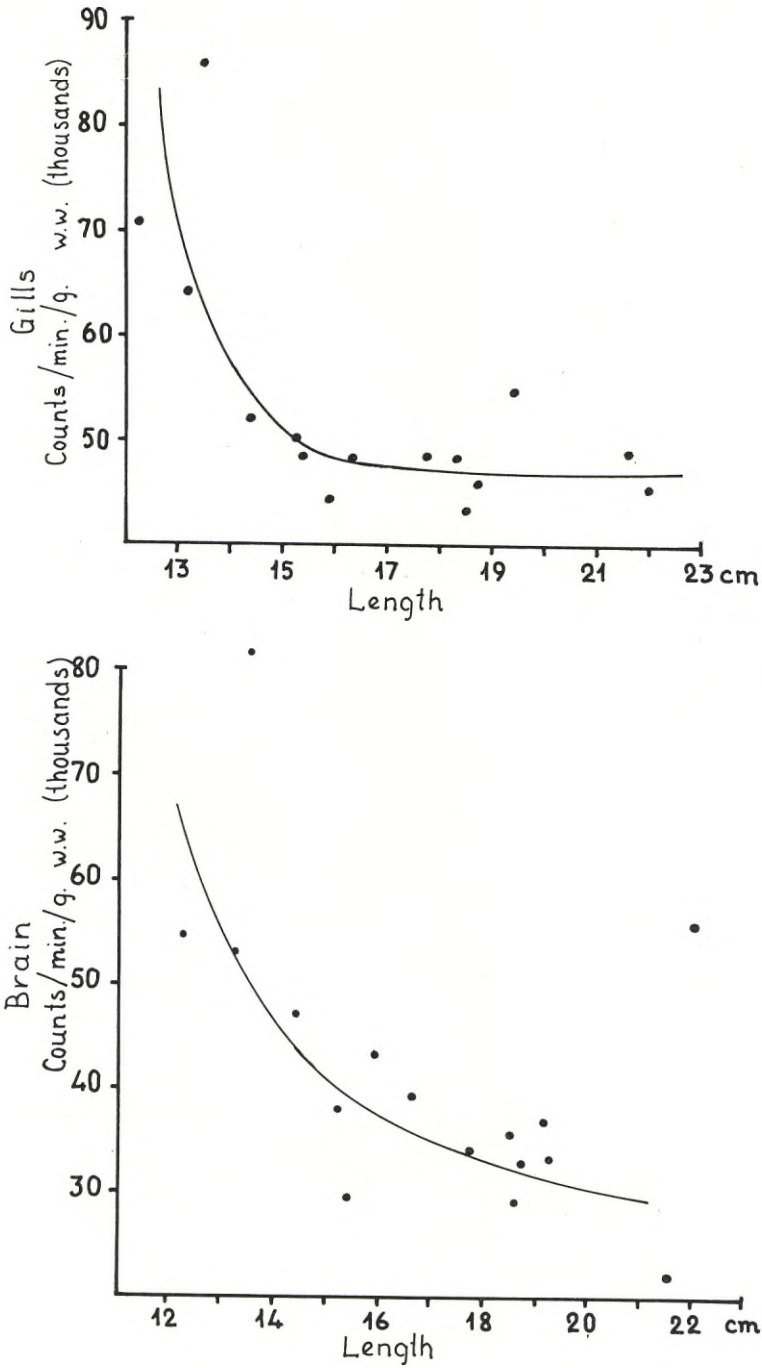|	Concentration factors after 10 days		Metylmercury
	Methylmercury	Methoxyethyl-mercury	Methoxyethyl-mercury
Blood	375	1,380	3.7
Heart	817	3,107	3.8
Liver	2,002	7,673	3.8
Spleen	2,455	6,573	2.7
Stomach	410	2,303	5.6
Kidneys	2,198	7,230	3.3
Eyes	108	597	5.5
Brain	620	2,457	4.0
Gills	2,133	6,883	3.2
Fins	765	2,883	3.8
Scales	365	1,620	4.4
Muscles	50	950	19.0
Bone	122	603	4.9

Fig. 14. The relation between the length of fish and the mercury concentration in gills and brain. (Exp. No. 1 Pike-perch).

Table 9. Variation in mercury concentrations in muscles of pike-perch from experiment no 1.

Concentration class ng/g	no of fish	Concentration class ng/g	no of fish
0— 250	—	2,751—3,000	2
251— 500	1	3,001—3,250	3
501— 750	11	3,251—3,500	1
751—1,000	16	3,501—3,750	—
1,001—1,250	7	3,751—4,000	—
1,251—1,500	7	4,001—4,250	—
1,501—1,750	5	4,251—4,500	1
1,751—2,000	1	4,501—4,750	—
2,001—2,250	1	4,751—5,000	—
2,251—2,500	—	5,001—5,250	—
2,501—2,750	1	5,251—5,500	1

The curves have been fitted by inspection. It is found that the curves are all of a more or less bent shape.

There are several possible explanations for this type of correlation.

1) Differences in metabolic rate could lead to differences in concentration factors, namely the smaller the fish, the higher the growth rate. The metabolic rate would be correlated in turn to the growth rate.

Arguing against this explanation of the sizebound variation found, however, is the fact that all the fish were of approximately the same length at the start of the experiment. Those which were largest at the time of sampling ought to have grown fastest and should have had the largest intake of food and the highest metabolic rate.

2) Differences in the selection of food objects in pike of different size could also theoretically explain differences in mercury concentration. The pike which had eaten food with the highest mercury concentrations would have accumulated the highest concentrations in its own body tissues. Against this explanation is the fact that the largest pike had remains of smaller pike in their stomachs. They had thus chosen food objects with the highest mercury concentration available in the pond and yet they had lower concentrations than the small pike which had mainly eaten invertebrates.

3) A third explanation is the most likely. This presupposes that the mercury is to a dominant degree taken up directly from the water also under conditions where there is a simultaneous uptake from the food.

The surface area of a fish is negatively correlated to its volume according to a bent curve. If it is supposed that the concentration in the fish is dependent of the relation $\dfrac{\text{surface area exposed to the water}}{\text{volume}}$, then curves of the type observed ought to be obtained. The role of the uptake of mercury directly from the water is confirmed by other experiments and will be discussed below (p. 163).

Table 10. Concentrations of ^{203}Hg (thousands of imp/min/g) in individual pike from experiment no 2.

Organ	Length															
	22.0	21.6	19.2	19.1	18.7	18.5	18.3	17.7	16.3	15.9	15.4	15.2	14.4	13.5	13.2	12.2
Heart	29.9	28.8	49.3	25.4	39.2	41.7	22.7	36.4	51.7	88.8	95.2	73.1	19.3	97.4	114.5	110.5
Liver	80.1	70.4	74.5	110.1	96.4	77.3	78.8	92.1	67.9	56.8	65.0	87.5	67.8	92.4	175.2	91.0
Stomach ..	57.9	55.9	71.0	69.9	75.3	55.8	82.5	35.4	85.8	64.4	33.1	67.3	71.0	42.0	57.8	129.8
Kidneys ..	170.8	126.5	150.3	158.7	140.4	150.3	135.9	153.7	152.2	135.4	132.3	185.5	131.2	147.0	285.7	190.7
Eyes	7.4	7.6	8.9	3.6	17.0	8.7	9.9	8.3	8.5	12.0	9.8	14.4	8.5	15.9	30.8	21.0
Brain	36.4	23.8	36.2	36.5	28.1	35.3	28.1	34.2	39.4	46.7	28.4	37.7	47.1	53.0	81.4	40.7
Gills	45.2	48.9	47.1	51.6	45.8	43.4	48.3	45.9	48.7	44.7	47.5	50.2	52.3	64.3	85.8	52.7
Fins	19.4	18.4	45.4	24.3	23.2	23.0	20.6	22.5	22.4	30.0	27.1	38.6	20.8	38.3	50.9	41.3
Muscles ...	18.1	12.5	23.3	18.4	20.4	19.5	18.0	19.1	21.8	23.2	28.4	36.8	22.7	43.4	83.6	46.4
Bone	6.0	5.5	8.9	3.9	10.7	10.1	8.9	8.1	9.4	11.5	10.8	16.2	6.7	10.9	21.5	9.9

The effect of dissolved solids on the accumulation

It is well-known that the uptake in organisms of many radionuclides from the water is influenced by the concentration of some electrolytes in the water. The concentration of radionuclides is inversely related to the concentration of corresponding elements in the water. The reason for this is that the stable and radioactive nuclides of the same element behave in the same way from a chemico-physiological point of view and that there exists what may be called a competition between all atoms, stable or radio-active, of the same element in the uptake.

As caesium and potassium have a similar chemistry, the uptake of radio-active caesium will be influenced by the potassium concentration of the water. A similar relation exists between e.g. calcium and strontium.

A considerable variation in the concentration of mercury in pike from lakes from the same region has been established by JOHNELS and WESTER-MARK (1967). This variation cannot entirely be explained by differences in the supply of mercury.

It was postulated as an experimental hypothesis that the concentration of electrolytes in the water could exert an influence on the accumulation of mercury in fish. Experiments Nos. 7, 9, 11, 13, 15, 16, 19 and 20 were carried out to elucidate this problem.

In these experiments, methylmercuric hydroxide and methoxyethylmer-curic hydroxide were tested in fresh water (Lake Mälaren water), in brackish water (Baltic Sea water), and in salt water (Skagerak water). In all of the experiments, which lasted 8 to 10 days, the mercury compounds tested were given only in the water and not by the food. The experimental conditions must be regarded as very similar. Pike were used as test organism in a number of fresh water and brackish water experiments, while cod from the Baltic and from the Skagerak coast were used respectively in a number of brackish water and salt water experiments. In one fresh water experiment, mercuric chloride was tested in the same way.

The concentration factors calculated from the experiments are expressed graphically for pike and cod in Figs. 15 and 16 respectively.

It is clear from the figures that the uptake rate in pike of methyl mercury from brackish water is lower than that from fresh water. If the mean concentrations for all the organs are compared, it is found that the uptake in brackish water was only about 60 per cent of that in fresh water. The relative distribution of concentrations among the organs, however, was fairly similar in the two experiments.

When the uptake rate of methoxyethyl mercury in fresh water and brackish water is compared in the same way, no significant difference is found. Methyl mercury was accumulated to 3.4 times higher levels than methoxyethyl mercury in the fresh water experiments, but only 1.9 times more in the experiments with brackish water.
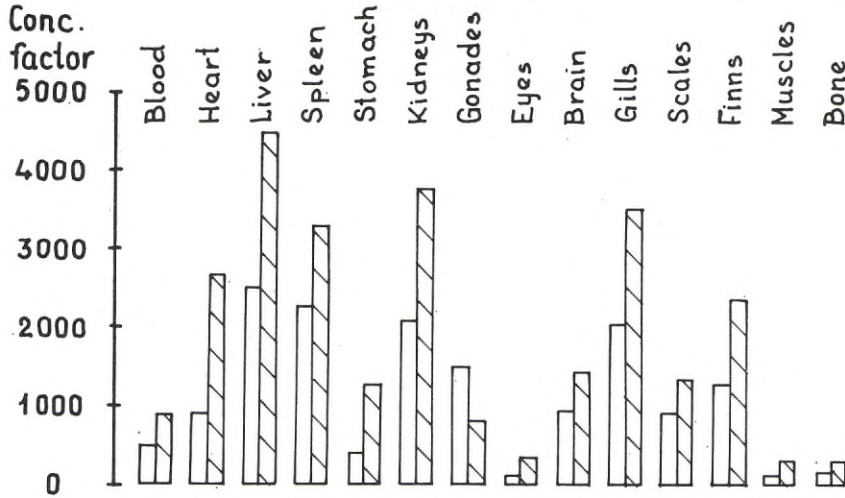
Fig. 15. Tank experiments with methyl mercury, methoxyethyl mercury and mercuric chloride. Uptake directly from the water in pike.

The accumulation in the experiments with mercuric chloride was insignificantly less than that of methoxyethyl mercury, though the distribution between organs was somewhat dissimilar.

The concentration factors in the experiments with cod are illustrated in Fig. 16. The uptake of both methyl mercury and methoxyethyl mercury was less in brackish water than in salt water. When the mean concentration factors are used in the same manner as for pike (p. 158), it is found that the uptake of methyl mercury in brackish water was only 44 per cent of that in salt water. The corresponding figure for methoxyethyl mercury was only 12 per cent. Very high concentrations of methoxyethyl mercury in the gills are found both in the experiment with brackish water and in that with salt water. The gills are known to be of importance for the salt excretion in marine fish. The higher figure for methoxyethyl mercury may, however, partly be explained by a greater tendency for this compound to form particles in salt water which are strained off in the gills.

Figs. 17—19 give curves for the uptake of the two mercury compounds, the two test fish species and the three different salinities. The more rapid uptake of methyl mercury than of methoxyethyl mercury is obvious from these figures. It is also seen that the uptake rate in pike of methyl mercury is significantly reduced in brackish water, while the uptake curves for methoxyethyl mercury largely coincide.

The uptake in cod of both methyl mercury and methoxyethyl mercury is lower in brackish water than in salt water. There is thus no general connection between the salinity and the accumulation of mercury in fish, as was supposed as an hypothesis for the experiments. The salinity exerts an influence on the direct uptake of methyl mercury from the water in pike, but it has no effect on the uptake of methoxyethyl mercury.

The uptake of methyl mercury in cod directly from the water was influenced by the salinity, but in an opposite direction to what was found for methyl mercury in pike. In this case also the uptake of methoxyethyl mercury was affected. The results show that several factors have an influence on the uptake.

If it is presumed that methoxyethyl mercury is available in the same chemical form in fresh water and brackish water, but methyl mercury in different chemical forms, the differences in uptake between the two compounds would be explained. It is well-known that methoxyethyl mercury is less stable than methyl mercury. If it is presumed that methyl mercury exists to a large degree as such in fresh water but not in brackish water, but that methoxyethyl mercury is largely changed to the same chemical form in fresh water and brackish water, the differences would be explained.

The relations between methoxyethyl mercury and methyl mercury when accumulated in cod from the water are about the same in salt water and brackish water, which shows that there is no difference in the relative avail-
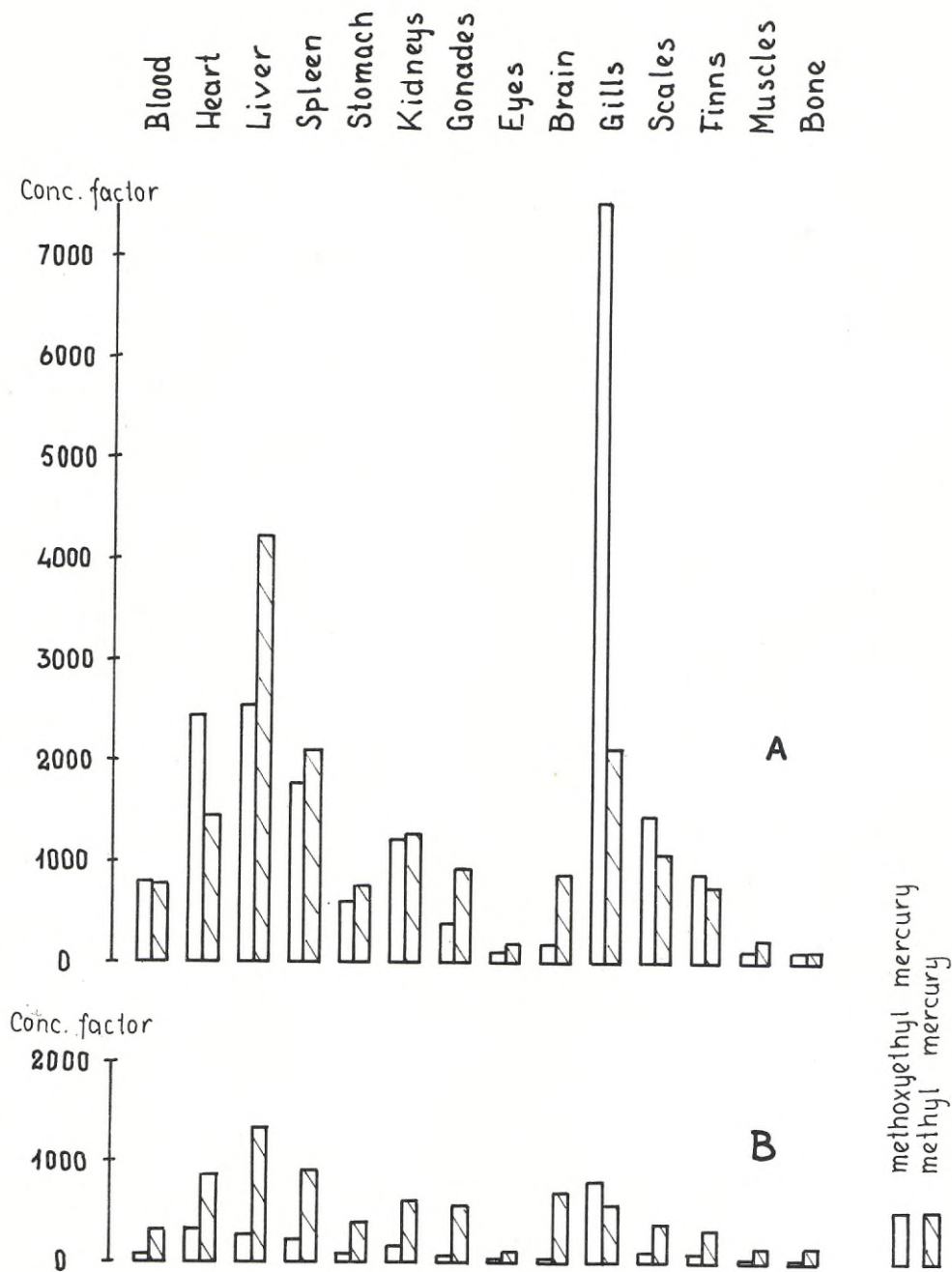
Fig. 16. Tank experiments with methoxyethyl mercury and methyl mercury. Uptake direct from the water in cod. A) Salt water B) Brackish water.
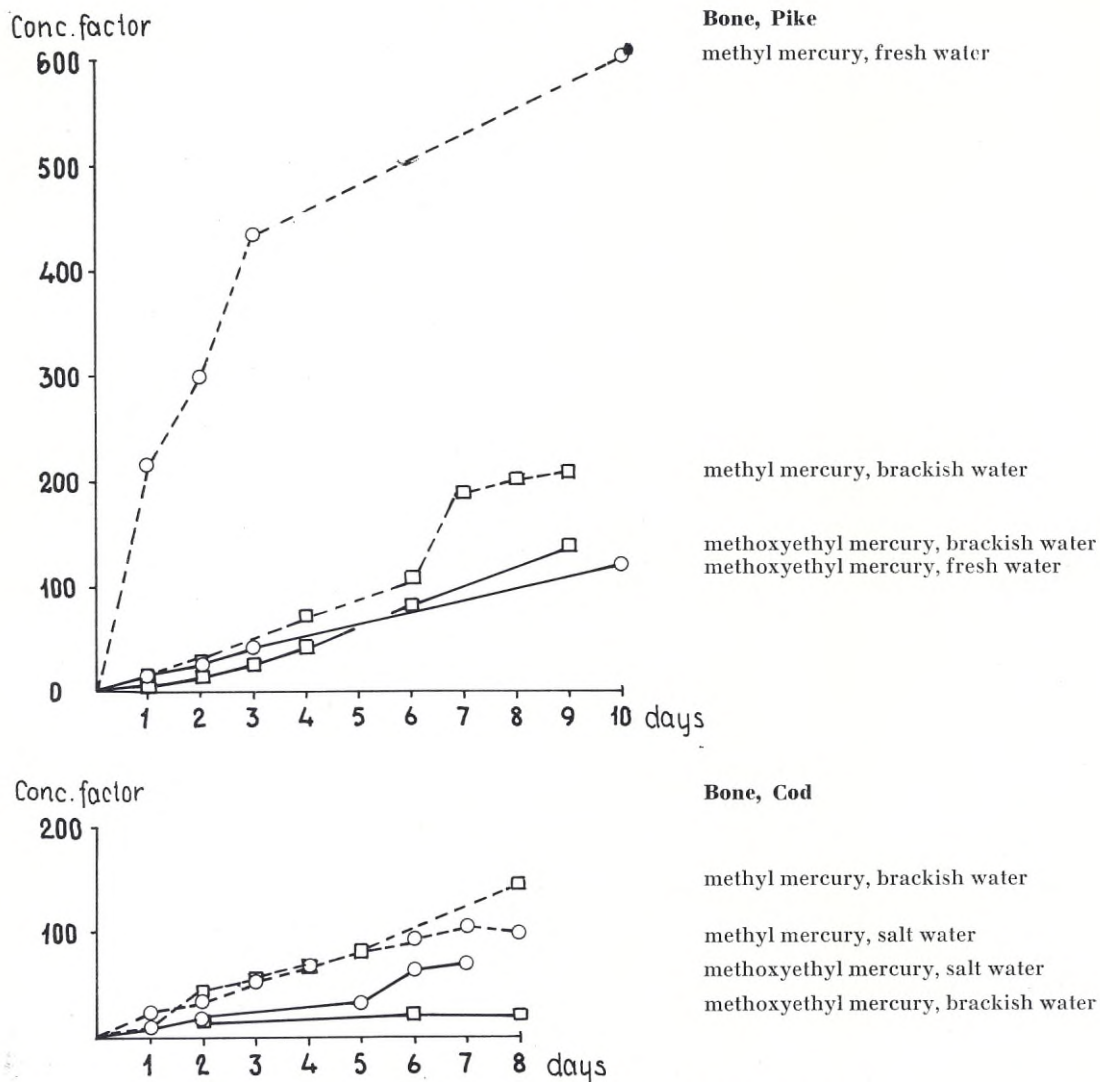
Fig. 17. Concentration factors in tank experiments.

ability of the two compounds. The reason for a less uptake in brackish water is thus not likely to be the result of a change in the chemical form.

The differences in accumulation in brackish and saline water may be connected with differences in the osmoregulative functions in the fish. In saline water (33—34 per mille salinity) the fish live in a hypertonic environment, whereas the fish in the Baltic (5—7 per mille salinity) live in an environment that is nearly isotonic. It must be supposed that the uptake and secretion of water in cod is very different in the two environments, and as a consequence

Conc. factor

Muscles, Pike

methyl mercury, fresh water

methyl mercury, brackish water

methoxyethyl mercury, brackish water
methoxyethyl mercury, fresh water

Conc. factor

Muscles, Cod

methyl mercury, salt water
methyl mercury, brackish water
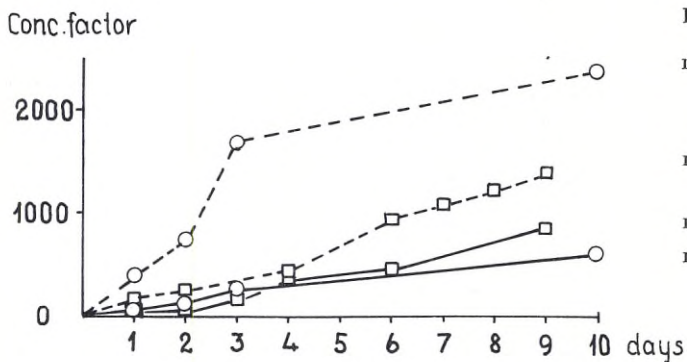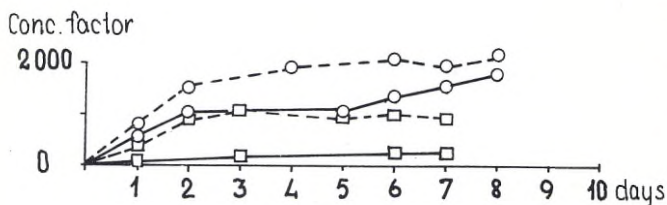methoxyethyl mercury, salt water
methoxyethyl mercury, brackish water
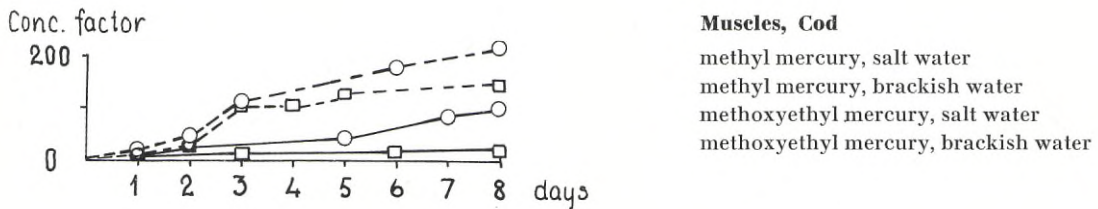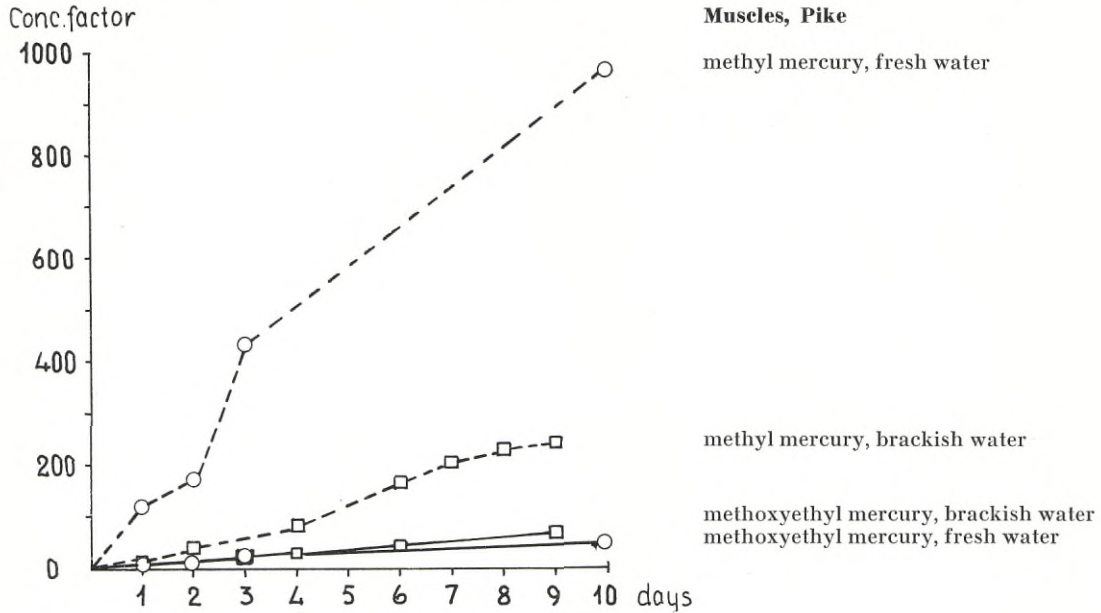
Fig. 17. Concentration factors in tank experiments.

of this also the uptake and secretion of dissolved salts. A greater tendency
to drink water in a saline environment than in a brackish would probably
result in a larger uptake, as a larger surface area is exposed to the water.

The uptake of mercury from the food compared with that
from the water

In the pond experiments, the fish accumulated mercury both from the
water and from the food.

A series of experiments has been carried out to elucidate the relative role
of these two routes of accumulation for various organic and inorganic mer-
cury compounds.

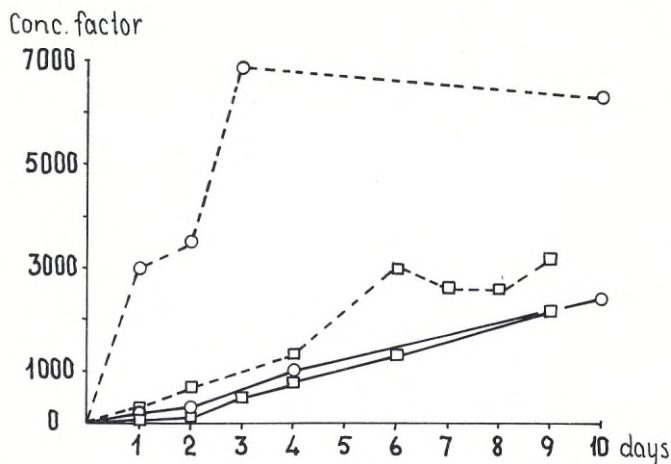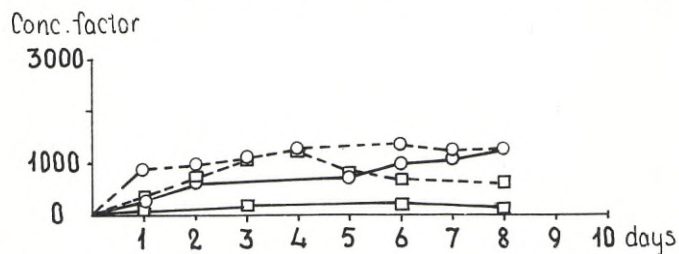All the feeding experiments carried out had in common that the food

Fig. 18. Concentration factors in tank experiments.

Fig. 19. Concentration factors in tank experiments.

Table 11. Accumulation of mercury in cod when given as methoxyethyl-mercuric hydroxide in the food and in the water.

	Uptake after 2 days			
	from the water (0.06 ng/g)		from the food (3.900 ng/g)	
	ng/g	concentration factor	ng/g	concentration factor
Blood	237	395	108	180
Liver	324	540	134	223
Spleen	635	1,058	131	218
Kidneys	385	641	98	163
Brain	21	35	9	15
Muscles	14	23	9	15
Bone	16	27	8	13
Mean		388		118

organisms had been cultured in water with the same mercury concentrations as the water of the experiments in which the direct uptake was studied. The food organisms were given in excess to fish which had been starved for some time. The concentration factors were calculated in relation to the concentration of the water in which the food organisms had been cultured. These concentration factors have been compared with the concentration factors calculated for fish which had accumulated mercury directly from the water during the same period of time.

When methoxyethyl mercury incorporated in mussel (*Mytilus edulis*) meat was given to cod, the resulting mean concentration factor for seven organs was about one third of that resulting from a direct uptake from the water during the same time of exposure (Tab. 12).

Table 12. Accumulation of mercury in cod when given as methylmercuric hydroxide in the food and in the water.

	Uptake after 2 days			
	from the water (1.1 ng/g)		from the food (5.250 ng/g)	
	ng/g	concentration factor	ng/g	concentration factor (in relation to water)
Blood	758	690	1,221	1,110
Liver	1,141	1,037	2,857	2,597
Spleen	1,415	1,286	2,471	2,246
Kidneys	1,051	955	1,575	1,432
Brain	211	192	232	211
Muscles	55	50	105	95
Bone	37	34	65	59
Mean		606		1,107

Table 13. Accumulation of mercury in pike when given as methylmercuric hydroxide in the food and in the water.

	Concentrations after 3 days	
	Accumulated from the water conc. factor	Accumulated from the food [1] concentration factor (in relation to water)
Liver	1,519	688
Spleen	1,341	573
Kidneys	1,057	451
Brain	416	221
Muscles	90	190
Bone	74	83
Mean	750	367

[1] The fishes had been refrigated for about one month before the analyses.

When the same type of experiment was carried out with methyl mercury it was found that the mean concentration factor in the feeding experiment was almost twice that of the "direct uptake" experiment (Tab. 12).

In one of the experiments, fry of perch and roach had been allowed to accumulate methyl mercury from the water for three days. They were then given to pike during a three day period. It was found that the mean concentration factor for 6 organs (Tab. 13) was about half of that obtained in an parallel experiment in which the fish had accumulated the mercury directly from the water. The corresponding figure for methoxyethyl mercury was about 40 per cent (Tab. 14).

A similar experiment was carried out with mercuric chloride in fresh water, using pike as the test fish. (Tab. 15).

Table 14. Accumulation of mercury in pike when given as methoxylethyl-mercuric hydroxide in the food and in the water.

	Concentrations after 3 days			
	Accumulated from the water		Accumulated from the food [1]	
	ng/g	concentration factor	ng/g	concentration factor
Liver	304	217	92	66
Spleen	677	484	240	171
Kidneys	299	214	145	104
Brain	205	146	78	56
Muscles	21	15	5	4
Bone	32	23	32	23
Mean		183		70

[1] The fishes had been refrigated for about one month before the analyses.

Table 15. Accumulation of mercury in pike when given as mercuric chloride in the food and in the water.

| | Concentrations after 8 days (uptake from the water) and 13 days (uptake from the food) | | | |
| | Uptake from the water (0.30 ng/g) | | Uptake from the food (231 ng/g) | |
	ng/g	concentration factor	ng/g	concentration factor
Blood	176	587	4	13
Heart	258	860	4	13
Liver	377	1,258	39	130
Spleen	608	2,027	12	40
Gut	199	663	137	457
Kidneys	496	1,653	42	140
Gonades	107	357	7	23
Eyes	36	120	1	3
Brain	284	947	3	10
Gills	878	2,928	5	17
Scales	214	713	2	7
Fins	406	1,353	3	10
Muscles	26	87	1	3
Bone	56	187	1	3
Mean		981		62

In this experiment, the uptake by way of the food was less than a tenth of that directly from the water. The only concentration factor for a single organ that approaches that of the direct uptake experiment is the factor for stomach tissue, which indicates that the pike actually had preyed upon the fodder fish. Also in this experiment there was food in excess. Finally, two experiments were carried out in which mercuric nitrate was given to cod in water and by the food (meat of mussels) (Tab. 16). It is seen from the table that the differences in concentration factors are not nearly as large as those from the experiments with mercuric chloride and pike. In contrast to what was found in the last-mentioned experiment the concentration factors for muscles and bone were even higher when the mercury was given in the food. This is supposed to be due to a lower availability of the mercury for the direct uptake from the water, which in turn should be the result of the fact that the mercury was largely in particulate form. It is obvious from the experiments that all the mercury compounds studied can be taken up both directly from the water, and from the food. The relative ability to be accumulated, however, differs between different compounds. The experimental conditions are naturally artificial and the experimental results cannot be used to make any conclusions as to the relative role of the uptake from the food and from the water in nature.

The cod, for instance, were given a food that is not commonly eaten by them in their natural environment. Cod in shallow water near the shore

Table 16. Accumulation of mercury in cod when given as mercuric nitrate in the food and in the water.

	Concentrations after two days			
	Uptake from the water (0.06 ng/g)		Uptake from the food (223 ng/g)	
	ng/g	concentration factor	ng/g	concentration factor
Blood	0.29	4.8	0.05	0.8
Heart	0.58	9.7	0.15	2.5
Liver	0.08	1.3	0.06	1.0
Spleen	0.35	5.8	0.30	5.0
Kidneys	0.21	3.5	0.76	12.7
Gut	0.20	3.3	29.02	483.5
Brain	0.15	2.5	0.04	0.7
Eyes	0.05	0.8	0.07	1.2
Gills	47.8	796.6	0.92	15.3
Fins	1.46	24.3	0.32	5.3
Scales	2.99	49.8	—	—
Muscles	0.03	0.5	0.05	0.8
Bone	0.07	1.2	0.19	3.2

have been found to live mostly on crustaceans or fish. Neither were the experiments of a sufficient duration to reach an equilibrium in the exchange process, nor in the feeding experiments or in the experiments where the mercury was given in the water. The results of the experiments may lead to an overestimation rather than an underestimation of the role of the accumulation from the food. Fish do not feed with the same intensity all the year around. For long periods (during the winter and the spring) they grow slowly and feed relatively little, while the direct water and salt exchange through the epithelia goes on continuously, even if it is hampered by low temperature.

It is possible, however, to draw conclusions from the experiments concerning differences between different compounds when they are tested simultaneously under identical test conditions.

Methyl mercury is thus more readily accumulated from the food than methoxyethyl mercury. The difference between these two compounds was much greater in the experiments with cod and mussels than with pike and fish fry. The reason for this is not known.

In fresh water fish, the uptake of inorganic mercury from the food seems to be negligible.

The elimination of mercury from fish

In experiment No. 5, pike-perch which had accumulated mercury given as phenylmercuric acetate were used for elimination studies. Samples consisting of about 20 fish each were analysed after two days, after 34 days, after 42 days and after 48 days in clean water (Figs. 20 and 21).
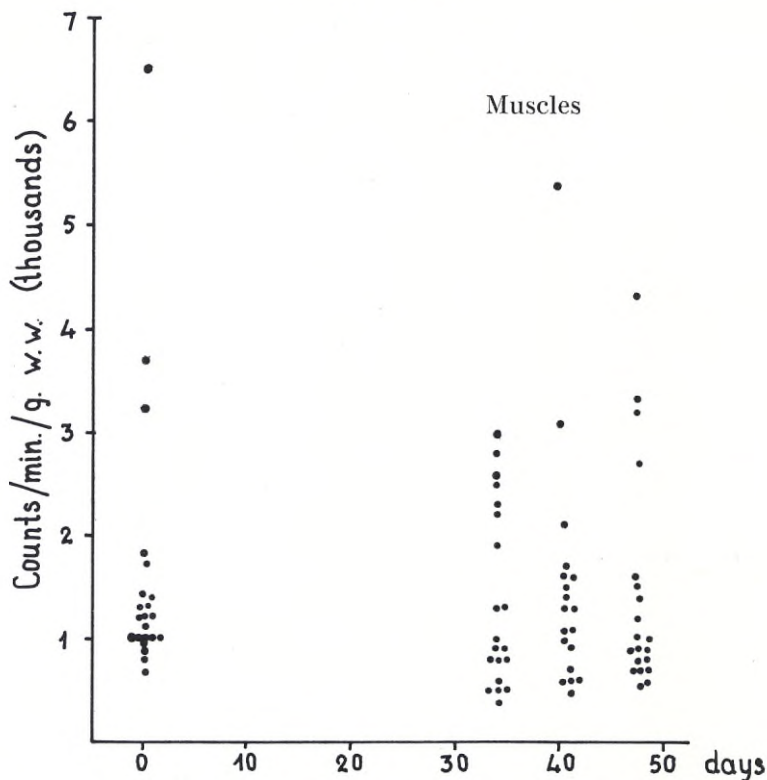
Fig. 20. Individual concentration values in pike-perch at different times after the discontinuation of the mercury supply.

The figures show a slow elimination. If it is assumed that the elimination follows an exponential curve it can be calculated that the biological half-life of mercury in muscles of pike is in the order of 65—70 days. As a consequence of the considerable individual variation, however, it is impossible to calculate a reliable figure for the elimination rate. For liver and spleen, the elimination rate is appreciably higher than for muscles. The biological half-life seems to be in the order of 35—40 days. There were indications of a slight increase in the concentrations of the bone during the experiment. Such an increase could be interpreted as the result of a redistribution of the mercury within the fish.

The differences in elimination rate between different organs find expression in the quotients $\frac{\text{conc. in muscles}}{\text{conc. in bone}}$ and $\frac{\text{conc. in muscles}}{\text{conc. in liver and spleen}}$. The former decreased from 1.92 to 1.16 and the latter increased from 0.105 to 0.173.

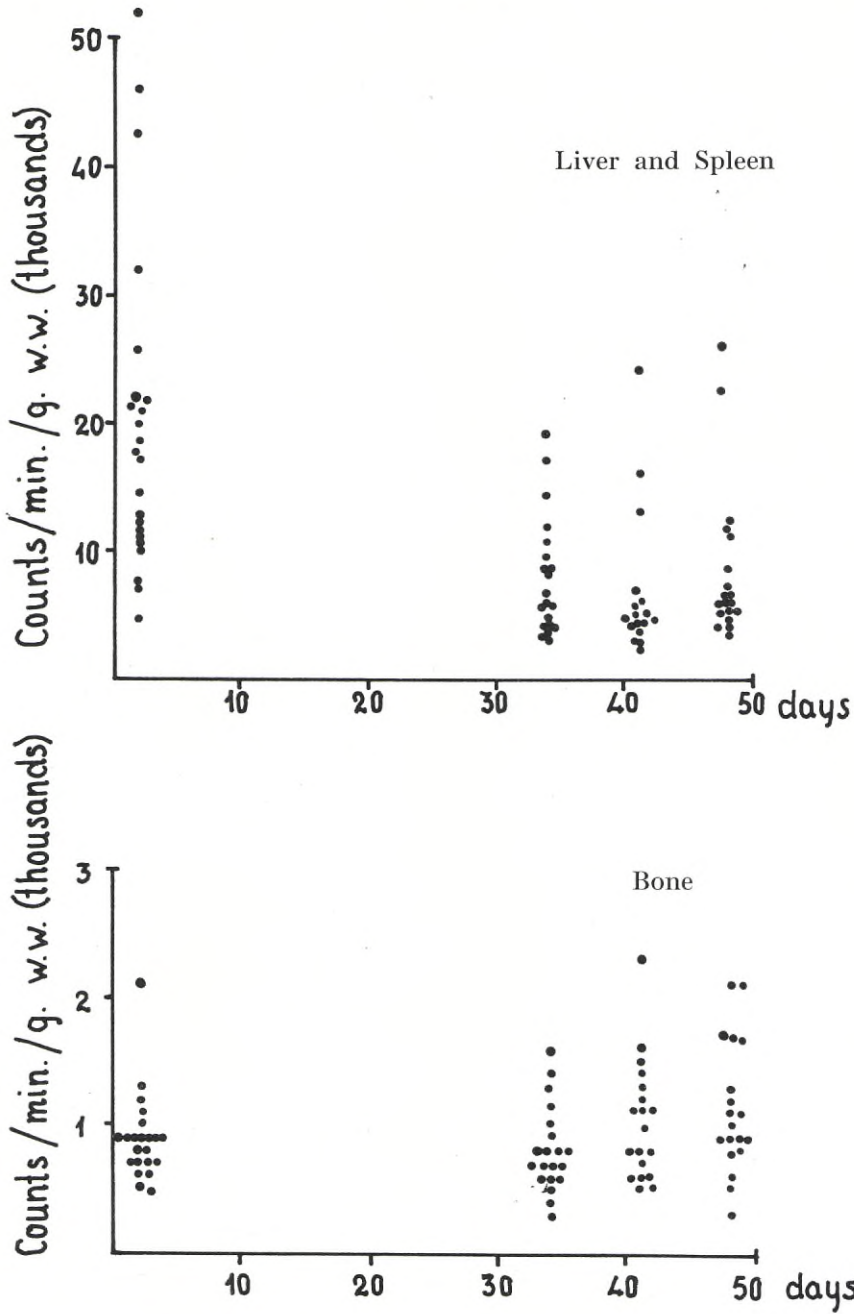Five pike from experiment No. 4 which had accumulated mercury given

Fig. 21. Individual concentration values in pike-perch at different times after the discontinuation of the mercury supply.

Table 17. Percentage elimination of mercury in pike from experiment No. 4
after 27 days in lake water.

Date No of fish Mean length	5 Oct. 10 22.1 cm	1 Nov. 5 21.7 cm	Percentage elimination
Blood	10	7	30
Heart	31	24	23
Liver	109	95	13
Spleen	77	59	23
Stomach	60	39	35
Kidneys	103	115	—
Gonads	15	16	—
Eyes	7	7	0
Brain	32	28	13
Gills	32	31	3
Scales	12	10	17
Fins	16	13	19
Muscles	23	19	17
Bone	10	10	0

as mercuric chloride were carried over to net cages in Lake Mälaren at the
end of the pond experiment. They were left for 27 days in the cages, after
which they were killed and analysed. Ten fish had been analysed in the
same way at the beginning of the elimination experiment. The concentrations
are compared in Table 17.

The number of fish analysed on 1 Nov. is too small to allow any reliable
conclusions as to the elimination rates. It is obvious, however, from the table
that the largest elimination had taken place from the stomach wall, the
blood, heart and spleen. The elimination seems to have been quite small in
bone, gills and eyes. The mercury accumulated in these organs thus seems
to be very little exchangeable.

On the whole, it can be said from the elimination experiments that the
elimination rate is low in relation to the accumulation rate. Such a relation
between accumulation and elimination rates results in high concentration
factors.

The chemical form of the mercury

In the experiments, the mercury has been given as methyl mercuric
hydroxide, phenylmercuric acetate, methoxyethylmercuric hydroxide, mer-
curic chloride or mercuric nitrate. It has not, however, been possible to
analyse the mercury in the water, in the sediments or in the organisms.

The chemical stability in earth of some of the compounds used has been
studied by BOOER (1944). With the aid of plant toxicological methods BOOER
has demonstrated strong indications for a decomposition in the earth of
mercuric chloride into a metallic form bound to the clay mineral.

He has also been able to show that there are profound differences in chemical stability between methoxyethyl mercury on one hand and ethyl mercury and phenyl mercury on the other, the latter being much more chemically stable.

The methoxyethyl mercury is easily decomposed in soil. BOOER, however, found also that ethyl mercury, after a sufficient period of time in the soil, decomposes and that the mercury is finally bound to the soil in metallic form. Booer's results indicate also that phenyl mercury behaves in a similar way when in contact with earth.

WESTÖÖ (1967) and NORÉN and WESTÖÖ (1967) have reported high concentrations of methyl mercury in fish where no methylmercury in the water could be expected but where industrial wastes containing phenyl mercury were known to have been released.

This speaks in favour of a theory that a change of the chemical form of phenyl mercury to methyl mercury can take place in the water.

Such a change has been verified in direct experiments by JENSEN and JERNELÖV (1967). In their experiments, mercuric chloride was mixed with bottom sediments. After a short period of time, the samples were analysed with the aid of the gas chromatographic method and the presence of methyl mercury could be established. Sterilized samples could not produce methyl mercury, which proves that the change of chemical form is connected with microbiological activities.

It would be rather surprising if changes of this kind had not taken place in the pond experiments, where the mercury compounds were introduced into biotop models with bottom mud, plants, organisms and untreated water from Lake Mälaren. There is also much that speaks for such changes having taken place, e.g. the similarlity in the distribution between different biotopic components and between the organs of the fish from different experiments. The rapid uptake of mercury in plants in the pond experiment with mercuric chloride at the refilling of the pond after a partial drainage during several weeks can also be explained by a change of the chemical form of the mercury that had been concentrated in the sediments, and which was suddenly made available at the refilling of the pond. The bottoms had been partly uncovered for a considerable time and exposed to a much higher temperature than when the pond was filled with water. The environmental conditions had thus been drastically changed for the microbiota, and this is believed to have furthered their biochemical activities.

In those experiments where the fishes were given the different mercury compounds in clean tanks, greater differences in the uptake and distribution pictures between different mercury compounds were found than in the pond experiments, indicating differences in availability for uptake. In these experiments, it may be supposed that the mercury compounds largely accumulated as such, without any change in their chemical form.

Certain differences in the availability for uptake in fish from the water of different salinities indicate that the electrolytes of the water can have an effect on the chemical form of the mercury. The uptake in pike of methoxy-ethyl mercury was not affected by the salinity, whereas the uptake of methyle mercury was retarded in brackish water. This has been interpreted as an effect of a chemical change of methyl mercury in brackish water.

There are indications that much of the mercury, no matter what its chemical form at introduction, becomes insoluble and forms particles in saline water.

The tank experiments, however, show that mercury can be accumulated from the water in all of the compounds studied. In the pond experiments, the mercury was presumably available for uptake in the biota as a mixture of compounds, no matter what the chemical form of the mercury introduced.

Summary

The accumulation of methylmercuric hydroxide, phenylmercuric acetate, methoxyethylmercuric hydroxide, mercuric chloride and mercuric nitrate in water organisms has been studied with the aid of labelled compounds in pond, tank and aquaria experiments.

None of the compounds is taken up to any appreciable degree in the tissues of water plants. A considerable surface adsorption, however, can cause high concentrations in submersed plants.

No general connection between the concentrations of the animals and their trophic level was found. The concentration in an organism seems to be the result of several factors, as for instance its metabolic rate and feeding habits.

The concentration factors of the invertebrates in the different pond experiments varied, being highest in the experiment with methyl mercury and lowest in the experiment with mercuric chloride.

The sediment had always high concentrations of mercury, showing a tendency to adsorption on and sedimentation with particles in the pond water.

The exchange of mercury between the plants and the water was found to be rapid in the two pond experiments where this phenomenon was studied. The exchange was less rapid in invertebrates. In the sediments, a considerable portion of the mercury seemed to be little exchangeable.

All of the mercury compounds are taken up in fish both directly from the water, and from the food. The accumulation rate is fast while the elimination rate is slow, which leads to high concentration factors.

The highest concentrations are usually found in the kidneys and the liver, medium-high concentrations in the heart muscles, the spleen, the gills and the brain, and low concentrations in muscles and bone. The uptake rate is

different in different organs, being most rapid in the blood and least rapid in the bone.

Of the compounds studied, methyl mercury is the most readily taken up. The concentration factor for methyl mercury in fresh water and muscles of pike is in the order of 2,000. The corresponding figure for kidneys is 9,000.

There is a considerable variation in the rate of uptake in different individuals of one and the same species of fish.

The size of the fish has been found to be of importance for the uptake rate.

The concentration of electrolytes of the water excerts an influence on the accumulation. The uptake of methoxyethyl mercury, for instance, is lower in brackish water than in salt water.

Differences in the osmoregulatoric functions are believed to be responsible for these differences. The ability of fish to concentrate it from the water has been studied. Differences were found in this respect between different mercury compounds.

The most important route of accumulation seems to be directly from the water through the outer epithelia.

The elimination rate of mercury in fish has been studied in experiments where the mercury has been given as phenyl mercury and inorganic mercury.

Much speaks in favour of a theory that organic mercury compounds are easily changed as to their chemical nature in natural waters.

In the pond experiments, the mercury was probably available for uptake in the organisms as a mixture of different compounds, no matter what the chemical form of the mercury introduced in the experiment.

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Growth Rates of the Char *Salvelinus alpinus* (L.) in the Vardnes River, Troms, Northern Norway [1]

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Abstract

The instantaneous rates of growth in weight and length of the char *Salvelinus alpinus*
in the Vardnes River, Northern Norway were estimated from data on weight and length
taken on multiple recaptures of tagged fish.

Introduction

The char, *Salvelinus alpinus,* in the Vardnes River migrate to sea in spring,
where they remain to feed during summer. They return to the river in early
fall to spawn and winter in a small lake of the watershed. Weight increases
with age throughout the lifespan of the fish, though changes in growth rate
occur within the year due to spawning and change in residence from fresh-
water to salt water. Summer growth is usually rapid and sufficient to offset
any weight loss from spawning and freshwater residence. Thus the smooth,
monotonic growth-in-weight functions commonly used in yield calculations
will not always hold for this stock of fish. A more adequate description of
the weight changes occurring in the two above-mentioned periods every
year in the life of this char seems warranted, therefore, to supplement a
recent description of the life history of the char by NORDENG (1961).

Material and procedure

The Vardnes River is located on the island of Senja at approximately
69°N and 16°E (Fig. 1). It is about 3 kilometres long and drains Vardnes
Lake. This lake has a surface area of about 30 ha and an average depth of
between 2 and 3 metres.

Angling is permitted in the lake, but the river is closed to fishing. The
catch is largely taken in the sea with commercial gear during the feeding
period of the char.

From 1956 through 1963 one trap was operated for downstream migrants

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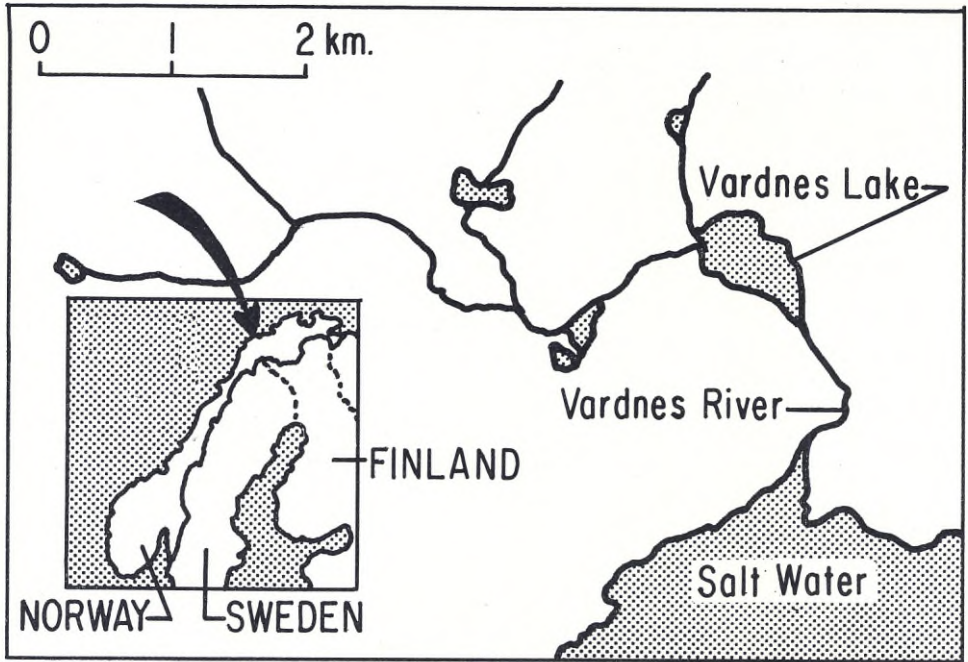[1] Contribution No. 246, College of Fisheries, University of Washington.

Fig. 1. Map of the Vardnes River.

and another trap for upstream migrants. Both traps were fished from April 1, before the beginning of the spring migration, until September 15, after completion of the fall migration. The traps were emptied daily. All untagged fish, descending or ascending, were tagged with a numbered Carlin tag (CARLIN, 1955); and recaptures of previously tagged fish were always recorded. Total live length was measured to the nearest centimeter and live weight to the nearest 10 g. No scale samples were collected for age determination, and sex could only be determined when secondary sex characters had developed. The growth rate is determined, therefore, for males and females combined.

The fishing power of the traps depended heavily on the water level of the river, and in the spring, also on the flow of ice. Consequently, the catches (listed in Table 1) were not in proportion to the total run. However, a sufficiently large number of tagged char were recaptured on subsequent occasions (Table 2) to enable the assessment, from observations of length and weight, of the instantaneous rate of growth in summer and in winter.

All length and weight data for individual fish at the time of tagging and on subsequent recapture dates were transferred to punch cards. Population size, mortality rates and other parameters are not discussed here. This study is concerned only with changes in weight and length observed in recaptured fish.

Table 1. Trap catches of char in the Vardnes River, 1956—1963.

Year	Downstream migrants	Upstream migrants
1956	19	86
1957	35	11
1958	279	110
1959	318	282
1960	629	272
1961	496	270
1962	544	262
1963	68	79
	2,388	1,372
Grand total		3,760

Duration of the feeding season in the sea and the wintering period in freshwater

Seaward migration is initiated, as in many salmonoid fishes, by the break-up of lake ice and rapidly rising temperatures. When the cumulative daily trap catches in a season were plotted as a function of time, the resultant curves were similar to logistic curves. A comparison between timing of seaward migration, duration of sea residence and timing of spawning migration in fall, can be made by fitting curves of the form

$$y = \frac{1}{1 + e^{-(a+bt)}}$$

to the cumulative daily trap catches by means of a computer program such as FRG 709 (Gales, 1964), which through a series of iterations converges to the best estimates of the parameters a and b. The given equation was brought into linear form through a log transformation

$$\ln\frac{1-y}{y} = -(a+bt).$$

Initial trial values of the two parameters a and b were obtained from intercept and slope of a straight line fitted to the cumulative daily trap catches plotted according to time on logarithmic paper.

The time periods needed to complete 10 %, 50 % and 90 % of migration,

Table 2. Summary of tagging and recapture data.

	Male	Female	Sex not determined
Tagged	131	296	1,657
Recaptured (one or several times)	233	594	849

Table 3. Calculated timespans of passage 10, 50 and 90 per cent of upstream and downstream migrations of char in the Vardnes River, 1957—1963.

	Percentage of migration	1957	1958	1959	1960	1961	1962	1963
Downstream migration ..	10 %	May 8	May 14	April 26	May 17	May 29	June 2	May 17
	50 %	May 29	June 14	May 14	June 2	June 8	June 11	June 2
	90 %	June 11	June 26	June 5	June 8	June 17	June 20	June 17
Upstream migration ..	10 %		July 5	July 5	June 29	July 8	July 11	June 17
	50 %		July 14	July 14	July 11	July 17	July 23	July 17
	90 %		July 23	July 23	July 20	July 26	Aug. 5	Aug. 14

upstream and downstream, are listed in Table 3. The predicted proportions from the logistic time entry curve were computed by a program prepared for this purpose by DAHLBERG (1966). The months were made equal to 30 days. The time period needed to complete from 10 to 50 per cent of the total seaward migration varied from 9 to 30 days, and the time span needed to complete from 10 to 90 per cent ranged from 18 to 42 days. For the upstream migration the corresponding figures were 9—30 days and 18—27 days, respectively. The yearly variations reflect changes caused mainly by varying temperature and water level associated with varying catchability of the traps. Since these sources were confounded, a better alternative appeared to be to combine all years and compute one common curve for downstream migrants and another for upstream migrants. Since there are always a few early and a few late migrants the distributions were censored by eliminating approximately the upper and lower 10 per cent. The migration curves estimated in this manner and plotted on probability paper approximated straight lines, as would be expected when the daily migration is normally distributed (Fig. 2). From June 4 to July 15 or a time period of 41 days, 50 per cent of all descending and ascending fish passed. Therefore, the feeding season in the sea was set equal to 40 days and the stay in freshwater to 320 days.

Growth in weight

A total of 706 char, tagged either for the first time in the spring on seaward migration or recaptured from previous taggings, were recaptured on their next fall ascent. Data on length and weight in the spring and in the fall for the same fish provided the basis for estimating the instantaneous rate of growth. During the summer, growth was assumed to be exponential (Ricker, 1958). Hence for each fish,
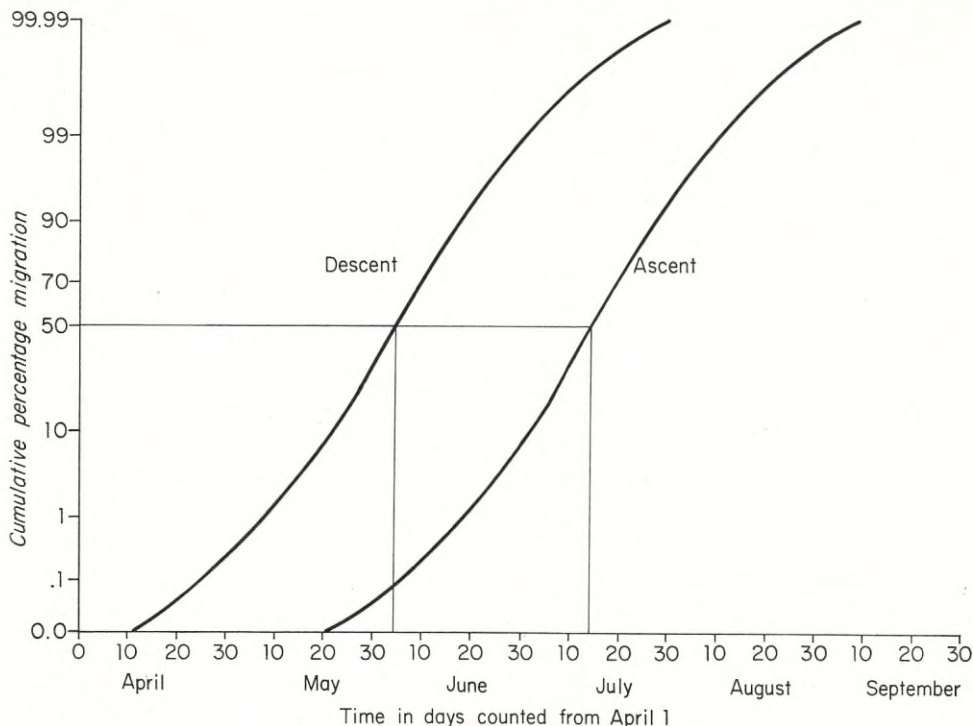
Fig. 2. Average cumulative migration curves of descending and ascending char in the Vardnes River for all years (1957—1963) combined.

$$W_{t_{i+1}} = W_{t_i} e^{g(t_{i+1} - t_i)},$$

$$\text{or } g = \frac{\ln(W_{t_{i+1}} - W_{t_i})}{t_{i+1} - t_i},$$

where W_{t_i} = observed weight in the spring,

$W_{t_{i+1}}$ = observed weight in the fall,

$t_{i+1} - t_i$ = duration of feeding season in the sea measured in days and

g = instantaneous rate of increase in weight.

The value of g for each fish in every year for the period 1958—1963 was calculated by means of a special computer program.

The same method was used to measure rate of increase or, more commonly, decrease in weight during residence in freshwater from fall to spring. Data on 568 fish from the year 1959—1963 were used. A mean was calculated for each year and for all years combined for both the instantaneous growth rate in the sea and in freshwater. The results are summarized in Table 4.

Table 4. Average instantaneous rates of growth in weight of char per day, during marine and freshwater residence.

Year	Marine residence			Freshwater residence		
	Number of fish observed	g_s	Days	Number of fish observed	g_f	Days
1958	61	.017137	37.0	—	—	—
1959	99	.012300	59.8	70	—.001129	292.5
1960	232	.020481	44.2	179	—.000402	313.2
1961	167	.012551	36.4	198	—.000278	321.5
1962	147	.012312	45.5	121	—.000132	319.6
All years combined	706	.015467	44.2	568	—.000391	315.0

There are significant year-to-year variations in growth rate and duration of stay in the two habitats. The cause can most likely be traced back to changes in the environment, but no attempt was made to introduce climatic factors as covariates since the object was to give a description of the average growth pattern of char at this locality.

A loss of weight was observed in every year, and the oscillating growth pattern is depicted in Fig. 3; average growth rates in all years for the summer and winter season were applied over 40 and 320 days, respectively.

The average weight of downstream migrants in all years was 195.7 g and that of upstream migrants 374.3 g. Based on an initial weight in the spring of 195.7 g, the growth in weight was calculated after the first summer in the sea, as well as the estimated loss in weight during the following winter, for four succeeding years as follows:

$$w = 195.7 \, e^{.01547(40i) - .00039(320j)}$$

where the values of (i,j) range from (1,0), (1,1) to (4,4), (5,4).

Growth in length

Basically the same procedure was followed to calculate growth in length, and the results are shown in Table 5.

The growth in length did not match the rapid increase in weight during the feeding period in the sea. During lake residence in winter no length increase or only a slight one was noted in mature char. Small immature fish, requiring less food than mature fish, manifested growth in length and weight even in the winter time. The material for this study involves primarily mature fish.

Using the average rates of growth in length for a period of 40 days during sea residence and 320 days for freshwater residence, the growth pattern was obtained from the data in Table 5 in the same manner as was done for weight changes with time. This curve is illustrated in Fig. 3, based on an initial length of 27.5 cm.
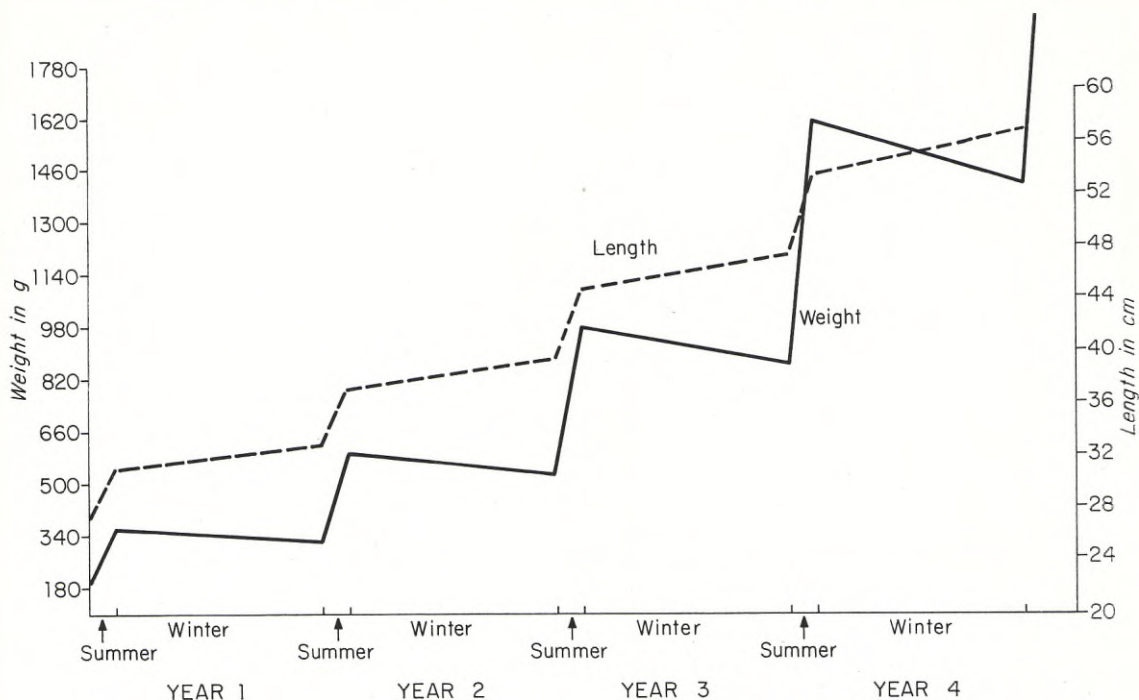
Fig. 3. Calculated growth in weight and length of char in Vardnes River.

Growth rates calculated over variable time periods

A number of fish escaped recapture for one, two or more times in succession on their migration upstream or downstream. Their growth rates were calculated from increases in weight and length for the entire time period. These parameter estimates were used to verify the estimates obtained for a single season either in the sea or in freshwater.

Table 5. Average instantaneous rates of growth in length of char per day during marine and freshwater residence.

Year	Marine residence			Freshwater residence		
	Number of fish observed	l_s	Days	Number of fish observed	l_f	Days
1958	60	.003433	37.0	—	—	—
1959	98	.002459	59.8	70	.000100	292.5
1960	234	.003231	44.2	180	.000211	313.2
1961	167	.003275	36.4	199	.000231	321.5
1962	155	.003006	45.5	122	.000107	319.6
All years combined	714	.003105	44.2	571	.000182	315.0

Table 6. Average instantaneous rate of growth in weight and in length per day.

Year	Number observed	g_w	Days	Number observed	g_l
Period: One summer plus one winter					
1957—58	5	.002716	360.8	6	.000458
1959	51	.001172	333.8	51	.000517
1960	56	.001209	372.1	56	.000420
1961	23	.001978	366.7	23	.000627
1962	42	.000433	351.9	42	.000277
All years combined	177	.001156	355.3	178	.000442
Period: One winter plus one summer					
1958—63	78	.001346	352.2	80	.000363
All data combined	255	.001214	354.3	258	.000418

For those fish where the time period between successive measurements was about one year, a distinction must be made between fish captured in the spring and recaptured the following spring and those captured in the fall and recaptured the next fall. In the latter case the average weight would be substantially higher because of the final summer's growth. The results are given in Table 6. No great differences were noted regardless of whether the year was counted from the beginning of the summer feeding season or from the beginning of the freshwater residence during the winter.

Finally, for a much smaller number of char, data on growth were available for time periods longer than one year. This could be either two summers plus one winter or two winters and one summer, or other combinations. The results are given in Table 7.

Discussion

The validity of the estimated growth rates can be compared against each other. First, the instantaneous growth rate in weight calculated over an entire year should equal the sum of the estimated growth rate for one summer, g_s, plus that of one winter, g_f, or

Table 7. Total instantaneous growth rate for variable time periods.

No. days	Estimated Period	g_w	g_l	Av. No. days	Observed g_w	g_l	No. observed
360	1 year	.001371	.000507	354.3	.001214	.000418	255
400	1 year+1 summer	.002781	.000852	393.9	.002364	.000658	41
680	1 year+1 winter	.000542	.000354	667.2	.000166	.000335	16
720	2 years	.001371	.000507	703.3	.000647	.000375	10
760	2 years+1 summer	.002113	.000644	743.8	.001232	.000472	5

Table 8. Comparison of observed and calculated growth rates for a char tagged on the spring descent, 1958.

Year	Migration	Weight		Length	
		Observed	Calculated	Observed	Calculated
1958	Downstream	200	—	27.0	—
1958	Upstream	375	371.3	34.0	30.6
1959	Downstrem	340	327.7	34.0	32.4
1959	Upstream	530	608.4	39.0	36.7
1960	Downstream	450	537.0	40.0	38.9
1960	Upstream	950	997.0	44.0	44.1
1961	Downstream	700	880.0	46.0	46.7
1961	Upstream	1,000	1,633.9	51.0	52.9
	Final capture in set net, July 3 [1]				
1962		1,600	2,294.0	51.0	63.4

[1] Final estimate on basis of 30 days spent in sea.

$$g_w = \frac{g_s \cdot 40 + g_f \cdot 320}{360}$$

The growth rate in length could be similarly checked. All other possible comparisons are assembled in Table 7.

The agreement between observed and calculated growth rates, both for weight and length, is quite satisfactory for the time period of one year. Beyond this time span discrepancies between observed and calculated values become more pronounced; the observed growth rate values were generally lower than the calculated ones.

Aside from normal random variability, there is another real source for the discrepancy. The average growth rate in one summer or in one winter was estimated as the arithmetic mean of all observations. Among the fish studied the younger ones predominated and influenced the mean value. Since, generally, growth rate decreases with increasing ages, the results follow a trend (apparent in Table 7) which could have been anticipated.

This observation can be further demonstrated by a comparison between observed weights and lengths for one individual char tagged on the spring migration in 1958 and recaptured every succeeding fall and spring until the fall ascent in 1961 (Table 8). Differences between observed and calculated lengths are small enough to be accounted for by chance variation for three years. After that time the calculated weight is overestimated. The discrepancy is further borne out by the fact that at the final capture of this fish in a set net in July in the fourth year, no length increase was noted and the final weight was 1,600 g.

The estimated parameters for the instantaneous rates of growth in weight and length during the summer season and winter season are therefore only applicable for the mature fish during their most active growing season; other

values probably would be found if age analysis and separation were performed according to sex. Nevertheless, the data indicate a variable growth rate of char in summer and winter, which is probably common to all diadromous fish which spawn repeatedly.

Results

1. The average feeding season in the sea of the char *Salvelinus alpinus* in the Vardnes River was estimated to be 40 days; and the lake residence, 320 days.

2. The average instantaneous rate of growth in weight per day in the summer was estimated to be $g_w = .01547$ and the average instantaneous weight loss per day in the winter, to correspond to $g_w = -.00039$.

3. The instantaneous rates of growth in length per day in the summer and winter were estimated to be $g_l = .00311$ and $g_l = .00018$, respectively.

4. These parameters give results biased upwardly when applied for two or more years.

Acknowledgments

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Seatrout (Salmo trutta, L.) of the River Istra, Western Norway

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Contents

Introduction

The River Istra has its outlet in the River Rauma in Romsdal, Western Norway. The two rivers join each other in the tidal zone of Rauma some three kilometres from Åndalsnes.

Istra's catchment area is 70.5 km², and much of it consists of more or less barren mountains with peaks exceeding 1,700 metres. As there are only a few, small lakes in the catchment area and there is forest only in the lower districts, spates or heavy floods are common. Bitter experience taught us that after heavy rainfall the river could rise one metre or more in a couple of hours.

While the upper reaches of the Istra are very steep, conditions change

abruptly as the river enters the flat, lower plain of the Romsdal valley. From this point and down to the confluence with the Rauma the river winds its way in numerous bends with pools and small rapids fenced in by clay banks with a very dense vegetation of alder, hazel and birch. So dense is the undergrowth and so steep and treacherous are the clay banks, that the river banks are hardly accessible on foot. Surveys of the lower part of the river are best made by canoe or some other small portable craft.

Seatrout and salmon have access to about 10 kilometres of the Istra before being stopped by waterfalls. Only a few specimens of adult salmon were caught in the river during the investigations and few salmon smolts leave the Istra in spring. The seatrout is the important fish in the river. In the tidal reaches sticklebacks and minute flounders abound. Small eels are found everywhere in the river up to the waterfalls.

The very few people in the lower parts of the Istra valley have taken some seatrout in traps, nets or on hook and worm, but the fishery has never been seriously exploited by the owners. Because of the difficult terrain and the huge amount of fallen alder trunks and other snags, illegal fishing is less attractive than in the neighbouring Rauma. The Istra has never been regarded as a particularly good seatrout river, but merely as a river where seatrout were known to enter — just as in hundreds of other small rivers in this part of the country.

In 1949 the late Inspector of Salmon and Freshwater Fisheries, Mr. SVEN SØMME, succeeded in hiring all fishing rights in the river on behalf of the Ministry of Agriculture. Our ambitious plan was to keep a check, by means of a weir incorporating traps, on all ascending and descending seatrout and by means of marking, tagging, age analysis, etc., to get more knowledge of the biology of seatrout and the dynamics of the seatrout population of a river.

Our first weir was constructed in 1949 in the tidal part of the river from 3″ wooden bars and wiremesh. It was completely wrecked by the first flood. Later constructions reinforced with iron bars were also broken down by the river, and no control of the fish was obtained in 1949.

Late in 1949 a new site some 300 metres further upstream was chosen for the weir, and a strong 25-metre-long construction was erected with a framework of timber and a grating of round 10 mm iron bars spaced with 15 mm openings. The weir had two openings for traps — one for ascending and the other for descending fish. In order to obtain a check on the descending seatrout smolts 0.5″ wiremesh netting was stretched over the iron bar grating in spring.

There was no possibility of obtaining a complete check on the fish passing the weir in the Istra, as we had to make the final weir construction in such a way that the heavy floods passed over the weir. A particularly severe autumn flood destroyed three or four of the bridges spanning the river and

wrought havoc on the road in the Istra valley, but the weir survived, though damaged.

The new weir was ready late in the autumn of 1949 and a fairly good check on descending and ascending seatrout was obtained in 1950. In 1951 and 1952 only a small fraction of the seatrout could be checked. After a final, vain attempt to check the kelt descent in spring 1953 the project was abandoned.

In spite of our failure to obtain a full control of the Istra seatrout some new knowledge of this fish was obtained, and as little is known of Norwegian seatrout we feel that publishing these incomplete data may still be worth while.

I. Tagging methods

Two types of tags were used, viz. a small LEA's hydrostatic tag and, as we were short of LEA tags, a home-made celluloid disc tag (ATKIN's tag, ROUNSEFELL and EVERHART 1953).

The LEA tags were yellow with blue ends. The diameter was 4 mm, the length about 30 mm and the weight approximately 300 mg. The home-made oval ATKIN's tags were white and weighed only about 50 mg. They were 20 mm long and 7 mm broad.

The LEA tags were attached by a 0.40 mm thread of stainless steel, while a stainless steel thread of only 0.25 mm diameter was used on the home-made tags.

Three different places for tag attachment were tried: (1) through the back at the front of the dorsal fin (the method commonly used on adult salmon in Norway), (2) around the left lower jaw and (3) through the back just behind the gillcovers. Only single-thread attachment was used.

All fish were tagged and released immediately after capture. Care was taken to handle the fish as little and as gently as possible. All tagging was done under water in a tub. Anaesthetics were not used.

As the descending kelts were not easily caught in the traps, other fishing methods were also used, such as chasing the fish on a trammel net, rod with spoon, spinner or worm; a few were taken by a ketcher. Chi-square tests for heterogeneity (SNEDECOR 1956) indicate that the probability of survival after tagging was independent of the kind of fishing gear used to secure the fish for tagging.

The Lea tags gave significantly more recaptures than did the home-made tags ($\chi^2=9.34$; d.f.$=1$). The inferiority of the home-made tags was probably partly due to the thin thread used on these tags and partly to a too thin celluloid cover on the tags allowing the water to penetrate.

The fractions re-observed (observed at the weir or caught by fishermen)

Table 1. Sea-trout kelts tagged in the River Istra 1950—53.

Tagging method	Type of tag	Date	Number	Fraction re-observed	χ^2	Degrees of freedom
Dorsal	Home-made	Spring '50	148	0.51	0.13	1
Dorsal	Home-made	Aut. '50	144	0.48		
Jaw	Lea	Spring '50	26	0.54	0.18	1
Jaw	Lea	Aut. '50	419	0.60		
Dorsal	Lea	Spring '50	262	0.66		
Jaw	Home-made	Spring '50	22	0.32		
Jaw	Lea	Spring '51	151	0.34		
Jaw	Lea	Aut. '51	90	0.43		
Jaw	Lea	Spring '52	20	0.35		
Neck	Lea	Spring '52	18	0.28		
Jaw	Lea	Aut. '52	22	0.45		
Dorsal	Lea	Spring '53	6	0.33		
Jaw	Lea	Spring '53	14	0.07		
Neck	Lea	Spring '53	14	0.36		
Total:	Home-made		314	0.48		
	Lea		1,042	0.54		

for the different tagging experiments are shown in Table 1. Tagging methods (1), (2) and (3) are called "dorsal", "jaw" and "neck" respectively.

Comparisons dorsal Lea *versus* jaw Lea ($\chi^2 = 1.05$) and dorsal home-made *versus* jaw home-made ($\chi^2 = 2.02$), all from the spring of 1950, indicate that the probability of re-observation is independent of whether the tags were attached through the back or around the lower jaw. However, the material is small, and it might therefore be desirable to include the autumn tagging of 1950 as well in the comparisons.

Unfortunately, all jawtagging in the autumn of 1950 was done with Lea tags and all dorsaltagging with home-made tags. Hence a direct comparison between the two tagging methods in autumn 1950 would be biased by the different efficiencies of the two types of tags.

This difficulty may be overcome by combining the spring and autumn taggings in 1950. As shown in Table 1 the probability of re-observation is not significantly different in these two tagging periods.

Pooling the spring and autumn 1950 taggings gives the following results (Table 2):

Table 2. Comparison between "jaw" and "dorsal" attachment of tags.

Tagging method	Number tagged	Fraction re-observed	χ^2	D. f.
Dorsal Lea	262	0.66	2.48	1
Jaw Lea	445	0.60		
Dorsal home-made ...	292	0.49	1.86	1
Jaw home-made	22	0.32		
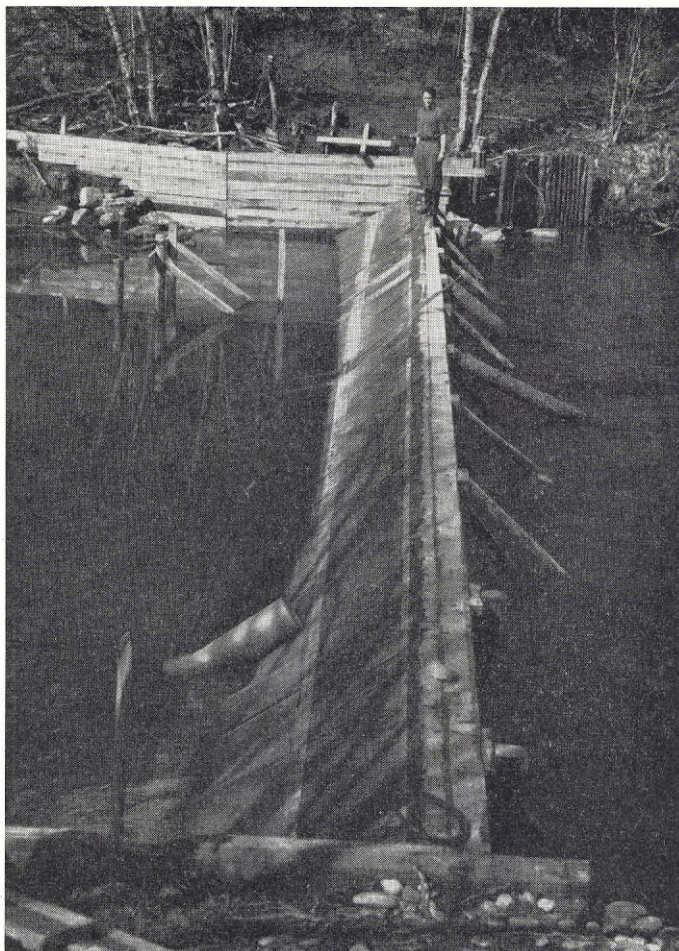
Fig. 1. The weir in the River Istra.

There is evidently a strong indication that the jaw attachment is inferior to attachment in front of the dorsal fin, but the difference is not statistically significant.

Too few fish were "neck"-tagged to allow any conclusion as to the efficiency of this kind of attachment.

II. Age and growth

The reliability of age determinations and growth calculations

The age determinations are based on the assumption that one close band ("winter" zone) is developed in the scales every year as long as the fish survives. As shown by NALL (1930) and others, exceptions from this rule may be rather common in seatrout.

To a certain extent the validity of age determinations of the seatrout could be checked, as scale samples were taken two or even three times during the life of a tagged fish. We have also a few scale samples from recaptures at the weir of fish which were marked as smolts in 1950.

The sea age could be read on 30 pairs of scales from kelts caught twice and with one year or more between the first and the second scale sample. From one specimen readable scales were secured in three successive springs. One fish had completely stopped growing during one year, and no close band had been formed in the scales. One fish had only formed one close band in the scales during two years. In the other 28 specimens the scales were in harmony with the known part of the life history of the fish.

Scale samples were secured from ten recaptures of seatrout smolts which were marked in the spring of 1950 by removal of the adipose fin. Nine of these had a sea age in full agreement with the number of years between smolt release and recapture. One fish had two sea summers in the scales whereas only one was expected. As the back-calculated length at the completion of the first sea winter (s_1) was only 22.5 cm, this fish may have been a finnock and not a smolt when marked in the spring of 1950.

For back-calculations of growth the following common symbols have been used:

L: The total length of the fish from snout to tip of caudal fin.

l_1, l_2 etc.: The calculated total length at the end of the first, second, etc., winters before smolt descent.

s_1, s_2 etc.: The calculated total length at the end of the first, second, etc., winters after smolt descent.

The back-calculations have been made on the assumption that the scale radius and the total length of the fish increase proportionally (LEA-DAHL's method). The bias resulting from this is believed to be small.

In salmon kelts back-calculations of growth will usually be heavily biased because of scale resorption. In the seatrout kelts from the Istra, back-calculations of growth from sets of scales taken from the same fish at different times indicated only a very slight bias (if any) due to scale resorption. As shown by the comparatively slight development, or even complete lack of spawning marks, the spawning migrations do not usually result in heavy scale resorption in the Istra seatrout.

Age and length at first descent

2309 seatrout smolts were captured and measured during their descent in the spring of 1950. Their length distribution is shown in Fig. 2.

More than 65 per cent of the smolts were between 14 and 16 cm but a few fish attained lengths of more than 20 cm before descending. However, as the
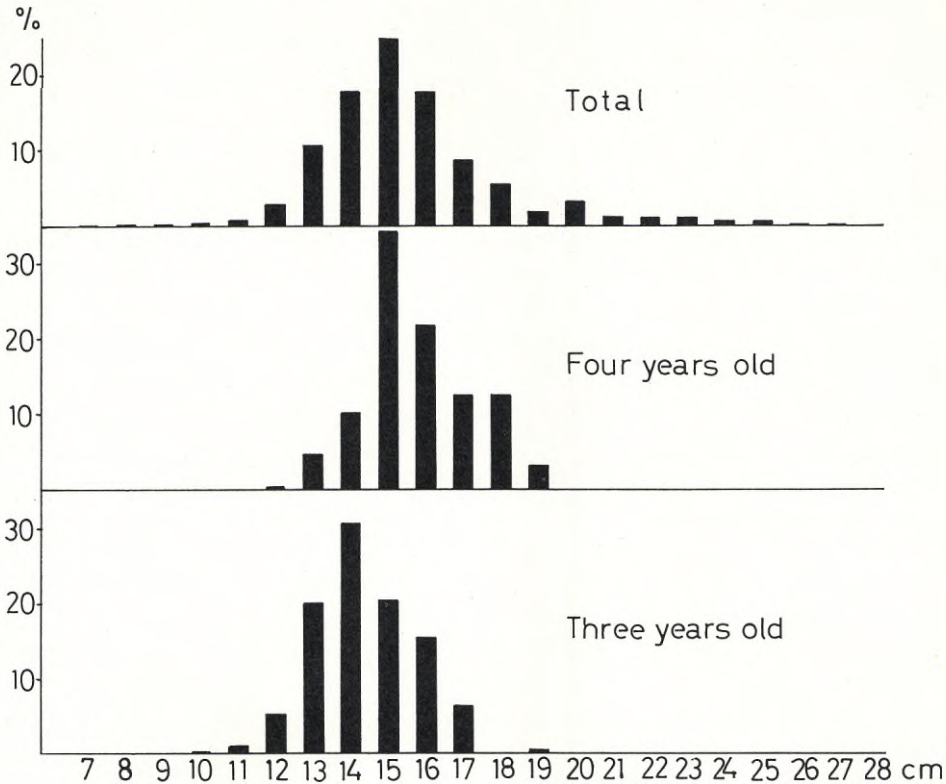
Fig. 2. Length distribution of 2,309 smolts descending in the spring of 1950.

scales were not checked on all fish, some of these big specimens may have been finnocks.

Scale samples were secured from 300 smolts, and by using these as a subsample the age distribution of the 2309 smolts was calculated. The results are shown in Table 3.

Table 3. Calculated age distribution of 2,309 smolts descending in the spring of 1950.

	Age in winters				
	1	2	3	4	5
Per cent:	0.3	1.6	51.2	44.7	2.1

More than 95 per cent of the smolts were three or four years old at migration. The few one-year-old fish in the sample were probably parr. One-year-old smolts scarcely exist in the Istra.

The growth of the smolts was determined from the scales by simple back-calculation. The results are shown in Table 4.

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Table 4. Calculated growth of three- and four-year-old smolts 1950.
Number of observations in brackets.

	l_1	l_2	l_3	l_4
Three-year-old smolts (139)	3.8	8.7	13.5	
Four-year-old smolts (100)	3.1	6.8	11.1	15.3

On average, four-year-old smolts had a slower calculated growth than have three-year-old smolts. The conclusion that fast-growing seatrout on average descend at a younger age than their slower-growing relatives (ALM 1950, WENT 1962) is probably correct, but not obvious, as LEE's phenomenon of apparent change in growth rate has probably biased the back-calculations of growth. Also in non-migratory populations of brown trout four-year-old fish will usually show a slower calculated average growth than will three-year-old specimens. LEE's phenomenon could easily be caused by misinterpretation of some of the scales, as both overlooking a true zone or marking down a check in the scale as a zone will tend to result in the "phenomenon". Omission of a true zone will make the fish in question younger and the calculated growth too fast, while marking down a false zone in the scale as a true zone will make the fish too old and correlate this with a too slow calculated growth.

The age at smolt descent can also be determined from the scales of adult fish. Scales from 470 older fish showed the following smolt ages (Table 5).

Table 5. Smolt age in per cent of 470 adult seatrout.

		Age in winters		
	2	3	4	5	6
Per cent	2.1	56.6	37.4	3.2	0.6

94 per cent of the fish were three or four years old at their first seaward migration. The results are in good agreement with the age determinations of smolts descending in 1950.

Smolt lengths can be back-calculated from the scales of older fish, but the results may be biased by the usual methodical errors inherent in back-calculations of this kind. There is also the possibility of bias due to differences in mortality correlated to differences in smolt size. However, back-calculations of smolt lengths were done on scales of 266 fish which had left the river when three years old and 176 fish which had left the river at an age of four years. The calculated lengths at smolt migration are shown in Table 6.

These calculated smolt lengths are 1—2 cm greater than the measured smolt lengths from 1950. Obviously the measured lengths from 1950 should be regarded as the more reliable of the two sets of observations, although some variation from year to year is probable.

Table 6. Back-calculated smolt lengths of seatrout adults (per cent).

	Smolt length cm								
	9	10	11	12	13	14	15	16	17
Three-year-old smolts	0.8	2.6	3.4	9.8	13.9	13.2	18.4	13.2	10.5
Four-year-old smolts	—	—	—	2.3	0.6	5.7	9.7	15.9	17.0

	Smolt length cm								
	18	19	20	21	22	23	24	25	26
Three-year-old smolts	9.4	1.1	2.3	1.1	0.4	—	—	—	—
Four-year-old smolts	15.9	11.4	8.0	9.1	1.7	1.7	0.6	—	0.6

Growth in the sea

As tagging may influence the subsequent growth, the best basis for an estimate of the sea growth is probably the length and age of the fish when caught at the weir for the first time. Measurements of tagged fish at ascent and descent have shown that no increase in length takes place during the kelts' sojourn in the river. However, as the winter zone is often not completed when the kelt descends in spring, some growth may take place between the descent and the completion of the zone. This will tend to make the empirical growth a little slower than the back-calculated growth.

The empirical-growth data are given in Table 7, where 2.3, 2.4, etc., stand for fish with two years' river life followed by three years in the sea, two years' river life followed by four years in the sea, and so on.

The table indicates that on average the males grow faster than the females. ALM (1950) found that in the Åva Stream stock females "grow a little faster

Table 7. Observed average length of different age groups. Number of observations in brackets.

	2.1	2.2	2.3	2.4	—	—	—	—
♀♀:	—	—	43.3(4)	63 (1)	—	—	—	—
♂♂:	—	—	49 (1)	43.5(2)	—	—	—	—
	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
♀♀:	—	40.2(28)	46.9(73)	51.1(36)	56.7(3)	55.5(2)	65.7(3)	64 (1)
♂♂:	—	41.4(17)	47.9(45)	59.1(21)	62.0(11)	70.0(3)	—	—
	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8
♀♀:	31.8(4)	39.8(40)	48.4(35)	54.9(21)	55.5(6)	59 (1)	67.5(2)	—
♂♂:	35 (1)	40.4(9)	49.9(16)	60.5(11)	61.7(7)	—	—	73.5(1)
	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8
♀♀:	38.0(2)	37.3(3)	57.0(2)	—	64 (1)	—	—	—
♂♂:	26 (1)	—	49 (1)	—	—	—	—	—
Sex unknown: 30.0(4)								
	6.1	6.2						
♀♀:	38 (1)	47.5(2)						

13*

Table 8. Back-calculated length at first, second, etc., winters after smolt migration. Number of observations in brackets.

	s_1		s_2		s_3	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
3-year-old smolts	27.0(147)	28.0(99)	38.6(147)	40.1(99)	46.3(135)	49.3(89)
4-year-old smolts	30.0(111)	30.0(46)	40.9(107)	40.9(45)	48.9(69)	49.9(37)

	s_4		s_5		s_6	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
3-year-old smolts	51.1(68)	58.1(40)	55.4(28)	62.2(16)	59.8(12)	66.8(4)
4-year-old smolts	54.0(40)	57.9(24)	58.0(16)	62.0(13)	57.8(8)	66.7(3)

than the males", while PIGGINS (1963) for Irish seatrout kelts states: "There appears to be little significant difference between the growth of males and females . . .".

Table 8 shows the average back-calculated lengths after the smolt migration of fish migrating as three-year-old and four-year-old smolts. This time the whole material has been used, regardless of whether the fish had been tagged one or more seasons before the scale sample was taken. We see again that on average the males grow faster than the females do.

Tables 7 and 8 may give an impression that four-year-old smolts grow faster in the sea than do three-year-old smolts, but this is not so. A closer examination of the yearly length increments gives no indication that four-year-old smolts grow faster in the sea than three-year-old smolts with the same length at smolt migration.

III.   Marking of seatrout smolts

In the spring of 1950 2092 smolts were caught at the weir, marked by removal of the adipose fin and released downstream the weir. The intention was to get an idea of the total mortality during the first years in the sea, but this failed because of the technical difficulties with the control at the weir.

Only 18 of these fish were observed at the weir at some later date. Details are shown in Table 15.

IV.   Reproduction biology

Sex distribution

DAHL (1910) found when he examined seatrout parr that females and males were fairly evenly distributed in the youngest age groups. Among the

Table 9. Sex distribution of descending seatrout smolts. Spring 1950.

Age	Females	Males	$\dfrac{\text{Females}}{\text{Males}} \times 100$	Sex unknown
2 years	0	5	0	—
3 „	75	59	127	5
4 „	58	41	141	—
5 „	1	1	100	—
Age uncertain	11	7	157	—
Total	145	113	128	5

elder fish which had never been to sea, the males dominated, and the oldest age groups of these fish consisted entirely of sexually mature males. He concluded that the young females had descended to the sea, while some of the males never left the river. In accordance with this, he found that females were more numerous than males in samples of post-migration sea-trout. This dominance of females among seatrout which have spent one or more years in the sea has been found by many later authors (ALM (1936), (1950), HESSLE (1935), SVÄRDSON and ANHEDEN (1963 b) and others).

Table 9 shows the sex distribution of a sample of descending seatrout smolts caught in the trap in the spring of 1950.

Females are more frequent in the sample than males; the average proportion is 128 females to 100 males. The numerical difference is significant (pooled $\chi_v^2 = 3.97$).

The sex distribution of all ascending (autumn) and descending (spring) adults when caught at the weir for the first time is shown in Table 10. There is again a dominance of females, and the difference is highly significant. The last column in the table contains fish with slightly developed or undeveloped secondary sexual characters and consists of a mixture of ripe (autumn) fish, spent (spring) fish and juvenile finnocks.

Table 10. Sex distribution of adult seatrout.

	Number of females	Number of males	$\dfrac{\text{Females}}{\text{Males}} \times 100$	Sex uncertain
Spring 1950	280	172	163	5
Autumn 1950	341	205	166	16
Spring 1951	59	56	105	36
Autumn 1951	43	37	116	10
Spring 1952	26	9	289	6
Autumn 1952	14	7	200	1
Spring 1953	19	15	127	0
Spring Total	384	252	152	47
Autumn Total	398	249	160	27
Grand Total	782	501	156	74

Table 11. Age of mature seatrout when first caught at the weir.

Smolt age	Sex	Summers in the sea							
		1	2	3	4	5	6	7	8
2-year-old smolts	♀♀	—	—	—	4	1	—	—	—
	♂♂	—	—	—	1	2	—	—	—
3-year-old smolts	♀♀	—	28	73	36	3	2	3	1
	♂♂	—	17	45	21	11	3	—	—
4-year-old smolts	♀♀	4	40	35	21	6	1	2	—
	♂♂	1	9	16	11	7	—	—	1
5-year-old smolts	♀♀	2	3	2	—	1	—	—	—
	♂♂	1	—	1	—	—	—	—	—
6-year-old smolts	♀♀	1	2	—	—	—	—	—	—
	♂♂	—	—	—	—	—	—	—	—
Total	♀♀	7	73	110	61	11	3	5	1
	♂♂	2	26	62	33	19	3	—	1

Age at first maturity

Scales from recaptured tagged fish have shown that spawning marks may be completely absent in seatrout kelts from the Istra. In many cases the interpretation of a slight scale erosion as a spawning mark is very doubtful. Analysis of spawning marks for ascertaining first age at maturity is therefore hardly worth while on this material.

Some conclusions about the age at first maturity can be drawn from the age distribution of mature fish when caught at the weir for the first time. This is shown in Table 11.

Most of the fish of both sexes had spent three summers in the sea before they were caught at the weir for the first time. As one- and two-sea-summers-old fish must be more numerous in the population, only a fraction of the population attains maturity after the first or the second summer in the sea. The table indicates that fish which mature after their first summer in the sea are more frequent among 4-, 5-, and 6-year-old smolts than among 2- and 3-year-old ones. There is also an indication that 4-year-old smolts will more frequently mature after their second summer in the sea than will 3-year-old smolts. This correlation between high smolt age and low seaage at first maturity was also found by ALM (1950) — maturation is partly a function of total age.

Spawning frequency

After the first spawning, either the surviving fish may spawn again the next year, or two years or more may pass before the next spawning.

NALL (1930, page 253) concludes: "When maturity is once reached . . . seatrout as a rule are annual spawners." ALM (1950, page 54) found that "Among the marked trout that were recaptured in the Åva Stream, 84.2 per

Table 12. Percentage recapture with different kinds of gear in the sea.

Kind of gear	Recaptures (%)
Trolling and spinning	36.8
Bag nets	27.1
Gill nets	14.4
Seines	14.4
"Not" [1]	6.4
Longline	1.1

[1] The Norwegian word "not" can mean both a bag net and a seine.

cent returned to spawn in the next autumn and 10.5 per cent during the following two years, while altogether 5.3 per cent have been away one, two or three years before their next spawning migration . . .".

JÄRVI (1940), on the other hand, for seatrout in rivers further north in the Bothnian Bay found that spawning in successive years is rather rare.

As shown in another connection, all or nearly all of the survivors from the kelt taggings in the Istra in the spring of 1950 returned on a new spawning migration in the summer or autumn of the same year. In spite of the incomplete control at the weir many fish were encountered there in three successive years. In some cases spawning marks are seen in the scales in as many as four successive years.

As the control at the weir was in all years incomplete, and as the negative evidence of missing spawning marks cannot be accepted as proofs, we have no way of ascertaining whether a few adult fish omitted to spawn in one or more years. However, our conclusion must be that usually the Istra seatrout will spawn every year after first maturity as long as the fish survives.

V. Recaptures with different kinds of gear

The kind of gear used is known for 276 of the tagged seatrout which were recaptured by fishermen. Of these 188 were caught in the sea and 88 in the River Rauma. The kinds of gear used in the sea are indicated in Table 12.

In the Romsdal fjords trolling and spinning from the shore take more seatrout than does any one commercial kind of gear. One of the reasons for this is that the smallest legal meshsize for bag nets in Norway is 58 mm from knot to knot, and in the Romsdal district this meshsize has been enforced for seines too. Hence most of the seatrout pass through the meshes.

Table 13. Percentage recapture with different kinds of gear in the River Rauma.

Kind of gear	Recaptures (%)
Fly	52.3
Spinning	33.0
Hook and worm	13.6
"Rod"	1.1

Table 14. Number of seatrout ascending 1950.

	July 16—31			Aug. 1—15			Aug. 16—31			Sep. 1—15			Sep. 16—30		Oct. 1—15		Oct. 16—30	
	♀♀	♂♂	?	♀♀	♂♂	?	♀♀	♂♂	?	♀♀	♂♂	?	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
	43	41	3	42	33	1	58	57	8	63	32	3	34	14	51	23	50	5
Total:	87			76			123			98			48		74		55	
$\dfrac{\text{Males}}{\text{Females}}$	0.95			0.79			0.98			0.51			0.41		0.45		0.1	

? = Sex unknown.

In the River Rauma all reported recaptures were made with sporting gear (Table 13). The salmon traps in Rauma have a minimum distance of 58 mm between neighbouring bars, and this allows most of the seatrout to pass through the traps.

VI. Migrations

The spawning migration

The number of ascending seatrout in the summer and autumn of 1950 is shown in Table 14. Fish which had been tagged in the spring of 1950 on descent are not included in the table.

The upstream migration began in July and continued through the summer and autumn. In 1950 the last ascending fish were caught on October 24. In 1952 two ascending males were caught as late as November 23. As can be seen from the table, most of the males enter the river in July and August and the ratio $\dfrac{\text{Males}}{\text{Females}}$ decreases towards autumn.

After spawning, most of the kelts remain in the river until spring. Ice conditions prevent observations during winter. The descent takes place mainly in spring. Shortly after the ice had broken in the spring of 1950, shoals of kelts were observed in the pool immediately upstream from the weir. Most of the descending fish were afraid of the weir and the trap, and had to be chased on a trammel net or taken on rod before being tagged and released below the weir. The fish avoided the weir and the trap in daytime when the water was low and clear. Small spates due to snow melting or rainfall immediately started shoals of kelts towards the weir, and under flood conditions they would try to jump over the weir or enter the trap even in daytime.

Spates always make the Istra turbid because of the clay banks. To test whether turbidity by itself might induce the fish to enter the trap, we tipped some bucketfuls of clay into the river upstream of the weir pool. The resulting turbidity did indeed induce some fish to move downstream towards the weir, and a small number entered the trap; but after a couple of days the trick ceased to work.
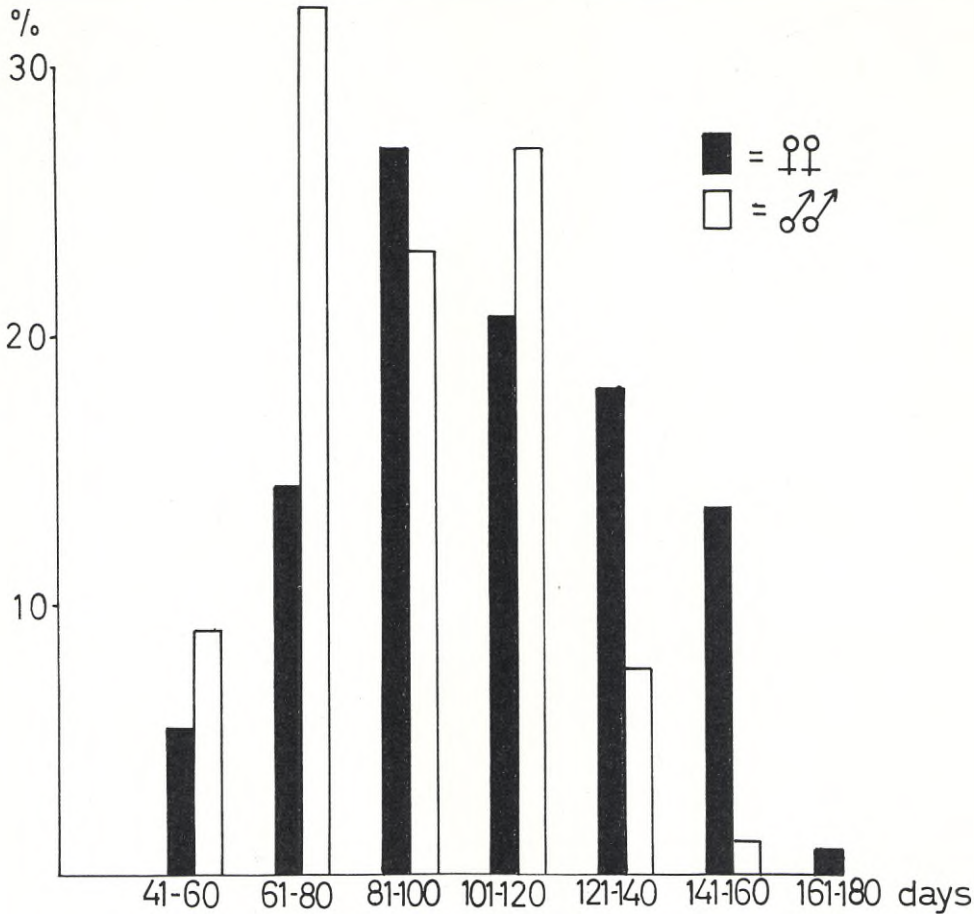
Fig. 3. Number of days between descent and new ascent of seatrout kelts controlled at the weir in 1950.

Doubtless the weir delayed the kelt descent, which in the Istra would probably normally be finished in May.

The duration of the sea sojourn of the kelts was in many cases very short. Fig. 3 shows the number of days between descent and ascent of fish control-led at the weir in 1950. The earliest return took place only 45 days after the fish had passed the weir on its seaward migration. Seatrout kelt returns to the river after only 43 days have been reported from Ireland (PIGGINS 1964).

In the Istra there is a tendency towards a shorter seastay for males than for females.

Migrations in the sea

Fig. 4 shows the recaptures by fishermen in the sea and in the Rauma of seatrout kelts tagged in the Istra. 35 specimens caught in Rauma between

Table 15. Recaptures at the weir of seatrout smolts marked spring 1950.

Date of recapture	Length	Sex	Date of recapture	Length	Sex
Oct. 1.1950	34	♀	May 28.1951	31	?
„ 19.1951	34	♀	„ 14.1951	34	♂
„ 3.1951	26	♀	„ 14.1951	32	♀
„ 4.1951	34	?	„ 3.1951	36	♀
„ 4.1951	28	?	„ 14.1951	42	♂
„ 4.1951	29	?	„ 5.1952	43	♀
„ 18.1951	27	?	„ 29.1952	38	♂
„ 19.1951	27	?	„ 21.1953	45	♀
„ 28.1951	28	?	„ 21.1953	49	?

the confluence with the Istra and the sea are indicated by the number 35 in a circle.

All recaptures in the sea were made in the Romsdalsfjords. Most of the fish were caught within 10—15 km of the outlet of the River Rauma, and the number of recaptures decreases rapidly with the distance from the river mouth. The longest migrations to Julsundet, Vatnefjord and Erisfjord cover only 60—70 km.

All recaptures in fresh water were made in the Rivers Rauma and Istra.

It should be borne in mind that only kelts were tagged. Experience from other countries indicate that young seatrout may frequently undertake much longer migrations than do seatrout kelts (SVÄRDSON and ANHEDEN 1963 a and others).

VII. Mortality

Mortality estimates from age distribution

No material is available for estimates of mortality during fry or parr life in the Istra. For the older fish it may be doubtful whether any of the age groups among the spawners can give unbiased estimates of the age distribution in the total seatrout population originating from the Istra. The attainment of maturity is probably not 100 per cent even after four years in the sea. The fraction of mature fish in the different age groups probably increases with age. Mortality estimates based on the age distribution of spawners (or on any other incompletely recruited biological group) will therefore be biased, and in this case they will probably be too low.

As most of the material was collected during only two years, mortality estimates from age distribution may also be seriously biased by variations in the magnitude of different year classes.

Readable sets of scales were secured from 471 adults and their seaage when caught at the weir for the first time was determined. The age distribution within the different two-centimetre groups was then calculated and the
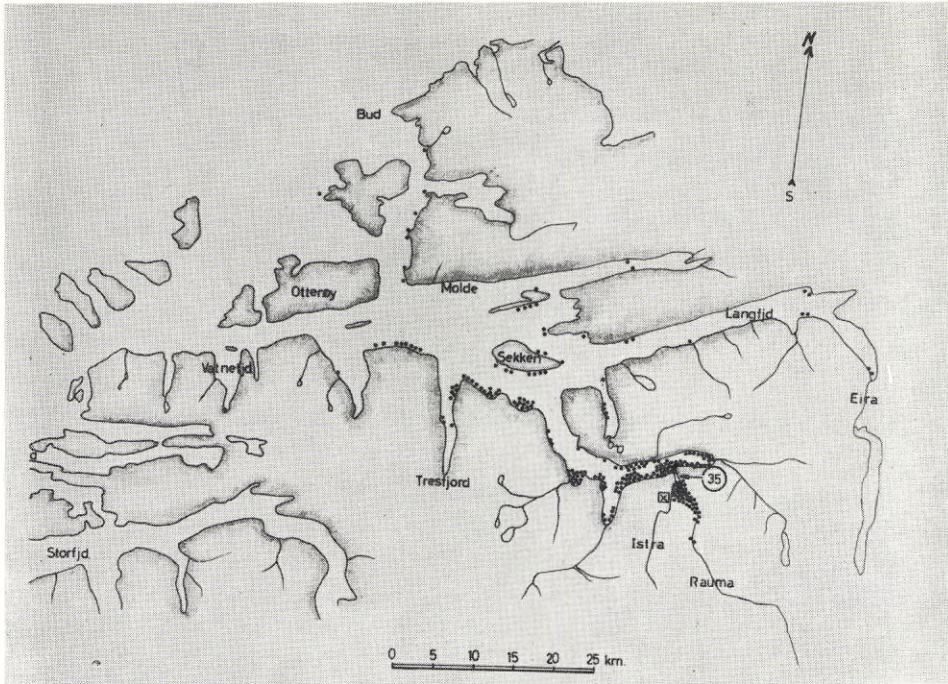
Fig. 4. Recaptures by fishermen of seatrout kelts tagged at the Istra weir.

results used to estimate the seaage when caught at the weir for the first time of 832 adults of known length but unknown age. The seaage distribution of the pooled sample of 1,303 fish can be seen from Table 16.

If we assume that from the fourth seayear the rates of recruitment to the spawning stock and of survival are constant, the annual mortality rate can be estimated as:

$$\hat{a} = \frac{N_4}{N_4 + N_5 + N_6 + \ldots}$$

(RICKER 1958). This gives an estimated annual mortality rate for females of $\hat{a} = 0.69$ and for males of $\hat{a} = 0.70$.

Mortality estimates from tagging

During the Istra investigations seatrout fishing in Romsdal was legal only from April 15 to September 5. Although some illegal fishing in the sea may have taken place, we can assume that all fishing was done between April and September. As we shall see, nearly all Istra seatrout kelts spend the winter months in the river; hence illegal winter fishing in the sea will not greatly influence our estimates. The Istra's topography and the presence of a paid guard made poaching in the river unusually difficult and unattractive.

Table 16. Estimated age distribution of adult seatrout when caught at the weir for the first time.

	Sea summers				
	1	2	3	4	5 or more
Females (number)	14	179	316	173	78
Males (number)	6	99	214	157	67

Evidently fishing mortality and natural mortality are not distributed proportionately through the year. As tagging and control at the weir were done both in spring and autumn, estimates of seasonal mortality are possible.

Table 17 shows the number of observations at the weir and of recaptures reported by fishermen from the different tagging experiments. Only LEA tags are included in the table.

The later observations at the weir and the fishermen's recaptures can both be used for mortality estimates. The observations at the weir include in some periods (autumn 1950) nearly the whole spawning run, while in other periods floods permitted control of only a small fraction of the migrating fish.

As to the recaptures by fishermen, the efficiency of reporting recapture is unknown. The Lea tags carry an inscription with instructions to the fisherman to report recapture, and a reward is promised. However, we do not know to what extent these instructions are followed.

Obviously estimates based on weir recaptures may be heavily biased if a significant fraction of the adults do not enter the river to spawn. As indicated in some fish by the spawning marks, spawning takes place yearly after the attainment of maturity. This can be verified by the observations at the weir.

Of the 288 kelts tagged in the spring of 1950, 138 were checked at the weir during their ascent the same year. During descent in spring 1951 only 40 of the spring-tagged fish from 1950 were checked, and of these 34 specimens had also been checked in the previous autumn. According to this 34/40 or 85 per cent (95 % confidence limits 0.69—0.94) of the spring-tagged fish were observed at the weir in the autumn of 1950. If this is a true estimate of the rate of observation of the surviving spring-tagged fish, we should expect to find that of all later recaptures by fishermen, or observations at the weir of fish tagged in spring 1950, about 85 per cent should have been observed at the weir in the autumn of 1950. If, on the other hand, a significant fraction of the kelts tagged in spring 1950 did not enter the Istra again the same year, but stayed alive in the sea, we should expect later observations at the weir and recaptures by fishermen of this group of fish to contain significantly less than the 85 per cent checked at the weir in the

Table 17. Number of observations at the weir (W) and number of recaptures by fishermen (F) from the different tagging experiments. (Only LEA tags.)

Time of tagging	No. tagged	F 1950	W Autumn 1950	W Spring 1951	F 1951	W Autumn 1951	W Spring 1952	F 1952	W Autumn 1952	W Spring 1953	F 1953	F 1954	F 1955	F 1956	F 1957	F 1958	F 1959
Spring 1950	288	41	138	40	19	12	5	5	1	1	3	—	—	—	—	—	—
Autumn 1950	419	—	—	182	46	40	17	22	7	1	10	5	—	1	—	—	—
Spring 1951	151	—	—	—	16	14	4	7	2	5	5	2	1	—	1	—	—
Autumn 1951	90	—	—	—	—	—	10	15	4	5	9	—	1	—	—	—	—
Spring 1952	41	—	—	—	—	—	—	6	—	—	6	1	—	—	—	—	—
Autumn 1952	22	—	—	—	—	—	—	—	—	4	7	1	1	—	—	—	—
Spring 1953	34	—	—	—	—	—	—	—	—	—	5	—	1	1	—	—	1

autumn of 1950. Of the later controls at the weir 15/17 or 88 per cent had been checked in autumn 1950. Of the 27 later recaptures by fishermen 26 or 96 per cent had been checked in autumn 1950. Hence we conclude that all, or very nearly all, survivors of the kelts tagged in spring 1950 ascended the river again the same year.

We can now estimate the number of surviving tagged fish from spring to autumn 1950 as 162 fish (95 % confidence limits 147—200). The corresponding estimated rate of survival is $\hat{s}=0.56$ (95 % confidence limits 0.51—0.69). The corresponding estimated rate of total mortality from spring to autumn 1950 $\hat{a}=0.44$ includes tag losses.

The rate of spring to autumn survival could also be estimated by means of RICKER's formula (5.2) (RICKER 1958):

$\hat{s}_1 = \dfrac{R_{12} M_2}{M_1 (R_{22}+1)}$ where M_1 and M_2 are the number of fish tagged respectively in spring and autumn 1950, R_{12} the number of spring-tagged fish re-observed at the weir in spring 1951, and R_{22} the number of autumn-tagged fish re-observed at the weir in spring 1951. The formula can only be used if the surviving spring-tagged fish had the same chance of being observed at the weir in spring 1951 as had the surviving autumn-tagged fish. Below we show that this condition is not fulfilled.

Of the 138 spring-tagged fish which were checked at the weir during their new ascent in autumn 1950 only 34 specimens, or 25 per cent, were observed at the weir during their descent in spring 1951. Of 419 autumn-tagged fish 182 specimens, or 43 per cent, were observed in spring 1951. The difference is highly significant (heterogeneity $\chi^2=14.67$; 1 d.f.). We had consequently a significantly better chance of observing the autumn-tagged fish. Possible reasons for the low rate of re-observation at the weir in spring 1951 of fish tagged in spring 1950 may be:

(1) High mortality during the winter of the spring-tagged fish.
(2) High rate of tag loss during the winter of spring-tagged fish.
(3) Different time of descent in spring 1951 of spring-tagged and autumn-tagged fish.

If winter mortality or winter loss of tags have been significantly higher for spring-tagged fish, we ought to be able to ascertain this from later observations at the weir and from later recaptures by fishermen. Of the estimated 162 spring-tagged fish that survived in autumn 1950, 19 specimens (11.7 per cent) were observed at the weir later than spring 1951, while 65 (15.5 per cent) of the 419 autumn-tagged fish were observed. The corresponding numbers of recaptures by fishermen from 1951 and onwards were 27 (16.7 per cent) and 84 (20.0 per cent). The differences are not significant. We may therefore assume that differences in time of descent, or in behaviour during descent of the two batches of seatrout, were probably the main reason why

comparatively few spring-tagged fish from 1950 were observed at the weir in the spring of 1951.

Evidently RICKER's formula (5.2) may give very unrealistic survival estimates when used on observations at the weir. As stated by RICKER (1958, page 129): "The attractive simplicity of this procedure is unfortunately often marred by the doubts occasioned by a possible lack of homogeneity among the group of fish being handled . . .".

We can, however, try the formula on the recaptures made by fishermen in 1951 of fish tagged in spring and autumn 1950, and get $\hat{s}_1 = \frac{19 \cdot 419}{288 \cdot 47} = 0.59$ (standard deviation 0.158). The corresponding estimated mortality rate from spring to autumn 1950 is $\hat{a}_1 = 0.41$.

The numbers of fish tagged in 1951—52 are too small to give worthwhile estimates of spring-to-autumn mortalities in these years.

RICKER's formula can also be used to estimate the *yearly* rate of survival of tagged fish. For the spring-tagged fish the condition that tagging in both years should be done at the very start of the fishing season would be violated. Estimates based on spring tagging in year 1 and year 2 and recaptures by fishermen in year 2 would be biased by the fact that fishing began before the tagging in year 2 was completed.

If we use RICKER's formula on autumn-tagged fish in 1950 and 1951, we violate the condition that tagging should be done right at the start of the fishing season. The survival estimates will not be biased because of this, however, if the surviving 1950 fish have the same rate of survival (and tag loss) during the winter 1951—52 as the 1951 fish. If this condition is fulfilled, the rate of survival from autumn 1950 to autumn 1951 for the fish tagged in autumn 1950 is:

$$\hat{s}_1 = \frac{90 \cdot 22}{419 \cdot 16} = 0.30 \text{ (standard deviation 0.094).}$$

If we assume that the rates of tag loss, natural mortality and fishing mortality are identical for the two groups of fish in all years after 1952, all recaptures by fishermen in 1952 and later years can be pooled, and we get:

$$\hat{s}_1 = \frac{90 \cdot 38}{419 \cdot 26} = 0.31 \text{ (standard deviation 0.078).}$$

The estimate is in good agreement with the yearly mortality rates of about 0.70 after the fourth seayear as estimated from the age distribution of the fish.

The number of fish tagged in autumn 1952 is too small to allow worthwhile estimates of $\hat{s}$ from autumn 1951 to autumn 1952.

As a further check on the estimated yearly rate of survival, we can use the relation $\hat{s} = \frac{R_2 + R_3 \ldots \ldots + R_n}{R_1 + R_2 + \ldots \ldots + R_{n-1}}$ where $\hat{s}$ is a weighted estimate of the

Table 18. Fractions of tagged seatrout recaptured by fishermen.

Time of tagging	Number tagged	Recaptured first year after tagging	Later recaptures
Autumn 1950	419	0.11	0.09
„ 1951	90	0.17	0.11
„ 1952	22	0.32	0.09
Spring 1950	288	0.14	0.09
„ 1951	151	0.11	0.11
„ 1952	41	0.15	0.17
„ 1953	34	0.15	0.09

yearly survival rate and R_1, R_2, etc., are the numbers of recaptures in later years (RICKER 1958, formula (4.2)). The conditions are that marking is done at the beginning of the fishing season in year 1 and that the total mortality rate does not vary appreciably over a period of years. Usually, in estimates of this kind, next to nothing is known about yearly variations in natural mortality; hence one postulates that this parameter does not vary significantly during a short sequence of years. Fishing mortality (rate of exploitation) from 1950 to 1953 can in our case be estimated from the recaptures.

Table 18 gives the fractions of tagged fish recaptured by fishermen in the first year after tagging and in all later years.

The spring taggings have given fairly even fractions of recapture in the first year after tagging.

Of the fish tagged in the autumn of 1952 a significantly larger fraction was recaptured than in the other experiments (heterogeneity $\chi^2 = 9.55$, d.f. $= 2$). However, spring-tagged fish from 1953 did not give unusually many recaptures in 1953. We will therefore assume that the high recapture fraction in 1953 of fish tagged in autumn 1952 was caused by chance or by some other factor than a more intensive fishing in 1953 than in the previous years. We will further assume that neither fishing mortality nor natural mortality varied significantly during the years the tagged fish were at large.

The autumn taggings were done about six months before fishing began again the next spring. This does not influence our survival estimates, provided the natural mortality from autumn to spring does not vary appreciably from year to year.

Our estimates of yearly survival rates from the three autumn taggings are:

From the autumn tagging 1950: $\hat{s} = \dfrac{22+10+5+0+1}{46+22+10+5} = 0.46$

„ „ „ „ 1951: $\hat{s} = \dfrac{9+0+1}{15+9} = 0.44$

„ „ „ „ 1952: $\hat{s} = \dfrac{1+1}{7+1} = 0.25$

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The last two estimates are based on too few observations to be taken as valid.

In the spring, tagging was still going on after the commencement of the fishing season. This will give too low values for R_1, and hence consistently too high values for $\hat{s}$. The results are:

From the spring tagging 1950: $\hat{s} = \dfrac{19+5+3}{41+19+5} = 0.42$

,,   ,,   ,,   ,,   1951: $\hat{s} = \dfrac{7+5+2+1+0+1}{16+7+5+2+1} = 0.52$

,,   ,,   ,,   ,,   1953: $\hat{s} = \dfrac{0+1+1+0+0+1}{5+0+1+1+0+0} = 0.43$

The last two estimates are obviously based on too few observations. The yearly rate of survival of the fish tagged in spring 1950 and spring 1951 should accordingly be smaller than 0.42 and 0.52.

We could eliminate, from this spring-tagged material the bias due to fishing beginning before tagging is finished, by using the formula

$\hat{s} = \dfrac{R_3 + R_4 + \ldots\ldots + R_n}{R_2 + R_3 + \ldots\ldots + R_{n-1}}$ but this leaves too few recaptures to give worthwhile estimates.

Let us, finally, review our best estimates of survival:

From age distribution: $\hat{s} = 0.30$—0.31 after the fourth year in the sea.

From tagging:

Survival from autumn 1950 to autumn 1951 of fish tagged in autumn 1950: $\hat{s} = 0.30$ (s.d. 0.094).

Weighted estimate of the average annual survival of fish tagged in autumn 1950: $\hat{s} = 0.46$.

Survival from spring to autumn 1950 of fish tagged in spring 1950 estimated from re-observations at the weir: 0.56 (95 % conf. lim. 0.51—0.69). The same rate estimated from recaptures by fishermen: 0.59 (s.d. 0.158).

Evidently the mortality rates are high among the seatrout kelts of the Istra.

As can be seen from Table 17 the rate of exploitation is low. The first year after tagging fishermen caught 12.8 per cent only of 531 autumn-tagged kelts and 13.2 per cent of 514 spring-tagged kelts.

VIII. The size of the spawning population

The best estimate of the size of the spawning population was obtained for the spawning run in 1950. The number of fish ascending the river during the summer and autumn of 1950 can be estimated from Table 19.

In spring 1951 a smaller fraction was observed of the spring-1950 fish than of the autumn-1950 fish. One reason for this may be a higher rate of tag loss during the winter of the spring-1950 specimens.

Table 19. Number of seatrout controlled at the weir in summer and autumn
1950 and in spring 1951.

	Observed autumn 1950	Observed spring 1951	Observed both 1950 and 1951	Fraction re-observed spring 1951
Tagged spring 1950. LEA tags	138	40	34	0.25
,, ,, 1950 "Home-made" tags ..	55	11	10	0.18
,, autumn 1950. LEA tags	419	182	(182)	0.43
,, ,, 1950. "Home-made" tags	144	60	(60)	0.42
,, spring 1951	—	151	—	—
Total	756	444	286	0.38

Of the S_{50} fish tagged with LEA tags, 138 were recaptured at the weir in
the autumn of 1950. 40 LEA-tagged S_{50} fish were observed on descent in
spring 1951, and 34 of these had been observed also in autumn 1950. From
these figures a Petersen estimate with BAILEY's correction (RICKER 1958,
formula (3.7) is:

$\hat{N} = \dfrac{138(40+1)}{34+1} = 162$ fish (95 % conf.lim. 147—200). This is the best estimate

of the number of LEA-tagged S_{50} fish ascending the river in autumn 1950.
The estimate is based on the fraction

$$\frac{\text{Observed spring 1951}}{\text{Observed spring 1951 and observed autumn 1950}}$$

As observation or non-observation at the weir of formerly tagged ascending
fish can hardly influence subsequent tag losses, the estimate is unbiased by
possible tag losses during the winter of 1950—51.

The number of S_{50} fish with home-made tags ascending in autumn 1950
was in the same way estimated at 60.

151 untagged descending seatrout were caught at the weir in spring 1951.
24 of these showed scars or had a string in the back from an earlier tagging,
probably in most cases from the spring of 1950. We will assume that all
these fish were tagged in spring 1950. Of the S_{50} fish with tags in place an
estimated fraction of $\dfrac{138+55}{162+60} = 0.87$ was re-observed in spring 1951. Hence
21 of the 24 fish with scars had probably been observed (with their tags in
place) in autumn 1950. The number of untagged fish and fish with scars
observed in spring 1951, but not observed in autumn 1950, is accordingly
corrected to 130 specimens. If we assume that in spring 1951 the same
fraction was observed of these fish as of the LEA-tagged A_{50} fish, our best
estimate of the number of fish in this group entering the river in autumn
1950 is 298.

Our best estimate of the number of seatrout ascending the river in autumn
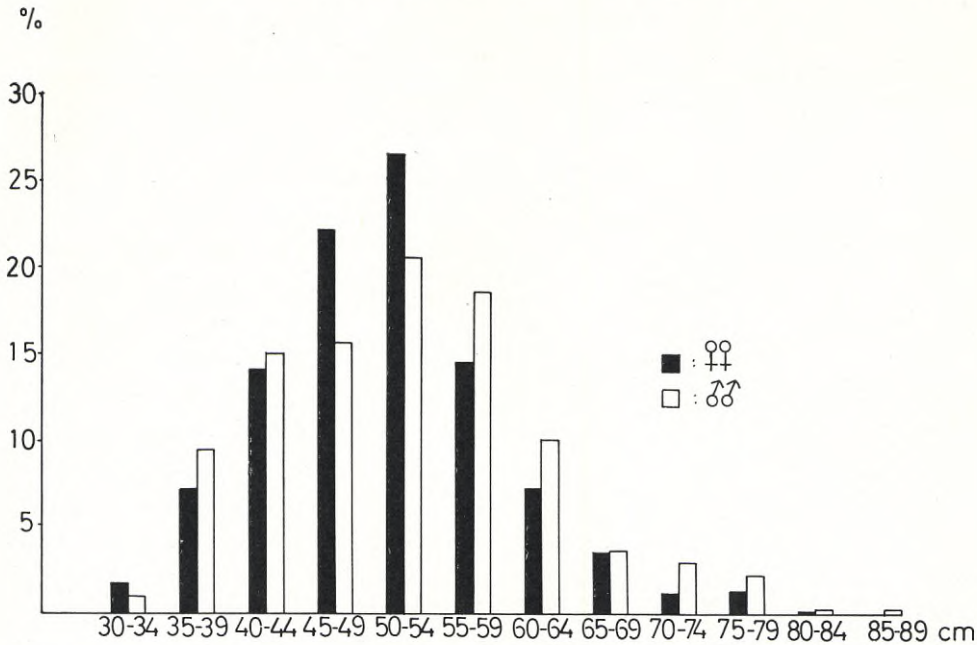1950 is then:

Fig. 5. Length distribution of adult ascending seatrout controlled at the weir in 1950.

S_{50} fish with LEA-tags .... 162 (95 % conf.interval 147— 200)
S_{50} fish with home-made tags .... 60 (95 %   ,,   56— 86)
Tagged in autum 1950 563
Untagged or with scars passing unobserved ...... 298 (95 %   ,,   241— 382)

Total .... 1,083 (95 % conf.interval 1,007—1,231)

The length distribution of the spawning run 1950 is seen from Fig. 5. More than half of the fish were in the length groups 45—59 cm. There is apparently no great difference in the length distribution of the sexes.

The average weight of the fish is about 1.5 kg, hence the total biomass of the 1950 spawning run was of a magnitude of about 1,500 kg — a quite astonishing figure for a rather insignificant seatrout river.

IX. Summary

The Istra is a small river (catchment area 70.5 km²) which has its outlet in the tidal zone of the River Rauma near Åndalsnes. Seatrout is the only fish of importance in the river. An experimental weir with traps was built, and the seatrout population studied in the years 1950—53. Heavy floods prevented complete control of the fish entering and leaving the river.

Age determinations and growth calculations were verified from the scales of fish with a known history and found reasonably reliable. In some cases spawning migration left no spawning mark in the scales.

The seatrout smolts leave the Istra in spring. In 1950 more than 95 per cent of the smolts were three or four winters old and more than 65 per cent of the fish were between 14 and 16 cm.

Four-year-old smolts had on average a slower calculated growth than three-year-old smolts.

In a sample of 263 descending smolts the sex proportion was 128 females to 100 males. In 782 adults checked at the weir for the first time, the proportion was 156 females to 100 males.

The calculated growth in the sea is shown in Tables 7 and 8. The males apparently grow a little faster than the females.

Comparisons of the first year's length increment in the sea of three- and four-year-old smolts with the same smolt lengths show no clear correlation between smolt age and sea growth.

The age distribution of the spawning fish indicates that only a small fraction of the population attains maturity after the first or the second summer in the sea. Most common among the spawners of both sexes are fish which have spent three summers in the sea. Usually the Istra seatrout will spawn every year after first maturity as long as the fish survives.

After spawning most of the seatrout remain in the Istra until spring, and usually leave the river in April—May. The stay in the sea may be as short as 45 days. The upstream migration begins in July and continues until October—November. The ratio of males to females among the ascending fish decreases towards autumn.

The migrations in the sea of the kelts are short. All recaptures of tagged fish have been done within a distance of 70 kilometres from the place of release. All recaptures in freshwater have been made in the Rivers Istra and Rauma.

The survival rate of adult fish was calculated both from age distribution and from tagging. As the material consists of only the sexually mature part of the population, survival estimates based on age distribution may be biased, and they are then probably too high.

From the age distribution the yearly rate of survival after the fourth year in the sea was estimated as $\hat{s} = 0.30$—0.31.

From the tagging data the following estimates were obtained:

Survival from autumn 1950 to autumn 1951 of fish tagged in autumn 1950: $\hat{s} = 0.30$ (s.d. 0.094).

Weighted estimate of the average yearly survival of fish tagged in autumn 1950: $\hat{s} = 0.46$.

Survival from spring to autumn 1950 of fish tagged in spring 1950: $\hat{s} = 0.56$ (95 % conf.interv. 0.51—0.69).

The rate of exploitation is low. During the first year after tagging, fishermen recaptured only some 13 per cent of the tagged fish.

The spawning run of 1950 was estimated at 1083 fish (95 % conf.lim. 1,007—1,231) with a total weight of about 1,500 kg.

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