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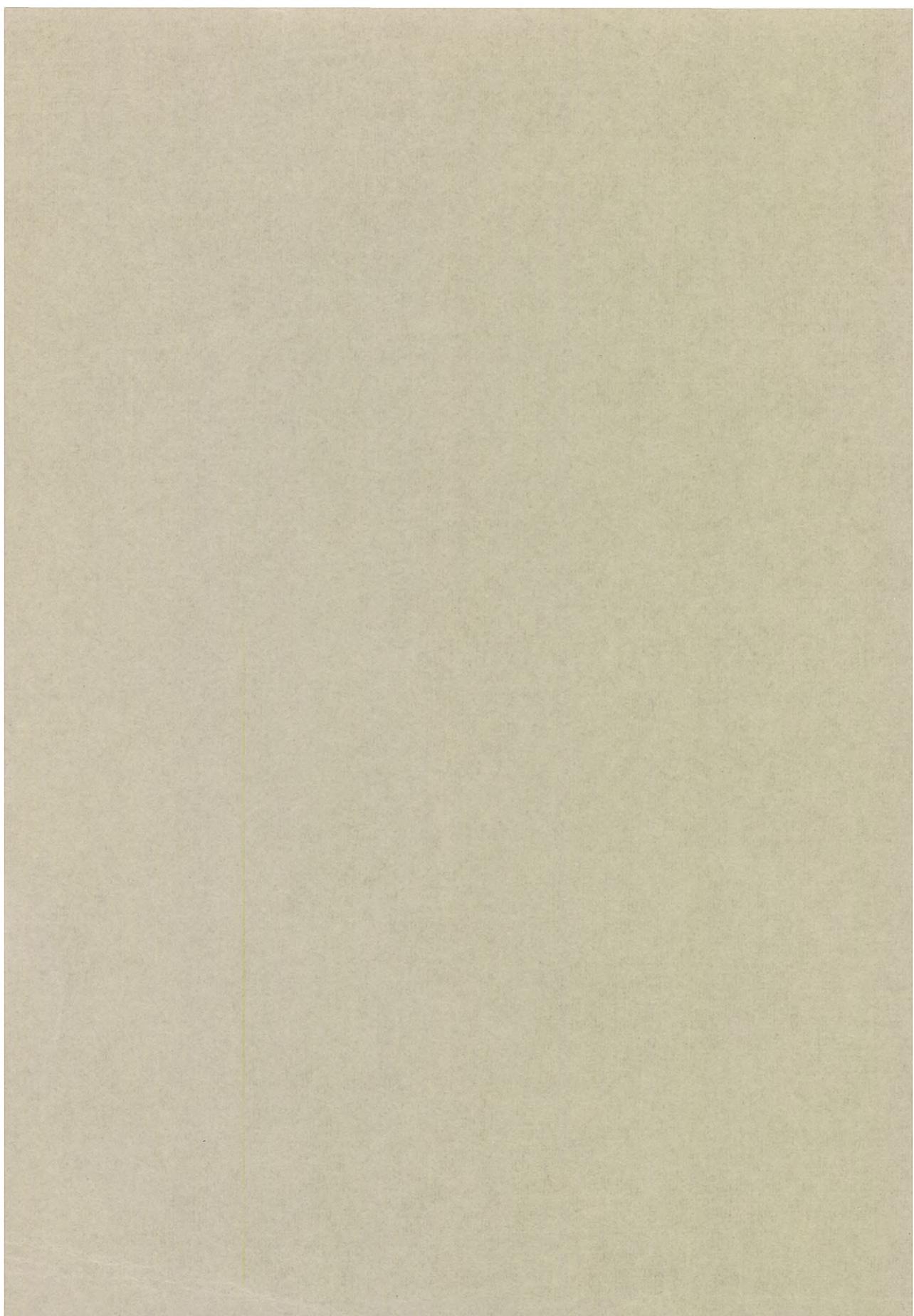
FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 50

LUND 1970
CARL BLOMS BOKTRYCKERI A.-B.



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Contents

The winter migrations of char, <i>Salvelinus alpinus</i> L., in the hydroelectric reservoirs Tunhovdfjord and Pålshufjord, Norway; <i>Per Aass</i>	5
On the ecology of the ide <i>Idus idus</i> (L.) in the River Kävlingeån, south Sweden; <i>Plutarco Cala</i>	45
Fishing pressure, growth and recruitment in a small high mountain lake; <i>T. Lindström, Å. Fagerström</i> and <i>K. J. Gustafson</i>	100
Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren, Sweden) with particular reference to interaction between <i>Coregonus albula</i> and <i>Osmerus eperlanus</i> ; <i>T. G. Northcote</i> and <i>H. Rundberg</i>	133
The food ecology and the annual food cycle in the Baltic population of fourhorn sculpin, <i>Myoxocephalus quadricornis</i> (L.). <i>Pisces</i> ; <i>Lars Westin</i>	168
Observations on the nest digging of fourhorn sculpin <i>Myoxocephalus quadricornis</i> (L.); <i>Lars Westin</i>	211

The winter migrations of char, *Salvelinus alpinus* L., in the hydroelectric reservoirs Tunhovdfjord and Pålsbufjord, Norway

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I. Introduction

The conversion into reservoirs of Scandinavian arctic or high boreal char lakes has a pronounced effect on the winter movements of the char, *Salvelinus alpinus* L. The water is stored mainly in spring and summer, while most of the draining and nearly all the lowering of the reservoirs take place in winter. Large-scale winter migrations are unknown in unimpounded lakes, where the winter dispersion of char apparently does not differ much from the autumn distribution. In reservoirs, however, the impoundments at once set off extensive and often far-ranging migrations, the char gathering upstream of the outlets and in sounds if such exist. The phenomenon is widely known, and the fishermen are quick to take advantage of the new situation. These migrations have been briefly described by AASS (1963), RUNNSTRØM (1964) and HANELL & HOLMBERG (1968) and in more detail by AASS (1965). The circumstances releasing the migrations and their extent and range are, however, inadequately known. A better understanding of the subject will have theoretical as well as practical consequences, as the altered dispersion of the char has a drastic effect on the fishing. The experiments undertaken were carried out in the lake reservoirs Tunhovdfjord and Pålsbufjord, which have long served investigations concerning the effects of impoundments on different aspects of fishing.

II. The lakes

The oligotrophic lakes Pålsbufjord and Tunhovdfjord are situated in the upper course of the River Numedalslågen, which drains the north-eastern parts of the Hardangervidda mountain area. Their position appears from Fig. 1. Another big tributary of Pålsbufjord is the River Skurdalselv. Into Tunhovdfjord runs the River Rødungselv, which originates in the reservoir Lake Rødungen. The natural catchment area of Tunhovdfjord is 1,809 sq. km, and the mean flow 42 m³/sec. (FOSSEDIREKTØREN 1932). In 1968 three

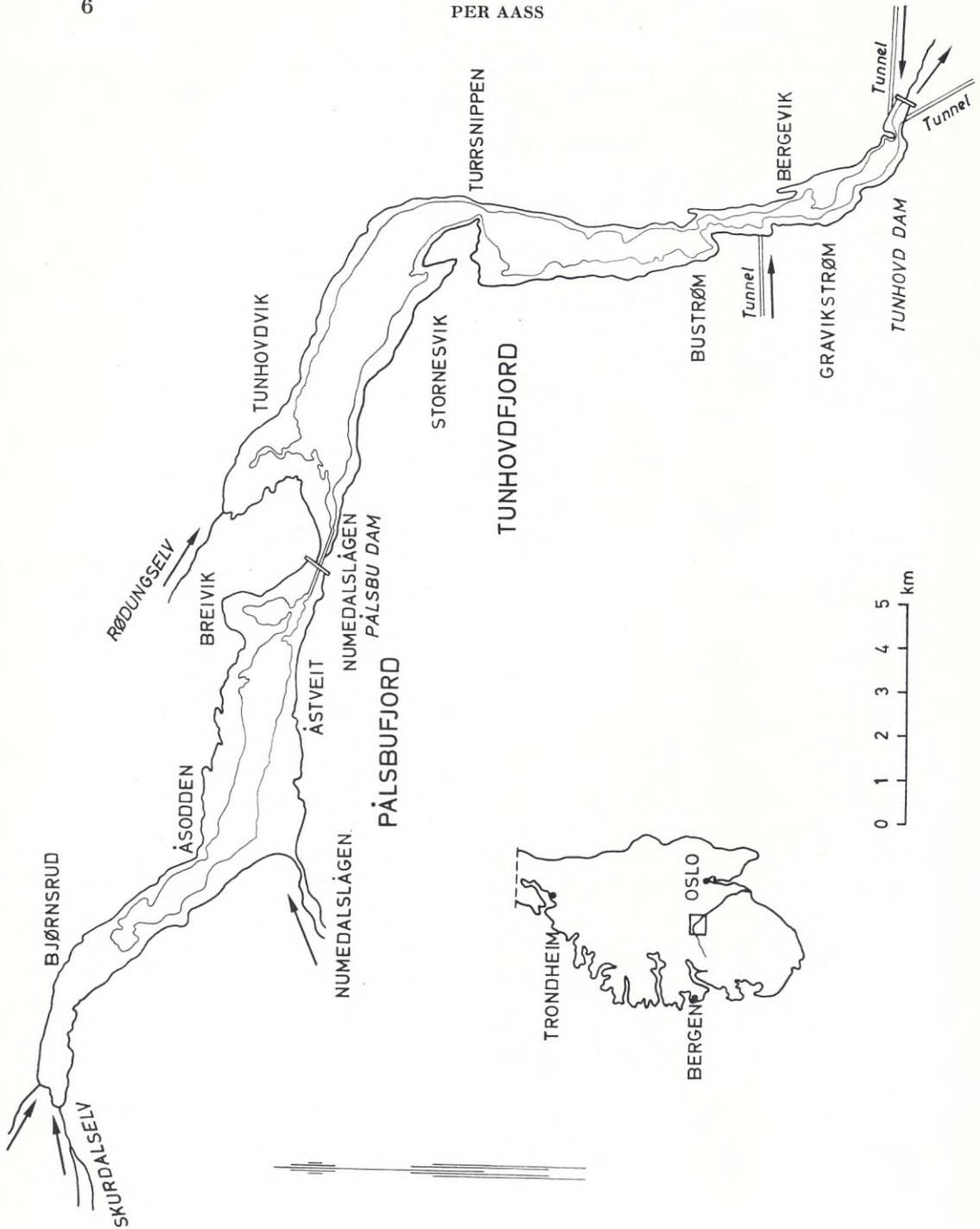


Fig. 1. The lake reservoirs Tunhovdfjord and Pålbufjord and their position. The two outlines indicate areas at maximum and minimum regulated levels. Place names of interest in connection with char winter migrations.

Table 1. Tunhovdfjord and Pålbufjord. Particulars of impoundments.

	Start of impoundment	Damming	Lowering	Annual amplitude in metres	Regulated levels metres above sea level		Areas in sq.km	
		in metres			Mini-mum	Maxi-mum	Mini-mum	Maxi-mum
Tunhovdfjord	1919	18.00	—	18.00	718.00	736.00	14.25	25.35
Pålbufjord	1927	—	9.00	9.00	—	—	—	—
	1946	12.50	—	21.50	—	—	—	—
	1958	—	12.00	24.50	726.00	750.50	5.25	19.50

small rivers running to the east and west of the lake were transferred to Tunhovdfjord by means of tunnels, the drainage area being thereby increased by 271 sq. km.

Originally Tunhovdfjord consisted of one big and two small basins, connected by short rapids. In 1919—20 the level of the lake was raised 18 metres above normal level, and in order to drain the reservoir completely the rapids were canalized, thus forming narrow sounds at low water. Pålbufjord, situated immediately above, was lowered by 9 metres below normal level in 1927—28. Later the lowering was increased and the lake level also raised by damming. Since 1958 the maximum amplitude has been 24.5 metres. Particulars of the impoundments will be found in Table 1. The reservoirs are filled mostly in spring and summer, and the water levels are relatively stable until the lowering starts in late autumn or early winter. Both reservoirs are emptied by tunnels situated close to their natural outlets and they are at their lowest in late April (Fig. 2). Tunhovdfjord serves as intake

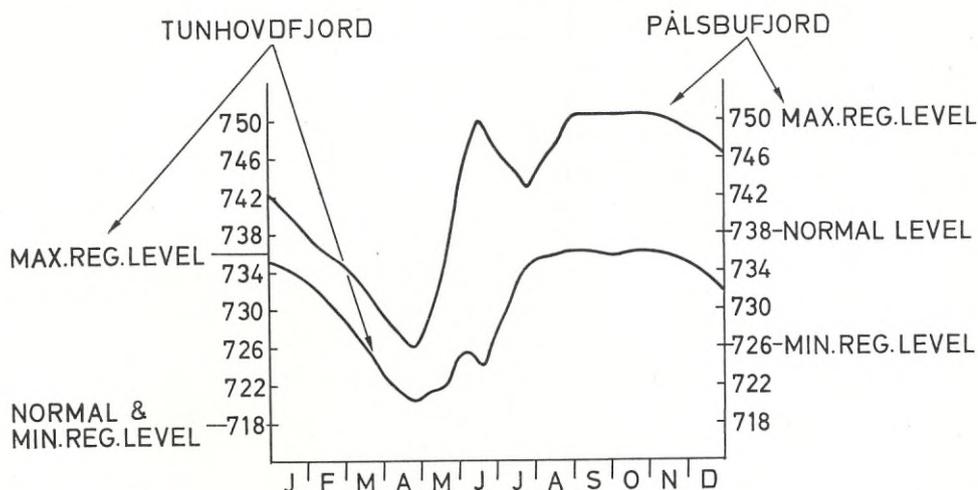


Fig. 2. Water-level fluctuations of Tunhovdfjord and Pålbufjord 1963. The lowering of Pålbufjord in June—July is due to draining to facilitate floating.

reservoir for the Nore power plant. The section of the River Numedalslågen connecting the two lakes is about 400 metres long when Tunhovdfjord is at its highest level, but lengthens to about 1,800 metres when the reservoir reaches low-water level. In winter the upper half of the riverbed is laid dry, the water running instead through the tunnel which empties in the middle of the course. Only when the reservoir in Pålbufjord has reached its original level can water run through the whole section.

Winter comes early, and shallow bays freeze in the middle of November. The main basins are mostly covered with ice from December to the first half of May.

Brown trout (*Salmo trutta* L.) was for a long time the only fish species present in both lakes. About 1915 minnow (*Phoxinus phoxinus* L.) was introduced by fishermen who used this species as living bait. In summer 1910 char fry was planted in a mountain lake that drained into the River Numedalslågen, about 35 kilometres upstream from Pålbufjord. Char was first caught in this lake in 1919 (DAHL 1920). No records exist of the first appearance of char in Tunhovdfjord, but probably they entered this lake at about the same time. That is at the start of impoundment of Tunhovdfjord. In Pålbufjord the stock was of considerable size when this lake was impounded. In both lakes char is now the predominant species, constituting about 85 per cent of the total yearly catch in weight.

III. Material and methods

During the years 1951 and 1954—68, in all 21,073 char were tagged in the two lakes and the connecting river. Of these 10,475 were tagged in winter, 8,714 in autumn and 1,884 in spring and summer. For details of number and tagging places, see Table 2 and Fig. 1.

A small home-made celluloid disc tag was used in 1951, and LEA's hydrostatic tag in 1954—55. During the winter taggings in 1956—58, difficulties over the supply of LEA tags led to comparisons with CARLIN tags (CARLIN 1955) and modifications of this type. Tags with and without an inserted wire between the tag and the attachment were tried, and some tags were also strengthened by a steel thread running along the tag. No significant difference in recapture was found between the LEA tag and the modified CARLIN tag without an intermediate link. CARLIN tags with an inserted wire gave a high first-year recapture, owing to their high tendency to fasten in nets. Reinforcing the tags did not increase the rate of recapture over the years. Different kinds of thread were also compared, *viz.* monofilament nylon, stainless steel and surgical steel. Nylon attachment gave the highest recapture rate, because of the greater tendency of the tags to fasten in nets. With the rather stiff nylon it was difficult to get the tag as close to the

Table 2. Numedalslågen watercourse. Tagging of char 1951—68.

Season	Place tagged	Number
<i>Pålsbufjord</i>		
Summer 1951	Åstveit	42
Autumn 1955—64	Åsodden	2,913
" 1965—68	Bjørnsrud	1,211
Winter 1951, 1954—64	Åsodden	1,179
" 1951, 1958—64	Near tunnel intake	1,083
" 1964	Åstveit	84
<i>Tunhovdfjord</i>		
Autumn 1955—68	Tunhovdvik	3,828
" 1965	Bustrøm	237
" 1961—64	Transferred from Tunhovdvik to different places in the lakes	525
Winter 1955—65	Near Tunhovd Dam	3,735
" 1957—65	Bustrøm	3,142
" 1957, 1963	Tunhovdvik	495
" 1961—62	Stornesvik	400
" 1961	Gravikstrøm	107
" 1964	Turrsnippen	250
<i>Numedalslågen</i>		
Spring—summer 1957—61, 1965—66, 1968		1,842

body as it was with steel thread. From 1959 onwards, only CARLIN tags without an inserted wire have been used. They are attached with double 0.3 mm stainless steel wire passed through the back of the fish in front of the dorsal fin. Anaesthetics are used in spring, summer and autumn, but not in winter.

The tagging places were selected with the intention of obtaining information on the extent and range of the movements and their importance to the fishing. They are rather few in number, because it was considered that series of long duration and populations that were to some extent homogeneous would show the general pattern and possible changes better than would many short-term experiments scattered along the lakes. The tagging was performed in the periods when it is possible to catch char in large numbers, mainly autumn and winter.

During spawning in October char was caught with gill nets. Fishing depths were about 15—20 metres in Tunhovdfjord and 30 metres in Pålsbufjord. The nets were regularly set in the afternoon and lifted early in the morning, but occasionally the occurrence of a gale meant that the nets had to stand for two or more nights. When the nets were lifted, the fish were removed one by one and placed in water, either in tubs or in the half-filled boat. Fresh water was constantly supplied. The procedure could take up to 2—3 hours, especially in windy or snowy weather, but the fish evidently took little harm. After the fish had been transported to the shore, immature and resting mature specimens and all fish with poor scales or floating belly up

were discarded. The rest were placed in immersed wooden boxes and kept for control for about a week. During the stay about 1—2 per cent of the fish died. To avoid immediate mass recapture, tagging and releasing took place when most of the commercial fishing had ended. The fish were placed in shallow water and allowed to make for deeper water by themselves. All fish in bad condition were killed.

Most of the fish tagged were males. Their well-attached scales prevent scratches and the slender and slimy bodies do not stick firmly to the nets. The females mostly get firmly entangled and stand the pressure of the meshes poorly. The slime secretion of females is less than for males and the scales are more easily lost. Most die on the nets or immediately after lifting; the rest are subject to the attack of fungi in the scars. Of 1,159 male spawners tagged in the two lakes in the years 1961—66 a total of 46 per cent were recaptured, not counting returns from the spawning places shortly after tagging. The corresponding figures for females were 285 and 23 per cent. The inferiority of the females is possibly due rather to reduced tolerance to netting than to different behaviour after release. In the winter fishing, which accounts for the bulk of the total catch, the sex ratio is very nearly 50—50. Both sexes have served to illustrate the pattern of movements, but in estimating the extent of the migrations only males have been used. Non-spawning char are also very difficult to catch or keep alive when caught on nets. The scales tend to get lost, the bodies stiffen and most of the fish die before the fungi have made any visible impact. This category was never used in tagging experiments in autumn.

The char tagged in winter were all caught from the ice with spoons baited with prawn, worm or artificial flies. Both sexes were tagged, as in winter they may be difficult to separate by external characters and their bodies are equally slimy and unhurt by capture. The fish were tagged immediately, without being placed in water, which in the low temperatures soon becomes undercooled and is plainly detrimental to the char. They were rushed to the tagging table, a portable wooden box warmed by a primus stove.

Sometimes a tent was used for the comfort of the tagger, but the time taken to run to a permanent tagging centre might easily be too long. The climatic conditions were often unfavourable, and the technical difficulties could be considerable. Tagging was performed in temperatures mostly between minus 10—20°C, occasionally as low as minus 34°C, and sometimes gales tore the tent. After tagging, the char was put through a hole in the ice. Apparently the fish took no harm from the cold, even if they became glaciated during the short stay in the air. Of 4,258 char tagged in Tunhovdfjord during the winters 1961—65 the number recaptured was 1,971 or 46.3 per cent. The corresponding figures for males tagged in the autumn of the same years were 830 and 398 or 48.0 per cent. In shallow water tagged char could be observed through holes in the ice. They behaved like untagged

ones, and very soon became interested in the bait again. The shortest time recorded between tagging and recapture was a quarter of an hour.

In the river char was caught in spring and summer with baited spoons and kept in running water for control before tagging. In this case, too, both sexes were used.

When the tagging started, the short-term positive effects of the impoundments (DAHL 1926 & 1932) had expired (HUITFELDT-KAAS 1935, AASS 1957) and the lakes were crowded with the dwarfed char characteristic of many reservoirs. Preliminary experiments showed that fish shorter than 18 cm gave significantly lower returns than did bigger fish and were mostly caught in nets although there was also extensive fishing with hooks. The char tagged in Pålshovfjord were mostly of the size 22—28 cm and in Tunhovdfjord 20—25 cm. The age has varied considerably according to fluctuations in year-class strength.

The tags carried an inscription requesting the fishermen to report recapture, a reward being promised. From the start of the experiment the fishing public were also informed by posters, letters and personal communications. During the season controllers were stationed at the main fishing places and arrangements were also made for the handing in of tags at local shops. Twice a year, after the end of the summer and winter seasons, chalet owners were visited in search of tags and of information. Other persons known to have fished in the lakes were contacted by post. In spite of all these efforts, some tags were not handed in, but so far as we know their recording would not have altered the general picture of the migrations given in what follows. Their main trend is illustrated by a few characteristic years, and the mass of data in evidence of the description is not included. Exceptions from the general pattern are, however, dealt with. To supplement the tagging experiments with fishing statistics, the controllers recorded the catches daily or three times a week. The lakes and river are rather heavily exploited; fishing efforts, measured as daily visits, amount to about 12,000 a year. The winter fishing with spoon attracts most fishermen, but char are fished the year round, nets and fishing otter also being important gear. There is an active search for fish and concentrations of char are soon discovered. Their movements help to enable an impression of the migrations to be formed.

IV. Winter migrations in Lake Tunhovdfjord

Early winter movements

Char for the autumn taggings have chiefly been caught at the spawning places all round Tunhovdvik at the upper end of the lake. When released the fish have returned quickly to the original site of capture. After spawning

is finished in the second half of October, the concentrations of char at the spawning places slowly disperse. The first recaptures of spent fish indicate that the movements immediately following spawning are rather short, though a few stray fish are caught far away. The char move in great numbers into the upper littoral from the spawning areas along the shore or on shallows out in the lake. Sheltered coves with muddy bottom are preferred. When the bays and coves freeze up in the middle of November, a greater number of mature fish are found in shallow water than at any other time of the year. To illustrate the accumulation, the fishery in Bergevik, a little bay with an area of about 4—5 hectares and a maximum depth of about 2 metres, may be mentioned. The catch here, made in few weeks, may amount to 3,000 char. The proportion of spent fish heading for the littoral cannot be determined, as the ice conditions restrict fishing. The concentration of old fish in the upper few metres is of short duration. Most withdraw to deeper water from the middle of December. This very often coincides with a decline in the penetrability of the ice by light, caused either by a cover of snow or by growing thickness.

Simultaneously with the withdrawal from shallow water, char begin to accumulate just above the tunnel intake near the Tunhovd Dam. Ice fishing on a small scale starts here in the second half of December. The catch gradually increases, generally attaining its maximum during the last days of February. Thereafter the yield decreases rather rapidly, but in most years fishing continues until the end of April (Table 3). Owing to changes in ice conditions the fishing area shifts a few hundred metres during the winter, but it never measures more than about 100×150 metres. It is evident that char must be moving into this and the other main winter fishing places, all situated in the southern part of the lake. Most probably the fish that appear first come mainly from localities nearby, but only one tagging experiment directly showing this has been carried out. In this region spawning places are small and scattered and the char are difficult to come by in autumn. Spawners tagged in 1965 at Bustrøm, close to the fishing places, were recaptured earlier in winter than were char tagged in more

Table 3. Tunhovdfjord. Estimated numbers of char caught at Tunhovd Dam in winters 1960/61—1966/67.

Year	December	January	February	March	April	May	Total
1960/61	500	3,600	10,700	7,000	1,450	—	23,250
1961/62	750	4,750	6,900	4,300	1,550	100	18,350
1962/63	100	2,900	4,500	4,900	1,600	—	14,000
1963/64	900	2,050	1,300	500	200	—	4,950
1964/65	800	1,900	5,000	4,300	500	—	12,500
1965/66	1,400	7,500	7,300	10,250	900	50	27,400
1966/67	1,600	5,100	10,200	6,400	1,000	—	24,300

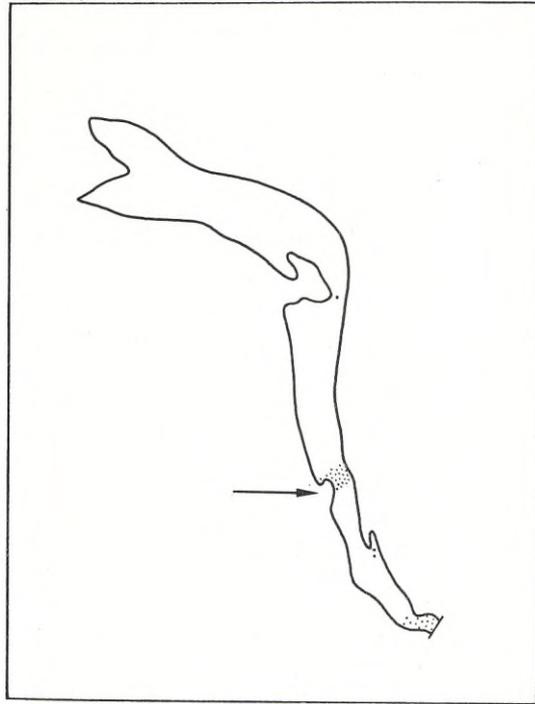


Fig. 3. Recaptures in winter 1966 of char tagged as spawners at Bustrøm October 1965. On all maps arrows indicate tagging place and a dot denotes one recapture. The recaptures are more concentrated than the figures indicate.

distant parts. The rate of winter recapture was high, but all the 1966 recaptures but one were made in the same part of the lake, indicating that the southern spawning populations move regularly in winter though not very far (Fig. 3). Through winter tagging it may also be possible to trace the region where the mature fish start their migration. The homing at their spawning areas is rather strong in the case of Tunhovdfjord char. Fish tagged near the Tunhovd Dam in January are recaptured as spawners mostly in the lower third of the lake, an indirect proof that the majority of the early entries belong to local populations.

Downstream migration

The growth in the catch at the Tunhovd Dam during midwinter is accompanied by an increased recapture of fish tagged as spawners at Tunhovdvik at the opposite end of the lake. From the upper part of Table 4, it will be seen that the recaptures are made mainly in February and March, the two months which account for the greater part of the total catch. Apparently char belonging to the spawning populations of the northern and largest basin of the lake constitute an increasing — possibly a predominant — part of the fish concentration above the dam as the winter proceeds.

Table 4. Tunhovdfjord. Winter recaptures 1960—67 at Tunhovd Dam, Bustrøm and Turrsnippen of char tagged as spawners at Tunhovdvik.

Year	Jan.	Feb.	March	April	May	Total
Tunhovd Dam						
1960	—	2	5	3	1	11
1961	2	16	11	3	—	32
1962	1	11	11	3	—	26
1963	4	3	5	2	—	14
1964	1	2	—	—	—	3
1965	—	2	3	—	—	5
1966	1	1	7	1	—	10
1967	3	7	5	2	—	17
	12	45	47	14	1	118
Bustrøm						
1960	4	2	22	16	1	45
1961	1	6	18	23	1	49
1962	—	4	17	17	—	38
1963	—	1	43	8	—	52
1964	10	14	5	4	—	33
1965	—	8	13	2	—	23
1966	—	3	10	7	—	20
1967	—	9	15	4	4	32
	15	47	143	81	6	292
Turrsnippen						
1960	—	—	2	—	—	2
1961	—	—	—	1	—	1
1962	—	1	—	—	—	1
1963	—	—	—	1	—	1
1964	—	5	13	4	—	22
1965	—	—	1	—	—	1
1966	1	—	2	—	—	3
1967	1	—	1	—	—	2
	2	6	19	6	—	33

The facts suggest that a migration from north to south takes place regularly every winter. The decreasing yield from the beginning of March is due to hydrological conditions and not to a reduction in fishing efforts. The fishermen are rather conservative and do not move to another fishing place until the downward trend is well established.

The place accounting for the greatest winter catch is situated at Bustrøm, about 6 kilometres above the Tunhovd Dam. Fishing starts as soon as the lake is covered, but during the first months the yield is inconsiderable. Normally a sharp increase in the catch occurs in late February and the daily maximum is obtained in the second half of March. April may also provide good fishing, but by the time the ice breaks in May the yield has for some time been insignificant (Table 5).

The interdependence of the fishing at the Tunhovd Dam and at Bustrøm is striking. When the yield starts to decline at the Tunhovd Dam, it improves

Table 5. Tunhovdfjord. Estimated numbers of char caught at Bustrøm in winters 1960/61—1966/67.

Year	Dec.	Jan.	Feb.	March	April	May	Total
1960/61	600	2,500	7,700	13,600	9,100	300	33,800
1961/62	550	1,050	3,200	9,000	8,800	500	23,100
1962/63	150	600	2,150	10,300	3,100	300	16,600
1963/64	500	4,750	7,850	4,100	1,900	100	18,300
1964/65	500	1,500	7,500	14,400	3,200	1,000	28,100
1965/66	100	1,800	10,300	19,800	6,000	300	38,300
1966/67	600	2,000	15,000	15,300	8,300	2,300	43,500

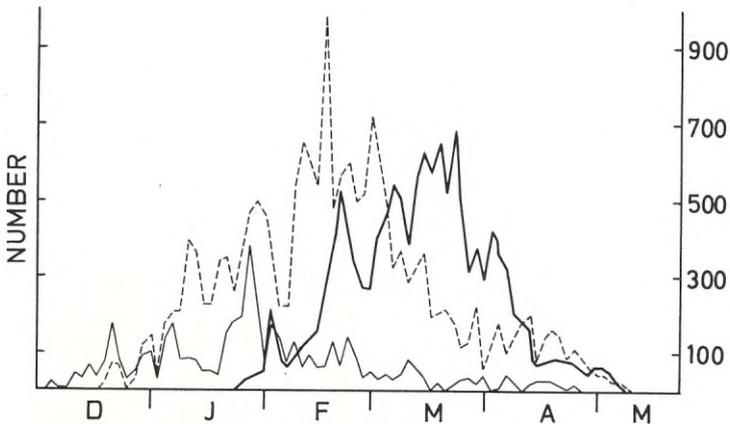
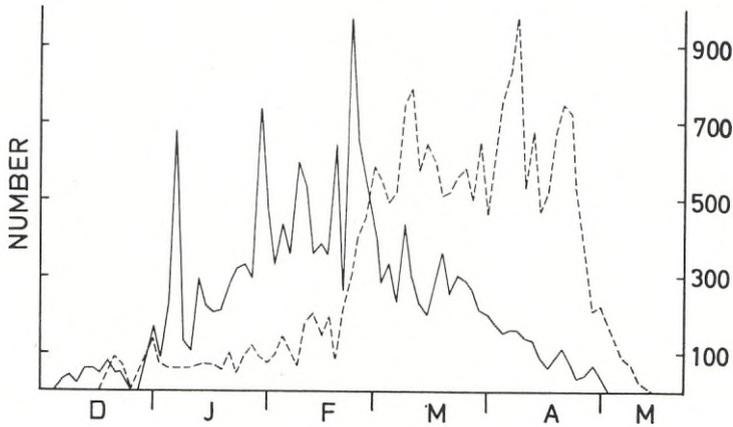


Fig. 4. Upper part. Number of char caught during winter 1961/62 at Tunhovd Dam and Bustrøm. Lower part. Number of char caught during winter 1963/64 at Tunhovd Dam, Bustrøm and Turrsnippen. The catches of two days are combined. Tunhovd Dam, - - - - Turrsnippen. —

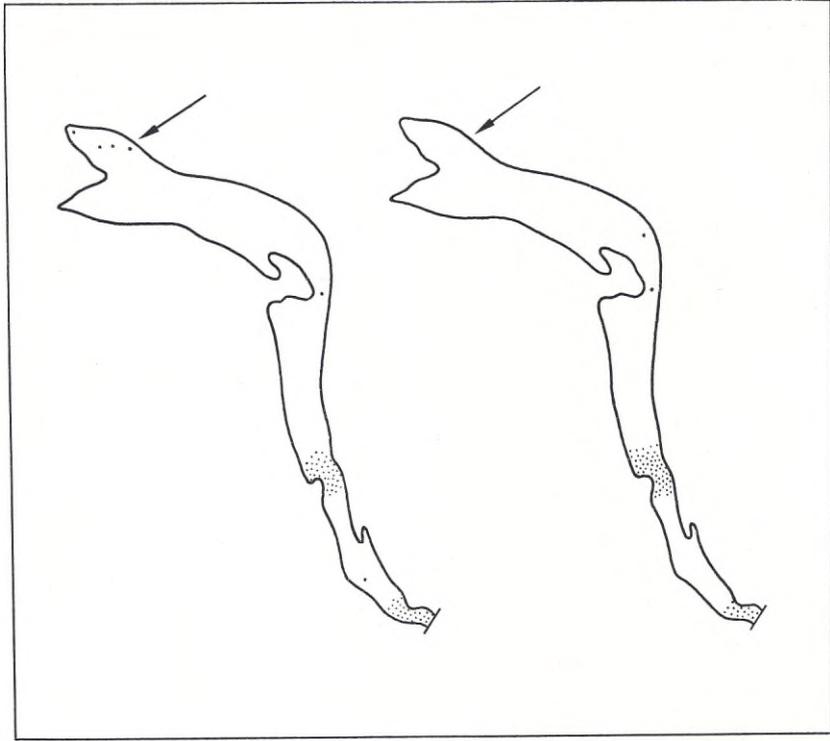


Fig. 5. Winter recaptures 1962 (left) and 1963 (right) of char tagged as spawners at Tunhovdvik, October 1961 and 1962.

greatly at Bustrøm (upper part of Fig. 4). The large number of recaptures of fish tagged in the north makes it evident that the fishery at Bustrøm, too, is largely maintained by char migrating southwards, and consequently the fish caught at the two places must in part belong to the same spawning populations. Fig. 5 shows the winter recaptures in 1962 and 1963 of spawners tagged at Tunhovdvik. In contrast to the Bustrøm tagging, Fig. 3, the recapture at the tagging place is insignificant.

During the fishing season the situation at the Tunhovd Dam and Bustrøm is characterized by a water velocity that is above the average for the reservoir. The currents formed at these places attract the char and the resulting concentrations form the basis of the rich fishing which develops. At high water early in winter the char can pass unimpeded from north to south. There are no currents strong enough to stop the fish, except at the intake near the dam. Some fish may interrupt their downward movement at Bustrøm, but both the fishing and the number of recaptures indicate that normally the char pass on. Tagging shows that many char that stop at Bustrøm in January and most of February are only halting on their way

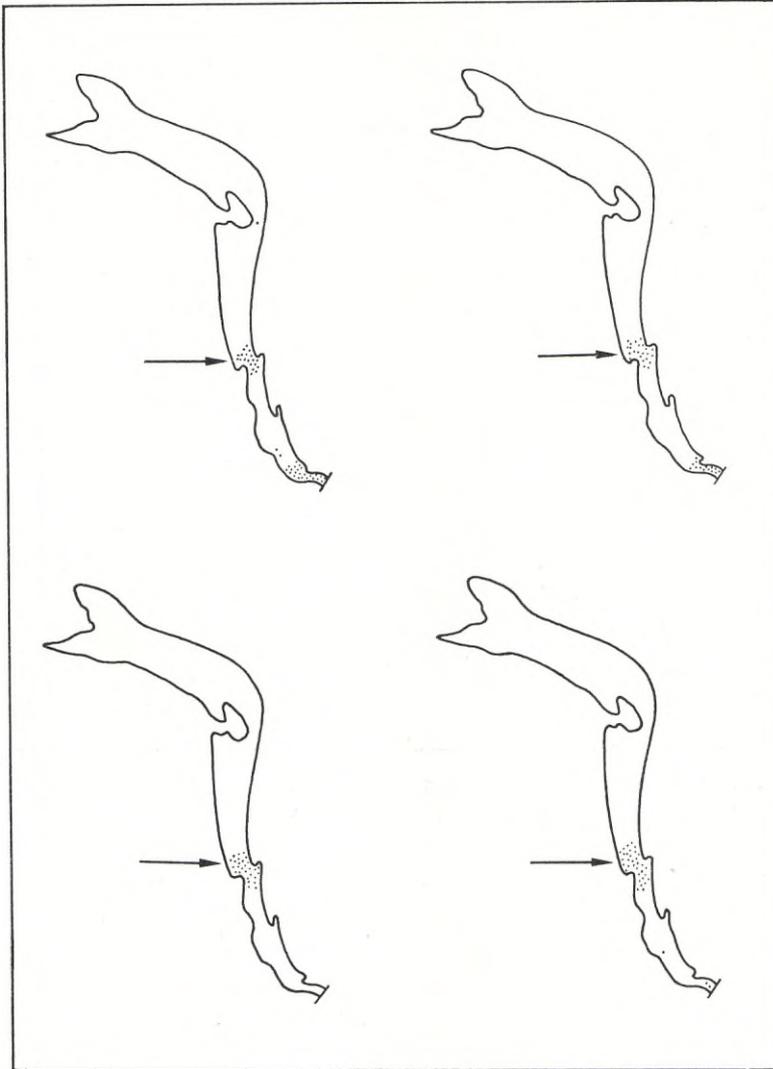


Fig. 6. Winter recaptures of char tagged at Bustrøm in January and March 1961 (upper and lower left) and 1965 (upper and lower right). Only returns from the tagging winters are marked off.

to the dam (upper part of Fig. 6). The proportion of fish permanently remaining at Bustrøm depends on the height of the water, and this is why the tagging experiments may give slightly different results in different years, *e.g.* 1961 and 1965.

When the reservoir is lowered during the winter a current is formed at Bustrøm, which is one of the old rapids transformed by canalization into a narrow strait at low water. In most years the current is observable from

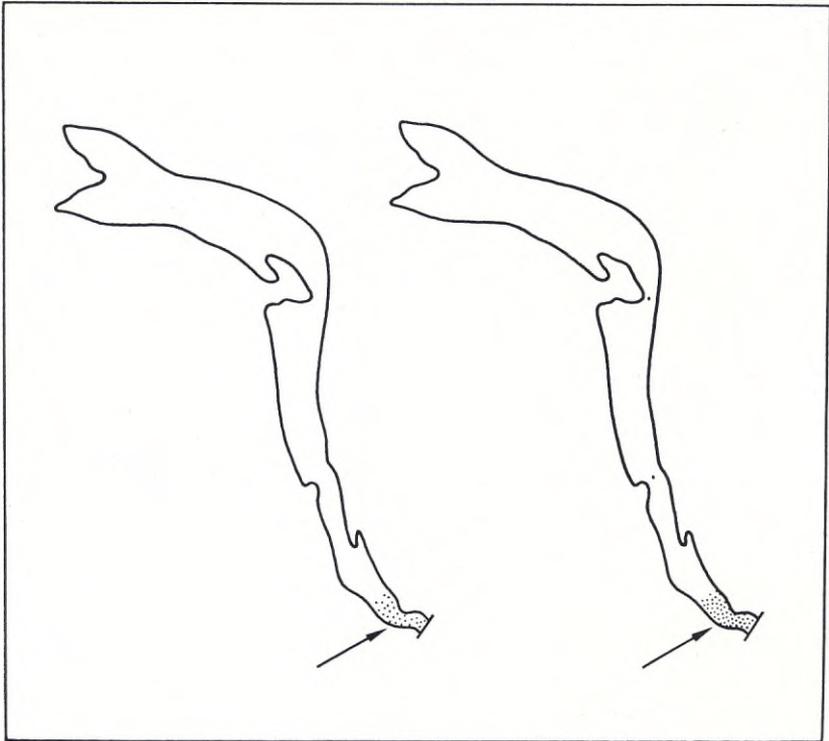


Fig. 7. Winter recaptures of char tagged at Tunhovd Dam in March 1962 (left) and 1963 (right). Returns the same winters.

the end of February. Tagging experiments at Bustrøm in March show the char to be strongly attached to the current (lower part of Fig. 6). Only a few stray fish move with the water to the dam, and char returning to the main basin late in winter have never been recorded. The fish standing above the Tunhovd Dam show the same preference for the current, although a few stray char have been recaptured later in the winter in currents higher up in the lake (Fig. 7).

Another of the former rapids, Gravikstrøm, is situated between Bustrøm and the Tunhovd Dam. The current here is less concentrated, and the tendency of the char to stop is not as great as at the places mentioned above. A small fishery develops in middle of winter, just when the decrease sets in at the Tunhovd Dam, and dwindles when the fishing at Bustrøm reaches its peak. The yearly catch may amount to 3,000—3,500 char. Returns from the Tunhovdvik taggings prove the fish to be partly of northern origin. A tagging experiment carried out in March 1960 showed a winter movement towards the dam. Recaptures from outside the tagging area were all made near the tunnel intake (Fig. 8).

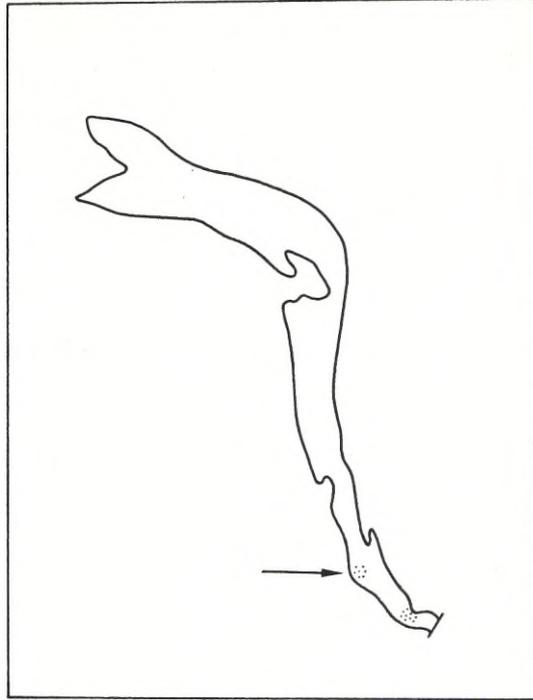


Fig. 8. Winter recaptures of char tagged at Gravikstrøm in March 1960. Returns the same winter.

Water level and char concentration

The tendency of the char to make a permanent stop at Bustrøm in the latter half of the winter must be the reason why the catch decreases drastically in the lake further south. Supply from the northern basin is severely reduced and the local populations are small and have been exploited through the whole season. Thanks to the close connection between water level and fishing output at Bustrøm, it is possible to predict when the change will occur. Usually the abrupt increase in catch starts when the reservoir is down 4—5 metres, but in some years the reaction is delayed until the lowering has reached 7—8 metres. The best fishing takes place when the reservoir is 8—10 metres below highest regulated level. This pattern is reflected in the recapture of northern spawners. Apart from a few stray individuals, tagged fish enter the catches when the reservoir is lowered 4 metres and most recaptures are made when the water level is down by 8—10 metres. Fig. 9 shows the relation between water level and recaptures at Bustrøm in the winters 1956—68.

The increase in both catch and recaptures is entirely dependent on the height of the water level, not on the time. This is best illustrated by the events in 1964. The reservoir was drained exceptionally early and rapidly to enable the Tunhovd Dam to be rebuilt, and the water level normal for

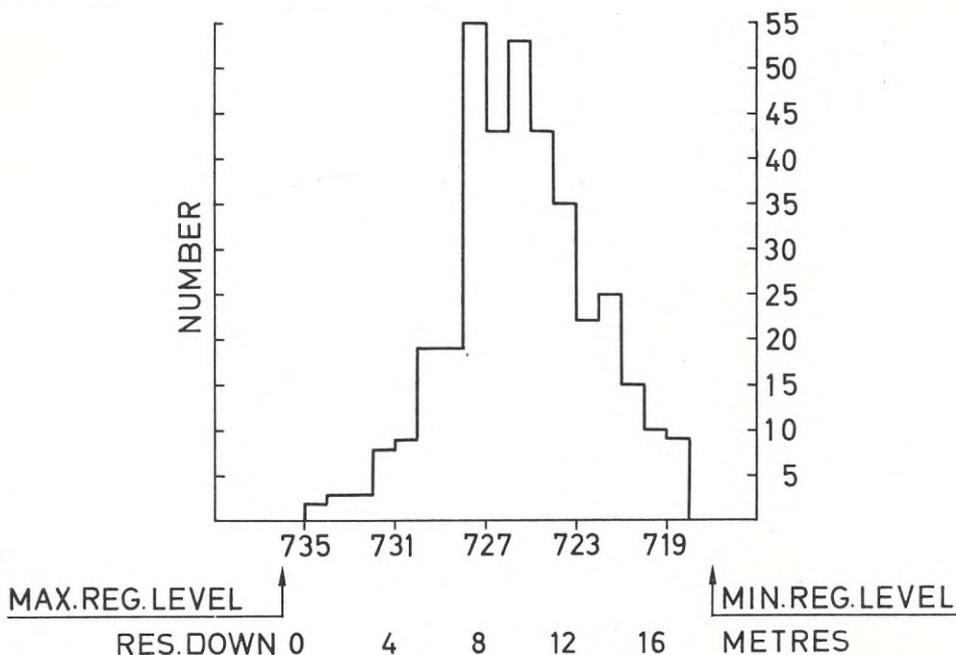


Fig. 9. Relation between water level and number of returns made at Bustrøm during the winters of 1956—68. The char were tagged as spawners at Tunhovdvik.

March—April was reached in the first half of February (Fig. 10). This put forward the catch at Bustrøm of char tagged in the north by more than a month, the majority being caught in January and February against March and April in an ordinary year (middle of Table 4). At the Tunhovd Dam only three northern spawners were recaptured, and the proportion between recaptures at the two places was 1: 10, compared with an average of 1: 3. Obviously very few fish got through to the dam in the winter of 1964. This is also reflected in the catch above the dam. Besides reaching its peak period as early as January, it was exceptionally small compared with the winter total for the lake. Comparisons between the numbers caught in the different years should be made with caution, in view of the varying strength of the year classes.

The winter fishing at Bustrøm also started exceptionally early in 1964 (Table 5). As only a fraction of the migrating population succeeded in getting down to the dam, a record catch was anticipated, but the expectations were not fulfilled. After a short peak period in February, which as usual coincided with a draw-down of 8—12 metres, the daily catches deteriorated in late winter as never before. As a result, the total winter catch at Bustrøm was well below the average for the period 1960/61—1966/67. Without doubt the unexpected outcome was due to a fishery

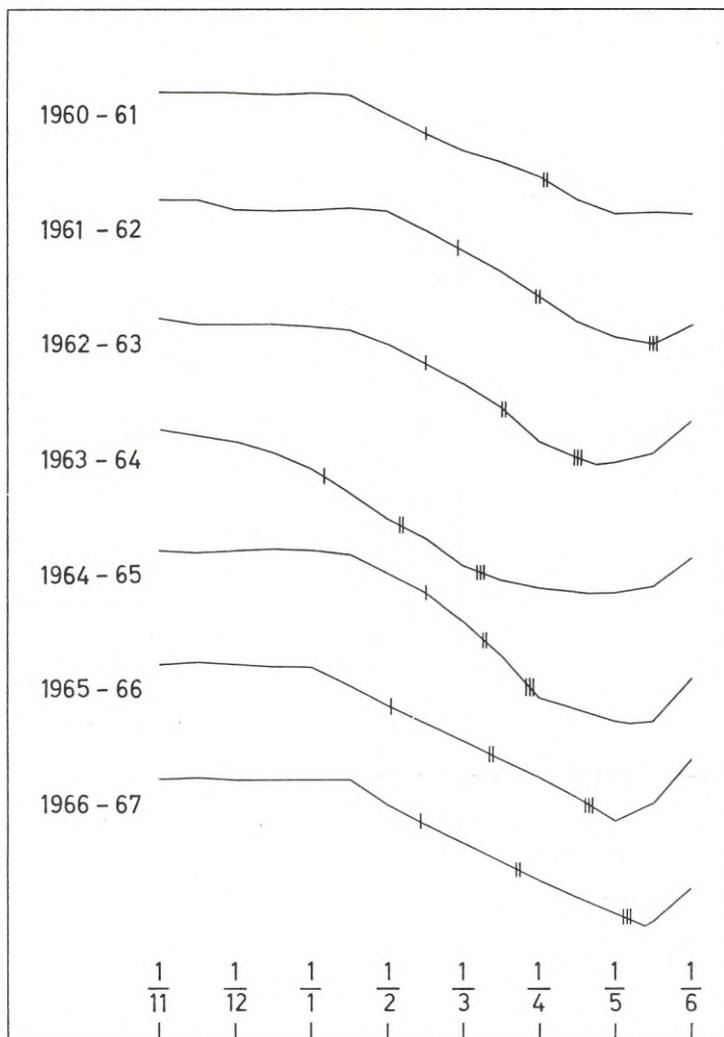


Fig. 10. Winter water-level fluctuations in Tunhovdfjord 1960/61—1966/67. Vertical lines indicate lowering of the reservoir by 5, 10 and 15 metres.

developing at a place called Turrsnippen, situated 5—6 kilometres to the north of Bustrøm. Here the lake narrows, and as a result of the great low-water flow a current was formed earlier in the season than usual. In previous winters the fishing at this place had been insignificant, the total catches amounting to only a few hundred fish. But now the char concentrated in great numbers in the strait. In consequence many fishermen were attracted, and the total catch in 1964 was estimated at about 13,000 char (Table 6). Many fish tagged as spawners in Tunhovdvik were recaptured

Table 6. Tunhovdfjord. Estimated numbers of char caught at Turrsnippen in winters 1960/61—1966/67.

Year	Dec.	Jan.	Feb.	March	April	May	Total
1960/61	—	—	—	100	100	—	200
1961/62	—	—	—	100	300	100	500
1962/63	—	—	—	—	250	—	250
1963/64	—	200	3,100	7,400	2,300	—	13,000
1964/65	—	—	200	2,900	2,100	—	5,200
1965/66	—	—	—	1,500	3,000	300	4,800
1966/67	—	—	—	700	1,600	200	2,500

at Turrsnippen (lower part of Table 4). Winter recaptures for 1964 are indicated in Fig. 11, and the distribution should be compared with winters with ordinary draining, such as 1961/62—1962/63, in Fig. 5. Undoubtedly a great proportion of the char accumulating at Turrsnippen in 1964 belonged to the northern spawning populations, which normally concentrate near the dam and at Bustrøm. Once halted, the char behaved just as at the other currents and stayed on for the rest of the winter, only a minority moving further down the lake (Fig. 12). Once more the interdependence of the fishing places is demonstrated. Just as the concentration of fish at Bustrøm

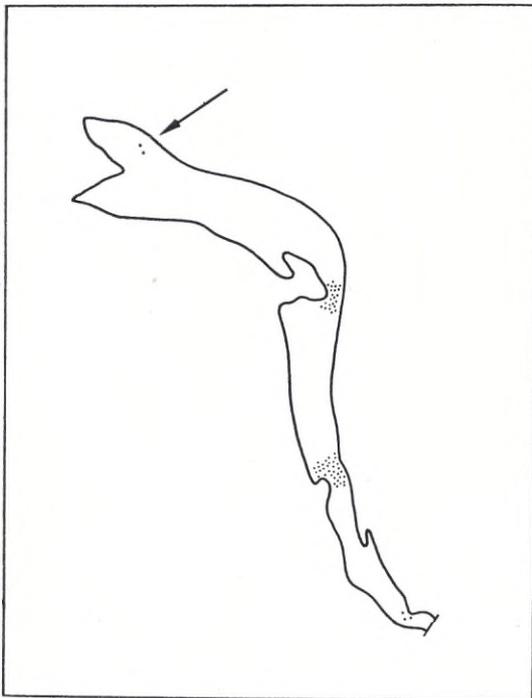


Fig. 11. Winter recaptures 1964 of char tagged as spawners at Tunhovdvik October 1963.

starts the decline in the fishing at the Tunhovd Dam, so the accumulation at Turrsnippen marks the turning point for the Bustrøm fishery (lower part of Fig. 4).

In the winter of 1965 the draining followed the traditional pattern until the middle of January, when the reservoir was lowered faster than ever before (Fig. 10). Near the Tunhovd Dam the fishing started and developed as usual, the draining apparently having occurred too late to stop the early migrants arriving from Bustrøm. Then followed a quick deterioration, and though the yield at Bustrøm did not suffer to such a degree as in 1964, the distribution of recaptures indicated that the char stopped at Bustrøm rather early in the season. Once again a considerable fishery developed at Turrsnippen, but this time at a later date and the total catch was smaller than the year before. Since the rebuilding of the dam, the draining has followed the normal pattern. Owing mainly to a great increase in fishing intensity, aroused by the two good years, the catch at Turrsnippen still exceeds the earlier years. There is, however, a distinct downward trend.

The facts mentioned suggest a close connection between currents and accumulations of char, and this is confirmed by a further circumstance. The local fishermen complain of a regular reduction in catches during Saturdays and Sundays, when draining is reduced because industries need

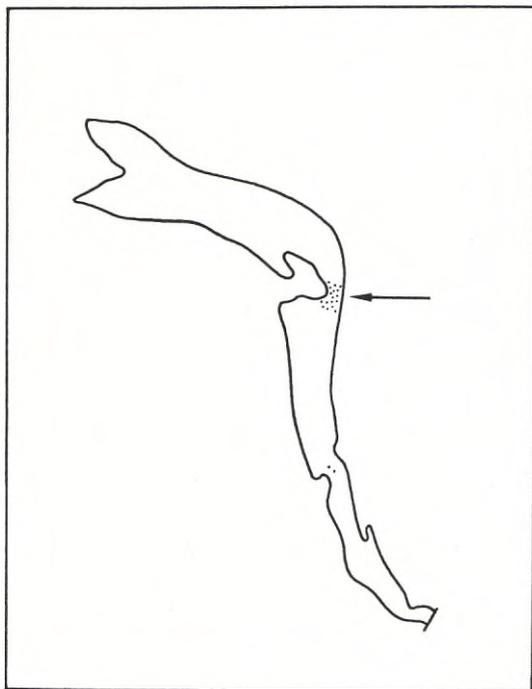


Fig. 12. Winter recaptures 1964 of char tagged at Turrsnippen in March 1964.

Table 7. Tunhovdfjord. Mean number of char caught per hour winters 1960—63. Experimental angling at Bustrøm.

Period	Number of hours	Mean number, weekdays	Mean number, weekends
22/2—31/3 1960	354	9.0	7.7
20/2—29/3 1961	326	6.5	4.9
21/2—30/3 1962	374	4.4	3.5
22/2—29/3 1963	349	3.4	3.3

less power. For many years a control fishing with spoon was carried out at Bustrøm six days a week, but only in the years 1960—63 were Sundays included. Every year the same two anglers were employed, the fishing duration, time of day, and locality being kept unchanged. The fishing results during the peak period when according to taggings the char make a permanent stop are outlined in Table 7. The catches per effort are significantly smaller during weekends, thus bearing out the fishermen's complaint. The reduction may be due to an increased total fishing effort, since during weekends more anglers take part than on weekdays. But the holiday fishers are of course less efficient than the local fishermen, as they are inexperienced and fish shorter hours. The fishing area is adequate, and it is doubtful whether the weekend influx had any effect on the control fishery. If it did not, the results suggest a weaker affinity between fish and current during weekends. Apparently the fish do not leave the current; had that been the case char tagged at Bustrøm in March would have been recaptured all round the lake the same winter, and this was not the case. When the water velocity is reduced, the char possibly disperse more freely in the water volume. During heavy draining the char tend to concentrate at a depth of about 8—10 metres, well above the bottom.

Speed of migration

The slow increase in the number of char caught, tagged and untagged, in the currents during early winter, imply that the char do not set out in one big shoal. The migration takes place over a period of several months, with maximum arrival in the southern region about early March. It is more difficult to establish when the bulk of the char leave the northern basin. Winter recaptures in Tunhovdvik of spawners tagged at the place in autumn are too few to show any trend, and for that purpose winter tagging was carried out on two occasions. In April 1957 and February/March 1963, respectively, 255 and 240 char were tagged. In all, 22 were recaptured during the winter they were tagged, but in each case close to the tagging

locality. The majority of the migrating fish had probably left the shores already, *i.e.* not later than the middle of February. This means that the fish take at least 2—3 weeks on their way to the southern region, a linear distance of 15—20 kilometres. Another indication of the travelling speed is given by the changing yield in the southern part of the lake. When all the moving char stop at Bustrøm, it takes barely a week before the effect is felt at the Tunhovd Dam. The distance between the places is 5—6 kilometres. At Stornesvik on the western shore near the middle of the lake, 200 char were tagged both in February 1961 and February 1962; 24 were recovered near the tagging place, in most cases fairly soon after being released, 3 had crossed the lake and 8 were recaptured at Bustrøm, 4—9 weeks after tagging. The small number of recaptures suggests that at this place, too, only a minority of the migrating fish had not left by the middle of February.

Size of migrating char

The existence of large-scale winter migrations can be demonstrated with certainty only for the tagged size group, *i.e.* fish measuring 20 centimetres or more. If the migrating population consisted of a well-defined size group, its departure and arrival could be observed by analysing the local catches, provided that the moving fish regularly entered into the catches. Regular length measurements of catches during the winter season were made at the various currents between 1955 and 1968. The results differ little from place to place and from year to year, char sized 20—25 centimetres constituting the bulk. The percentage length distribution at Bustrøm, where in all 82,610 char were measured, is listed in Table 8. To judge from this distribution, it is mainly the bigger fish that move into the currents. If this is the case, their departure should be observable as a reduction of this size group in the remaining population. Measurements made in March 1963 at Tunhovdvik and Bustrøm — Tunhovd Dam show a distinct difference in size distribution in north and south (Table 9). Small fish predominate in the northern bay, bigger ones in the currents. The result may be due to an uneven distribution of young fish belonging to the rich year class 1960. The investigation was repeated in 1966—68, when in all 2,499 char were measured in Tunhovdvik. In these years there was no significant difference in the mean length of northern and southern catches. This would mean that fish of all sizes left the northern basin. The selectivity of the gear, however, renders an interpretation of the result difficult. The small fish are not afraid of the spoon — on the contrary it is often difficult to avoid catching large numbers. But it can be clearly observed through the ice that the big fish dominate the small ones, which have little chance of being hooked until their superiors are reduced in number. As long as there exists

Table 8. Tunhovdfjord. Length distribution in per cent of char caught at Bustrom in winters 1955-68.

	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
Number measured . .	345	1,218	2,270	2,921	2,611	22,998	25,534	5,577	3,308	3,164	4,972	3,023	2,408	2,261
10-10.9 cm	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1
11-11.9 "	—	—	—	—	—	—	—	—	0.2	—	—	0.1	—	0.4
12-12.9 "	—	0.2	0.1	—	—	0.1	—	1.5	1.0	0.2	0.6	0.2	0.3	1.0
13-13.9 "	0.3	0.2	0.3	0.2	0.1	0.2	0.1	0.9	1.4	0.5	1.0	0.7	0.9	1.2
14-14.9 "	0.3	1.3	0.4	0.4	0.4	2.0	0.3	1.5	2.8	0.9	1.8	1.0	0.9	0.8
15-15.9 "	0.9	2.7	2.6	1.0	1.0	4.3	0.6	1.7	3.1	1.5	3.2	1.5	1.2	1.3
16-16.9 "	2.3	6.7	7.0	1.6	1.4	4.1	1.0	1.8	3.5	2.3	7.2	4.2	1.7	2.6
17-17.9 "	4.4	7.3	11.9	4.1	3.8	3.7	2.4	1.8	3.6	4.0	8.2	8.4	4.6	4.4
18-18.9 "	4.4	8.8	10.5	8.3	5.8	3.7	2.9	1.7	3.1	6.3	13.5	9.8	7.9	7.2
19-19.9 "	10.7	5.9	10.6	16.8	12.7	6.7	5.6	1.4	2.2	7.9	9.6	12.0	12.3	8.7
20-20.9 "	6.1	6.6	11.6	23.1	21.9	13.2	8.8	1.5	2.2	8.8	10.2	13.6	16.2	11.5
21-21.9 "	4.4	8.7	8.9	15.5	27.5	21.3	12.0	3.2	3.1	8.9	10.1	15.6	20.3	19.8
22-22.9 "	4.1	9.0	8.2	11.1	17.1	25.8	25.4	13.0	4.8	10.6	10.6	13.2	18.1	20.3
23-23.9 "	7.8	10.2	6.8	7.7	5.4	11.1	24.0	31.9	12.3	10.9	10.5	7.2	9.3	13.7
24-24.9 "	12.6	8.6	6.8	4.4	1.3	3.2	11.6	26.1	26.7	13.1	7.2	6.2	3.7	4.7
25-25.9 "	10.1	9.0	6.7	2.8	0.9	0.5	3.7	10.0	19.1	12.1	3.5	3.8	1.9	1.7
26-26.9 "	13.3	6.7	3.5	1.7	0.4	0.1	1.1	1.6	8.0	7.4	1.9	1.5	0.5	0.4
27-27.9 "	8.7	4.7	2.2	1.0	0.2	—	0.3	0.3	2.2	3.4	0.7	0.8	0.2	0.2
28-28.9 "	5.8	1.7	1.4	0.3	0.1	—	0.2	0.1	0.6	0.9	0.2	0.2	—	—
29-29.9 "	2.6	1.1	0.5	—	—	—	—	—	0.1	0.2	—	—	—	—
30-30.9 "	1.2	0.4	—	—	—	—	—	—	—	0.1	—	—	—	—
31-31.9 "	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—

Table 9. Tunhovdfjord. Length distribution in per cent of char caught by angling in March 1963.

	Tunhovd- vika	Bustrom	Tunhovd Dam
Number measured	907	3,308	1,025
10-10.9	0.8	—	—
11-11.9	1.8	0.2	0.2
12-12.9	5.3	1.0	1.8
13-13.9	4.8	1.4	1.8
14-14.9	5.5	2.8	2.0
15-15.9	12.1	3.1	3.4
16-16.9	12.8	3.5	4.4
17-17.9	11.5	3.6	4.0
18-18.9	10.2	3.1	2.4
19-19.9	7.8	2.2	2.4
20-20.9	8.6	2.2	3.3
21-21.9	3.1	3.1	2.9
22-22.9	3.6	4.8	6.8
23-23.9	4.1	12.3	13.1
24-24.9	3.7	26.7	27.9
25-25.9	2.1	19.1	14.4
26-26.9	1.5	8.0	6.5
27-27.9	0.7	2.2	2.0
28-28.9	—	0.6	0.4
29-29.9	—	0.1	0.2
30-30.9	—	—	0.1

a sufficient supply of big fish, these will constitute the greater part of the catch, thus concealing the presence of a supernumerary population of small fish. If this kind of selection occurs in the currents, the proportion of small fish ought to increase in late winter when the number of big fish is supposed to have been reduced by fishing. A test of catches made at Bustrøm in 1960—63, reveals no significant difference in mean length from January to April. But there is a slight tendency for smaller fish of 2—3 years age to be caught in April. The result does not imply a great influx of small fish to the currents, but the possibility of a winter movement directed towards the outlet cannot be excluded. In that case the young fish occupy the bottom, not being able to stay in the stream. The winter movements of the young char have not yet been explained.

The extent of migration

With few exceptions, the char accumulating in the currents must have moved into these from other places. To what extent the different populations migrate certainly depends on the situation of the spawning grounds in relation to the currents. The movements of the northernmost spawning populations are best known, and it is evident from the distribution of the recaptures that a high proportion of the population must leave for the currents in winter. But owing to the variable arrival of the fish during winter and the division of the migration population between several places, it is difficult to make a quantitative estimate of the stock involved. Table 10 shows the percentage winter recapture in the Bustrøm—Tunhovd Dam region of spawners tagged in Tunhovdviik during the preceding autumn. Immediate recaptures are deducted. The average for the years 1959—65,

Table 10. Tunhovdfjord. Winter recapture in the Bustrøm—Tunhovd Dam region of spawners tagged at Tunhovdvika the preceding autumn. Males only, with the exception of the 1958—60 material, when a few females were included. Recaptures made before the winter season have been deducted.

Autumn of tagging	Number tagged (after deduction)	Winter of recapture	Percentage recapture
1958	306	1959	8.8
1959	498	1960	10.4
1960	492	1961	8.9
1961	130	1962	13.8
1962	193	1963	23.3
1963	147	1964	12.4
1964	135	1965	9.0
1965	174	1966	12.6
1966	279	1967	11.5

which are supposed to give the most reliable results, is 12.3. This is a rather high rate of exploitation, but spawning populations belonging to the currents or nearby localities are possibly more drastically reduced, being exploited throughout the season. Only once has it been possible to tag a greater number of spawners at Bustrøm. Of the 237 tagged in autumn 1965, nearly one hundred were recaptured before the lake was frozen over. The remaining are supposed to have behaved and dispersed in just the same way as the early arrivals from the north. The winter recapture of these fish in 1966 in the Bustrøm—Tunhovd Dam region was 26.8 per cent, compared with the 12.6 per cent recapture of fish tagged at Tunhovdvik in autumn 1965. The difference in the returns is assumed to be due to the northern group being only partly present. The proportion suggests that about 47 per cent of the tagged population had moved southwards this winter. For three years char were tagged and released at Bustrøm early in January, just when fishing had started, and for several years in March at the time when maximum arrival from north was supposed to occur. The recapture percentages in the Bustrøm—Tunhovd Dam region in the winter of tagging are listed in Table 11. When combined with the percentage recapture of fish tagged in Tunhovdvik given in Table 10, the proportion of fish migrating from Tunhovdvik is estimated to be from 40 to 47 per cent when fish released in January are made the basis of the estimate. The corresponding figures when the March taggings are used are 51 and 86 per cent. The results in 1964 are not included, the whole migration rhythm being then upset by the unusual draining. The discrepancy is due to the migrating population not being exploited to the same degree as the fish released at Bustrøm. The majority of the migrators are present during only part of the season. The higher fishing mortality of the local fish tagged early in season results in an unduly low estimate of the proportion leaving the northern bay. Conversely, the fish released at peak arrival are less exploited than the migrating stock, part of which arrives earlier in the season. If this group

Table 11. Tunhovdfjord. Winter recapture in the Bustrøm—Tunhovd Dam region of char tagged at Bustrøm the same winter.

Year	January		March	
	Number tagged	Percentage recapture	Number tagged	Percentage recapture
1959	—	—	300	11.0
1960	—	—	230	13.5
1961	200	19.0	200	17.5
1962	—	—	250	16.0
1963	—	—	250	38.8
1964	250	30.8	250	9.2
1965	200	22.0	208	13.5

is used as a basis, the resulting estimate will be too high. As a rough estimate the proportion of spawners leaving the upper end of the lake may perhaps be put at 50—60 per cent.

Upstream migration

For years the recaptures showed only a downstream winter migration, and the location of the fishing places confirmed this impression. Recently a winter fishery has come into existence at the upper end of Tunhovdfjord, below the tunnel outlet from Pålbufjord. One year the catch amounted to about 3,000 char, and as a whole it is quite insignificant compared with the output at the other end of the lake. The fishing starts late in winter, after the downstream migration has begun, and the catch consists mostly of small fish. The outlet of the tunnel is situated only 2 kilometres from the tagging place in Tunhovdvik, yet recaptures here are few. In the winters 1965—67 only 3 out of 134 recaptures of spawners tagged at Tunhovdvik were made at this place, and the movement towards the tunnel outlet must be of small extent. It is unlikely that emigration from Pålbufjord contributes much to this fishery. No winter-tagged char from Pålbufjord have been recaptured the same season in Tunhovdfjord. A few fish tagged as spawners in Pålbufjord in the preceding autumn have been recaptured in the upper end of Tunhovdfjord near the outlet in winter. Probably they emigrated through the bottom gates in the Pålbu Dam already in the late autumn, and stayed in the pool below the outlet during the winter (Fig. 13).

In most years Pålbufjord is drained through the bottom gates until early winter, and the tunnel between the lakes is in use from the middle of January to May. As long as the water level in Tunhovdfjord exceeds 727.5 metres the fish can get at the outlet directly; at lower water they have to pass over a small rapid. The tunnel is about 1,300 metres long and the fall is 1:600. At full reservoir in Pålbufjord the flow is 30 cubic metres/sec. Under these conditions the tunnel is impassable for char migrating upstream. When approaching minimum regulated level the lower end of Pålbufjord is transformed into a river, which empties into the tunnel. The water flow is then reduced to about 5 cubic metres/sec. In this period char may have a chance to pass through the tunnel. Yet of a total of approximately 13,000 char tagged in Tunhovdfjord, immediate recaptures not deducted, only 5 have with certainty been recaptured in Pålbufjord. In addition some cases not verified are reported. The upstream migration is insignificant, whether because of difficulties in entering or leaving the tunnel, or of the reduced capacity of the fish to move against the stream in winter.

Char is, however, not reluctant to pass through tunnels upstream if the circumstances make it possible. The migration from Lake Breivatn to Lake Bonsvatn, county of Telemark, offers a striking example. The tunnel be-

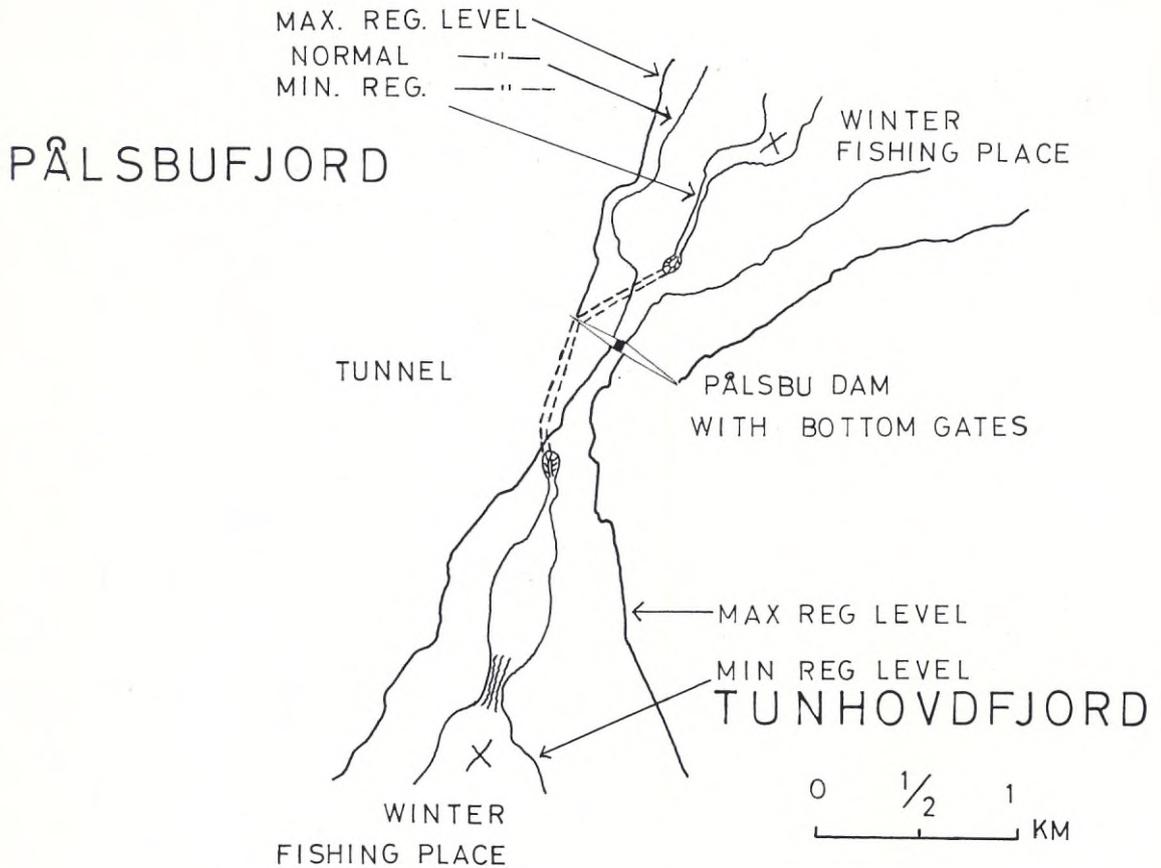


Fig. 13. Pålshufjord and the adjacent parts of Pålshufjord and Tunhovdfjord. Pålshufjord is drained through the bottom gates in the dam until approaching the old normal water level, then the tunnel is taken into use.

tween the lakes is 15.3 kilometres long, with an average fall of 1:4635 and a maximum water velocity in summer of 1 metre/sec. A mixed population of trout and stunted char occurred in Breivatn, while trout was the only species in Bonsvatn. The tunnel was brought into use in the winter of 1958 and during the following years many char were caught in Bonsvatn. The population is now well established and outnumbers the trout.

V. Winter migrations in Lake Pålshufjord

The migration pattern is much the same as in Tunhovdfjord, but deviates in some details. After spawning, the spent char approaches shallow water,

but the stay may be short and the fish move to a greater extent. To attain maximum power production, the water level of Tunhovdfjord is kept as high as possible and the lowering of Pålbufjord starts early, mostly in November (Fig. 14). The fish are continually compelled to change location, and in so doing some also move along the Pålbu Dam. If the bottom gates are open, a downstream migration to Tunhovdfjord takes place, but it involves only a minority of the population. The shorebound movement gives

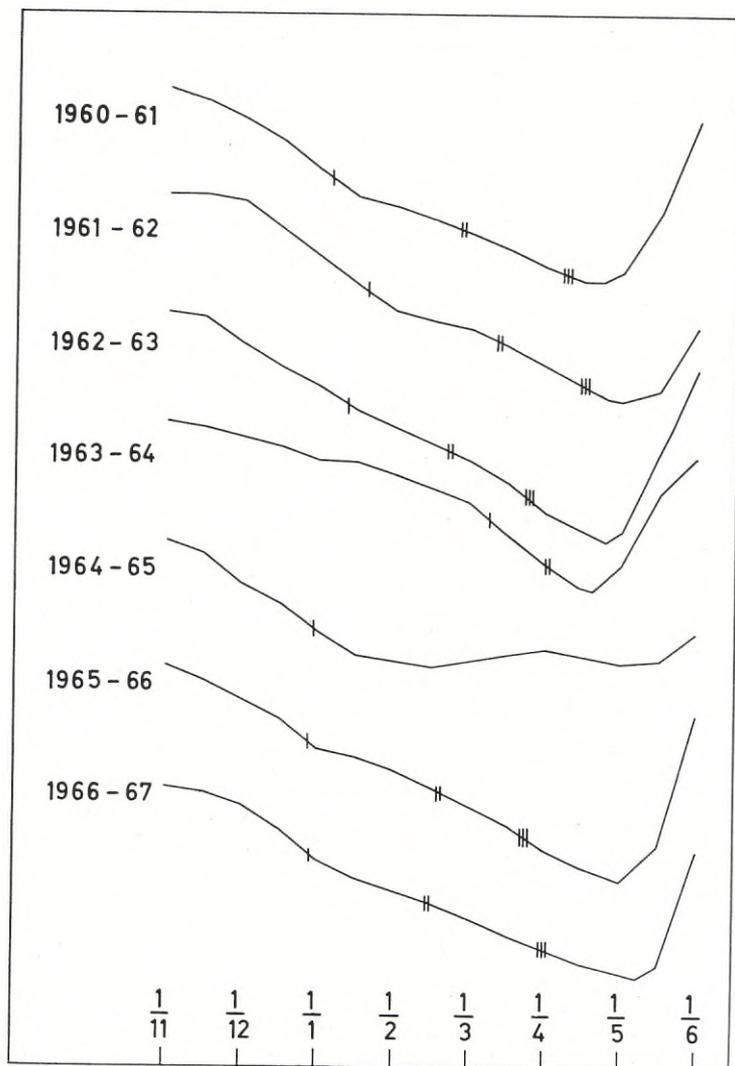


Fig. 14. Winter water-level fluctuations in Pålbufjord 1960/61—1966/67. Vertical lines indicate lowering of the reservoir by 10, 15 and 20 metres.

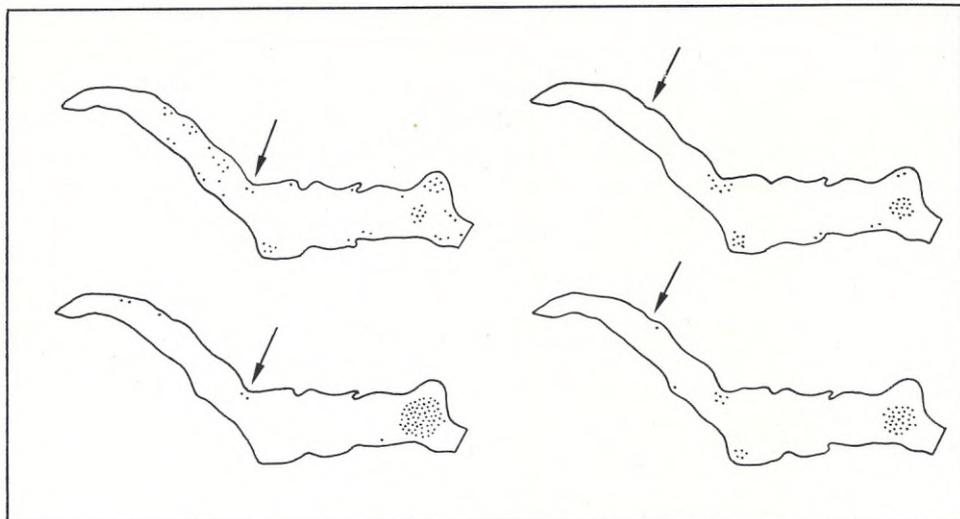
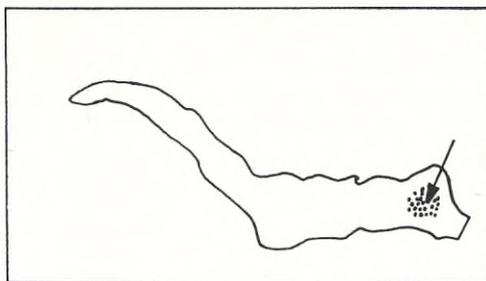


Fig. 15. Winter recaptures following tagging experiments on spawning char at Åsodden October 1958—60 and Bjørnsrud October 1965—67. Upper and lower left, recaptures in the periods December—March and April—May after the Åsodden taggings. Upper and lower right, recaptures in the same periods after tagging at Bjørnsrud.

rise to a fishery of short duration at depths of only 1—2 metres. In December the char return to deeper water, but the mobility is still rather high. Fig. 15 (upper part) shows the distribution of recaptures in December—March of fish tagged as spawners during the preceding autumn at Åsodden and Bjørnsrud. The reason for this greater spreading is certainly the fact that a current strong enough to accumulate the char does not develop until late in winter. When the reservoir approaches minimum regulated level the lake narrows to a sound, situated about 1,200 metres north of the tunnel intake. In years with normal lowering this happens in March—April, and for the rest of the season the fishing is largely concentrated in this place (Fig. 13). The accumulation of char can only be due to a gradual approach, and the migration involves fish from the whole of the lake, even the remotest part. Judged by the fishery statistics and the distribution of recaptures, a great proportion of the total population must stay in this restricted region in late winter (Fig. 15, lower part).

Once having arrived, the char remains firmly attached to the current for the rest of the winter. For several years char have been tagged at the place, but not even once in a year has a recapture outside the current been made in the tagging season, and — when this occasionally happens — always in the lower end of Pålbufjord (Fig. 16). Of the 2,346 char tagged in the lake in winter, nearly one half were released in the current. Seemingly nothing prevents the char from moving downstream to Tunhovdfjord, but

Fig. 16. Winter recaptures 1963 of char tagged near the tunnel intake in Pålbufjord March—April 1963.



no certain recapture has been made in this lake indicating a winter migration between the two lakes.

The gradual increase in yield suggests that the char enters the current over a period of a couple of months. The time for their leaving the upper regions for the current may vary greatly. In the period 1954—63 char were tagged about March 20th every year at Åsodden in the middle of the lake. In some years the recaptures the same winter were concentrated at the current; in other years the recaptures were mostly made at the tagging place or close to it, only stray fish being recovered from the current. The variations are apparently due to water-level differences. The time of max-

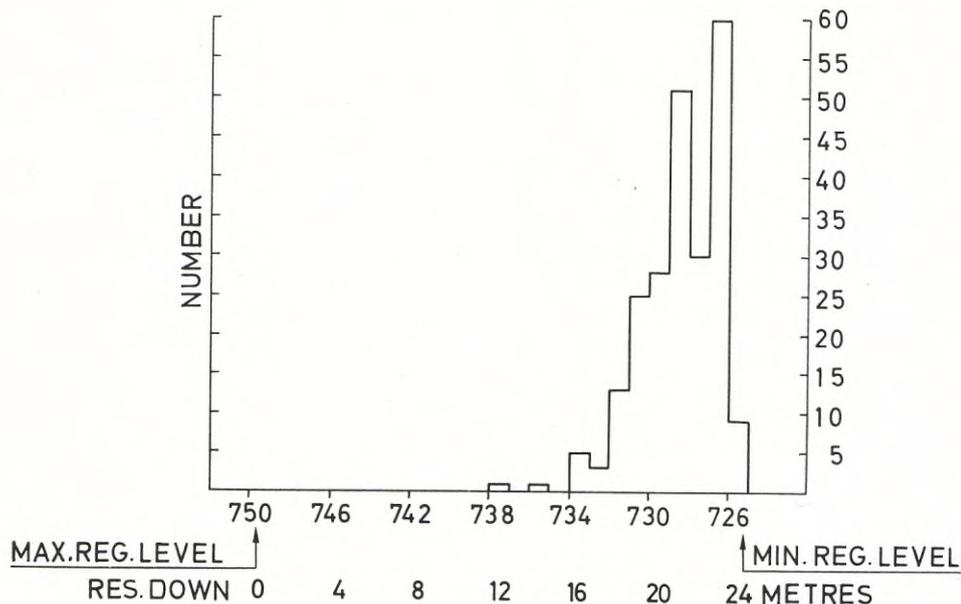


Fig. 17. Relation between water level and number of returns made near the tunnel intake in Pålbufjord during the winters of 1956—68. The char were tagged as spawners at Åsodden and Bjørnsrud.

Table 12. Pålbufjord. Winter recapture above the Pålbu Dam of spawners tagged at Åsodden and, Bjørnsrud the preceding autumn. Males only, Recaptures made before the winter season have been deducted.

Tagging location	Autumn of tagging	Number tagged (after deduction)	Winter of recapture	Percentage recapture
Åsodden	1961	209	1962	6.7
"	1962	194	1963	7.2
"	1963	94	1964	0
"	1964	117	1965	0
Bjørnsrud	1965	175	1966	9.1
"	1966	212	1967	7.1
"	1967	250	1968	2.8

imum arrival at the current of this and other northern spawning populations is easier to establish. Of spawners tagged in the upper half of the lake, in all 226 have been recovered in the current, including the winter of 1968. The rate of recapture, and most probably of arrival, is highly dependent on the water level. Apart from a few stray fish, recoveries were made when the reservoir was lowered 18 metres below maximum regulated level. The majority were recaptured when the reservoir was lowered 21—23 metres, *i.e.* close to the regulated minimum level. Fig. 17 shows the relation between water level and recapture. The yield has a trend similar to the rate of recapture.

In winters when the reservoir is not fully exhausted, the importance of the water level for the long-distance migrations is clearly demonstrated. In 1964 and 1965 the reservoir was lowered only about 18 and 14 metres respectively (Fig. 14), and no recaptures of the tagged northern spawning populations were made at the current in these winters. Table 12 shows the winter recapture percentages at the current calculated after deducting immediate recoveries near the tagging place. The downstream movements of the more local populations were certainly also influenced. Consequently the catch in the current declined, and its share of the total yield dropped (Table 13). But owing to the late concentration of char, the fishing does not depend on the current to the same degree as in Tunhovdfjord. On the whole, ice quality and yearclass fluctuations are as important for the fishery as is the formation of a current. The extraordinarily high yield in the remaining lake in 1964 was not due to the char concentrating at substitute places. The catch was made early in winter, before the current normally develops. Because there was little snow and the lowering was unusually slow it was possible to drive cars on the ice. This drew crowds of anglers to the lake and made the fishing more efficient.

Based on the rates of recapture in the current of fish released there and

Table 13. Pålshufjord. Estimated numbers of char caught in winters 1960/61—1966/67.

Year	Place		Total
	Near tunnel intake	Rest of lake	
1960/61	4,500	8,300	12,800
1961/62	6,700	5,800	12,500
1962/63	4,900	6,000	10,900
1963/64	3,600	15,700	19,300
1964/65	1,700	8,400	10,100
1965/66	8,000	9,100	17,100
1966/67	11,500	8,900	20,400

spawners tagged at Åsodden, the proportion of the spawning population from Åsodden entering the current may be estimated at 35—45 per cent for the years 1959—60 and 1962—63. In spite of the autumn tagging places being situated in the upper half of the lake, no recaptures were made in winter at the outlet of the River Skurdalselv, which empties further up in the lake. However, a winter fishing of some importance takes place at the outlet of the main tributary, the River Numedalslågen, in the middle of the lake. In most years some of the tagged spawners are recaptured at this place, and the accumulation may consist mainly of fish migrating from the northern regions. Outside the current, winter taggings in the southern and largest basin are few, but the results do not indicate an upstream migration of any importance.

VI. Discussion

Large-scale winter migrations of inland char in natural lakes have not been reported, but their existence cannot be ruled out. LINDSTRÖM (1954) reports of a winter fishery close to a current in an unimpounded Swedish lake. The char must migrate to the place from the spawning regions. In hydro-electric reservoirs, however, migrations occur regularly, commencing as soon as the impoundments are accomplished. The characteristic hydrological difference between Scandinavian lakes and reservoirs in wintertime is that the latter are drained, resulting in a water flow of unusual strength for the season. In the case of Tunhovdfjord the mean winter water flow at the outlet is 50—60 cubic metres/sec. Between the middle of November and the end of April approximately 750—800 million cubic metres flow through the lower end of this narrow lake. Currents develop upstream of the tunnel intakes and, depending on the topography of the reservoirs, may also arise far from the outlets when the lakes are lowered. From a long-term production point of view, the reservoirs are characterized by a reduced

bottom fauna production and the increased importance of the zooplankton as fish food (NILSSON 1961, NILSSON & ANDERSSON 1967, GRIMÅS 1965, AASS 1969).

Jointly, the two factors could explain the winter migrations, which finally end with the stay in the currents. The shorebound movements in early winter take place after spawning, when the spent fish exert a great demand for food. At this time the water level generally gains its maximum for the year (Fig. 2). This makes it possible for the char to exploit the food production of areas difficult to approach during most of the year: banks, moss islands and sheltered shallow regions with some organogenic sediments and a scarce vegetation, mostly consisting of *Ranunculus reptans* L. and *Littorella uniflora* (L) ASCH. The drained areas of Tunhovdfjord and Pålshufjord are still covered with stumps from the former forest, and the shores are littered with drifts of forest debris. The remnants are used as a food basis for the bigger insect larvae (GRIMÅS 1964). During a short period char feeds well on organisms typical of shallow water. The stomach contents consist mostly of semi-terrestrial *Chironomidae* larvae of the *Diamesini* group (det. M. HIRVENOJA) and *Macrocyclops albidus* JURINE. A few *Megacyclops viridis* JURINE and *Eucyclops serrulatus* FISCHER also occur (*Cyclops* det. KÅRE ELGMORK). In Pålshufjord and Tunhovdfjord the char mostly approach the shore close to their spawning sites. Recaptures show that stray spent fish are few. The majority possibly stay along the shores until the food resources are exhausted or the drainage forces the fish towards the barren stone and gravel bottom of the deeper impounded zone. The mature char of these crowded populations is no true bottom dweller and possibly turns to the pelagic zone in search of food when the bottom supply is short. In so doing the fish may be attracted by the water flow that passes along the entire whole length of the lakes, carrying the organic drift from the watercourse above. Following the drift, the char move down to the currents, and make them their wintering places. This may be due to the drift being concentrated in the currents by turbulence; the accumulation of char in the mid-water layers is a conspicuous feature.

In the Swedish reservoir Lake Jormsjön, RUNNSTRÖM (1964) showed that a considerable migration of spent fish took place from the only important spawning site to the main feeding ground. In this lake the two localities are distinctly separated. Owing to natural underwater barriers the feeding ground is not entirely drained during the winter and the char are not compelled to leave the region. In Jormsjön too, char accumulate near the outlet in winter and to a lesser degree in a sound dividing the lake into two parts. But it is not established by tagging experiments that the spent char, having once arrived at the feeding place, leave for the currents in winter. The remaining Scandinavian char-tagging experiments in reservoirs give little information about the immediate post-spawning

Table 14. Tunhovdfjord. Relation between water velocity and number of *Bosmina coregoni* in char stomachs. Tunhovd Dam January—March 1960.

Number of <i>Bosmina</i>	January Current		February Current		March Current	
	slow	strong	slow	strong	slow	strong
0	9	6	9	10	11	6
0—5	4	1	4	3	3	5
6—10	1	2	3	5	1	1
11—25	1	4	2	1	4	4
26—50	1	3	3	3	2	4
51—100	4	1	1	0	1	0
>100	7	13	2	2	2	5
Number of fish examined	27	30	24	24	24	25
Other organisms	1 <i>Cyclops</i>	1 <i>Cyclops</i> 1 <i>Chironom. l.</i> 1 <i>Pisidium</i>	2 <i>Chironom. l.</i> 1 <i>Planorbidae</i>	2 <i>Chironom. l.</i>	2 <i>Cyclops</i> 1 <i>Planorbidae</i> 4 <i>Trichoptera l.</i> 47 <i>Hydracarina</i>	6 <i>Cyclops</i> 2 <i>Chironom. l.</i> 2 <i>Pisidium</i>

movements. Renewed contact with the fish after tagging at the spawning places is mostly established later in winter, after accumulation in currents (AASS 1963). RUNNSTRÖM (1963) states from Borgasjön that a pronounced downstream migration of mature fish takes place in the non-spawning period, November—August, but he does not specifically mention winter movements. A pause in recoveries between spawning and winter concentration also applies to taggings performed in other seasons (HANELL & HOLMBERG 1968).

RUNNSTRÖM (1964) maintains that at the outlet of a reservoir the organic drift attains its maximum during winter, when the main draining takes place. The erection of dams and draining through deep-set tunnels or bottom gates has, however, extinguished the original filter fauna of the shallow outlets. Judged by the stomach contents the amount of drifting plankton must also be very scarce in winter. Up to the end of March the drift in Tunhovdfjord consists almost entirely of small individuals of *Bosmina coregoni* BAIRD. Table 14 shows the number of *Bosmina* in the stomachs of char caught near the tunnel outlet in January—March 1960. Most of the stomachs were empty or contained only small numbers of the crustacean, and none was quite full. Towards the end of winter the amount of *Bosmina* in the stomachs showed a downward trend. True bottom organisms are consumed only in small numbers, and it is questionable whether they form part of the drift. Only a few fish had eaten the odd *Pisidium* or *Planorbidae*. One stomach containing 47 *Hydracarina* and 4 *Trichoptera* larvae was a marked exception. A few observations suggest that *Bosmina* disappear in late winter, being replaced by *Cyclops* sp. as the main

food of the char. Of 19 fish caught at Bustrøm in April 1960, 12 had eaten *Cyclops* in small numbers, the stomachs of the remaining 7 being empty. When 62 stomachs of Pålshuffjord char, caught near the outlet in March—April 1967, were examined, 39 were empty, while 16 contained small numbers of *Bosmina*; 3 fish had eaten molluscs and chironomid larvae and 4 fish had, in addition to crustaceans, also consumed molluscs or chironomid larvae, the total number of these organisms amounting to 50 and 10 respectively.

The food consumption of char staying in the currents is obviously very small. Table 14 also shows there is no significant difference between the amounts eaten during heavy and slight draining, *i.e.* in periods with strong and weak currents, respectively. The deconcentration of fish during weekends is thus difficult to explain in terms of reduced food supply. But the digestion in winter may be so slow as to disguise any short-time fluctuations in consumption.

The stomach analyses indicate that another factor than the food supply may be active in concentrating the char in the currents. The winter migrations of char in reservoirs may be interpreted as a partly active, partly passive movement. The arrival at and departure from the shores in early winter would then be the active phase. But once the fish have passed into the pelagic zone, the transport down the lakes could be as passive movement with the gentle flow. The assumed speed of the fish, about 1 kilometre every 24 hours, does not imply an active migration. The fish moving in deep water under the ice are not provided with visual clues and navigation must be difficult. The char can only halt when the water attains a velocity which is perceived by the fish. This happens in the currents, and without such an instinctive reaction, nothing would prevent the char from drifting out of the lakes, with an extinction or severe reduction of the population as the result. The Scandinavian mountain reservoirs, being mostly small or medium-sized, rarely allow of migrations exceeding 20—30 kilometres a linear distance. This will not prevent the char from the most remote spawning place arriving at the outlets during winter, even if the movement is a passive one. The reluctance of the char to move down the rapid and open parts of the currents resembling rivers is established by the low rate of downstream recapture after winter taggings (Fig. 6, 12 and 16) and by gill-net fishing in the open water. This behaviour may be due to several factors, *e.g.* the increasing energy requirements, the often observed reluctance of the char to leave the protecting ice cover, but most plausibly by the disposition of the char to halt when the bottom appears to rush away. This behaviour is more easily observed in summertime when char are swept down through tunnels or bottom gates in dams. ERIC FABRICIUS, in a personal communication, was the first to explain the halt as a reaction of the char to the visual clue provided by the bottom rushing away.

The brown trout behave quite differently and are often observed in the open parts during winter, and, to judge by the catch, they rarely appear in the deep and slow currents. In the winters of 1966 and 1967 the proportion between trout and char in the catches made at Bustrøm and Tunhovd Dam was about 1:400, against 1:50 for the whole year. Aquarium observations show little or no territorial behaviour in the young stages of char. In still-water tanks the fry swim about when feeding starts after the yolk sack is finished, but they keep close to the bottom (FABRICIUS 1953, FROST 1965). Direct observations from the ice at Tunhovdfjord and Pålbufjord confirm this. The char appear to be benthic in their fry and parr stages. The change in body colour, the dark sides with parr marks shifting to a silvery hue, is accompanied by a change in habitat. The char become more pelagic and form bigger shoals. In this behaviour they resemble salmon rather than trout. The change from a benthic to a pelagic habitat takes place in the two lakes when the char are 3—4 years old. If the migration towards the outlet is a passive movement with the water, the moving populations would naturally consist mainly of fish in the pelagic stage, as these most easily come in contact with the heaviest flow. This may explain why the migrating populations apparently consist of the bigger fish. In Tunhovdfjord and Pålbufjord this impression is based on the composition of the winter catches (Table 8). But if it may be assumed that the scanty number of char leaving a current for further downstream migration is representative of the population migrating into it, then a check undertaken in the outlet should give some data about the size of the moving fish.

Such a check has been made in the impounded Lake Limingen, situated in the county of Nord-Trøndelag and close to Lake Jormsjön. During the observation period the lake was drained in winter only, and in the seasons 1954/55 to 1958/59 a grating was erected some hundred metres down in the drainage tunnel, barring the whole cross section. Char down to a length of 10 centimetres were detained, but apparently the grating worked effectively only on fish of 13 centimetres or longer. The fish had no opportunity to return to the lake, and every 24 hours the water was cut off and the char were caught in a trap. In winter char accumulate near the tunnel inlet, and the catch consists mainly of mature and larger immature fish, just as in Tunhovdfjord and Pålbufjord. The size and age of the fish differ, however, the char in Limingen being bigger and older. The seasonal catch in the tunnel trap varied between 1,701 and 3,739 char. Fish of 20 centimetres or more constituted the great majority, confirming the impression that the moving fish chiefly belong to the pelagic stage. But smaller fish occurred relatively more frequently than in the ice fishing catches. This may imply that more small fish take part in the downstream winter migrations than is generally supposed. By keeping close to the bottom they escape exploitation by the fishing that takes place in mid-water, concen-

trating on the bigger fish. Lake Limingen has an area of about 95 sq. kilometres and char is the main species. The number emigrating must be considered insignificant. The total recapture in the trap of spawners tagged at different localities in the lake was only 1 per cent (AASS 1963). This small winter emigration accords with the results obtained by tagging in Pålshufjord and recapture in Tunhovdfjord.

VII. Fish management applications

Generally, impoundments will alter the balance between populations of trout and char. As a result of the reduced bottom-fauna production in reservoirs, the segregation between the species will increase (AASS 1957, NILSSON 1965). The trout, mainly a bottom feeder, will be hardest hit, and in many cases reduced spawning facilities will accelerate the decline of the populations. Conversely, char of all stages may increase their consumption of planktonic crustaceans, the summer abundance of which is almost unchanged when the short-term impoundment effect is terminated (LÖT-MARKER 1964). Improved spawning possibilities in the eroded zone may theoretically lead to an increased recruitment of char, provided that the reservoirs are drained slowly. Data of char recruitment are, however, generally lacking. As a final result of impoundments, the mature char decrease in size and the traditional autumn fishing with gill-nets suffers a setback. In some places the decline is aggravated by the long-term difficulties of net fishing over drained areas (JENSEN & AASS 1958). Although the char utilize the food production of subarctic and high boreal reservoirs better than do the trout, stocking with char has not been recommended, one of the objections being the difficulty of exploiting char stocks. A satisfactory catch after impoundment is dependent on a change in fishing methods. In many reservoirs the winter migrations and the subsequent accumulations of char in the currents render this possible. The favourable conditions created make them outstandingly good fishing places, and ice fishing with baited hooks becomes the most important method, also when the reservoirs are situated far from densely populated districts. In addition to the local population, which derives a direct income from fishing, visiting anglers spend considerable amounts on building or hiring cabins, and everybody has to pay for a fishing licence. In Tunhovdfjord about 4,000—5,000 daily visits are paid to the Bustrøm—Tunhovd Dam region alone in an average winter.

Of the total catch of char in Tunhovdfjord during the years 1961—67 (Table 15), winter fishing with hooks was responsible for 87.8 per cent of the number caught, and as much as 74.8 per cent of the total was captured in the currents. The corresponding figures for the catch in Pålshufjord

Table 15. Tunhovdfjord. Total catch of char in numbers 1961—67.

Year	Winter fishing		Summer and autumn fishing	Total
	in currents	rest of lake		
1961	59,900	7,300	12,500	79,700
1962	44,650	6,100	10,000	60,750
1963	34,050	5,050	8,000	47,100
1964	36,900	7,600	6,900	51,400
1965	47,700	10,600	9,300	67,600
1966	73,800	12,500	7,500	93,800
1967	71,100	14,600	5,800	91,500
Total 1961—67 ..	368,100	63,750	60,000	491,850

(Table 16) were 71.9 and 27.8 per cent. In this lake there is only one current and no substitute for this exists if draining is late or incomplete, as it was in 1964—65. The average yearly rate of exploitation during the winter fishing in the currents in the Bustrøm—Tunhovd Dam region varies between 25 and 13 per cent for the local and the most distant spawning populations respectively. In Pålbufjord an average of 6—7 per cent of fish tagged in the middle of the lake is recaptured near the outlet in winter. Summer and autumn fishing being insignificant, the winter rates could be considerably increased without endangering the recruitment. A higher exploitation of the remote spawning populations is especially desirable, as this will have the greatest effect on the total yield. Theoretically the migrations may be speeded up or delayed by varying the velocity and level of the water, and the starting time and duration of the fishing season thus influenced. The char may be concentrated at one fishing place or distributed among several if possibilities for this exist. This seems to be a general effect, and should be taken into consideration by those who manage char reservoirs.

In the case of Tunhovdfjord the lowering should start in December, and the reservoir ought to be 5 metres below maximum regulated level in the

Table 16. Pålbufjord. Total catch of char in number 1961—1967.

Year	Winter fishing		Summer and autumn fishing	Total
	in currents	rest of lake		
1961	4,500	8,300	7,300	20,100
1962	6,700	5,800	5,200	17,700
1963	4,900	6,000	5,900	16,800
1964	3,600	15,700	5,900	25,200
1965	1,700	8,400	6,900	17,000
1966	6,400	9,100	6,250	21,750
1967	11,500	8,900	2,200	22,600
Total 1961—67 ..	39,300	62,200	39,650	141,150

second half of January. This is somewhat earlier than the general practice and should speed up the start of the longdistance migrations. After a period of gentle lowering, allowing a large proportion of the char population to reach the dam, the reservoir should be rapidly lowered to 8—10 metres below maximum from the middle of February. This will halt the char at Bustrøm, and create conditions for a long fishing season at the two places where the char are most effectively exploited. Further lowering should take place slowly and as late in the season as possible. Rapid drainage at this stage will disperse the fish to several different places, but the total catch is unlikely to increase. The ideal management of the reservoir from a fisheries point of view is likely to clash with the interests of power production. The latter is favoured by a high water level and early lowering is not desirable. Later in the season the conflict of interests should be of less importance.

For a maximum yield, Pålbufjord should be lowered almost to the minimum regulated level early in winter. But for two reasons it is impossible to speed up the draining as desired. First, the management of the reservoir is dependent on the water level of Tunhovdfjord; this must always be lower than in Pålbufjord if draining is to be possible. Secondly, the existing tunnel is not dimensioned for a rapid lowering of Pålbufjord. Such an obstacle is hardly met with in modern hydro-electric developments. But even if a rapid lowering had been possible, its accomplishment is not desirable every year, because of the consequences on the recruitment of the char. Many spawning places are situated in the impounded area, and early lowering will kill a large proportion of spawn and alevins, making the year class a poor one (AASS 1964). Every third or fourth year the draining should be slow or incomplete.

VIII. Summary

1. During the years 1951 and 1954—68, in all 21,073 char were tagged in the two lake reservoirs and the connecting river. Of these 10,475 were tagged in winter, 1,884 in spring and summer and 8,714 in autumn as spawners.
2. Post-spawning and early winter movements were shorebound feeding migrations, mostly covering short distances.
3. Later in winter, char accumulate in great numbers in the currents near the intakes of the drainage tunnels and in narrow sounds which come into existence with the lowering of the reservoir. The movements are nearly always downstream.
4. Char from neighbouring areas enter the currents first, the populations of distant regions chiefly arriving in middle and late winter.
5. There is a close connection between water level and dispersion of char.

When a current attains a certain threshold velocity the char interrupt their migration and keep to the current for the rest of the winter.

6. The catch in the currents consists mostly of fish in the pelagic stage, that is mature or older immature char. It is not proved to what extent the younger fish take part in the migrations.
7. The downstream migrations involve a great part of the total population. Of the more distant spawning populations in Tunhovdfjord, more than 50 per cent take part. A fish may participate in several subsequent years.
8. The food supply in the currents is negligible, and the downstream movements make little sense as active feeding migrations. The lowering of the water level brings about a movement of the pelagic char towards deeper water and in contact with the flow through the reservoirs. The further migration is possibly a passive downstream displacement.
9. Important winter fishing arises in the currents. In Tunhovdfjord, the annual rate of exploitation varies between 12—25 per cent for distant and local spawning populations respectively. On average, 75 per cent of the total char catch in Tunhovdfjord is made by angling in the currents. The corresponding figure for Pålbufjord is 28 per cent.
10. The affinity of char to currents may be exploited to improve the fishing. When managing the reservoirs, the distribution of char most favourable to the fishing should be considered.

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X. References

- AASS, P. 1957. Fiskeriundersøkelsene i Pålbufjord og Tunhovdfjord 1949—1956. Årsberetning for fiskeriundersøkelser i regulerte vassdrag. Inspektøren for ferskvannsfisket. 36 pp. (Mimeographed in Norwegian.)
- 1963. Limingenreguleringens virkninger på fisket. 40 pp. (Mimeographed in Norwegian.)
- 1964. Reguleringer og røyerekuttering. *Norges Jeger- og Fiskerforbunds tidskr.* 93: 378—381.
- 1965. Rödingvandringar i Pålbufjord och Tunhovdfjord. *Inform. Sötvattenslaboratoriet, Drottningholm* (4). 17 pp. (Mimeographed in Swedish.)
- 1969. Crustacea, especially *Lepidurus arcticus* Pallas, as brown trout food in Norwegian mountain reservoirs. *Rep. Inst. Freshw. Res. Drottningholm* 49: 183—201.

- CARLIN, B. 1955. Tagging of Salmon Smolts in the River Lagan. *Rep. Inst. Freshw. Res. Drottningholm* 36: 57—74.
- DAHL, K. 1920. Studier over røje i ørretvand. *Norges Jeger- og Fiskerforbunds tidskr.* 49: 233—248.
- 1926. Undersøkelser ved Tunhovdfjorden angaaende fiskens næringsforhold før og efter reguleringen. *Medd. Norges Vassdrags- og Elektrisitetsvesen. Foss.* 1. 1—18.
- 1932. Influence of water storage on food conditions of trout in Lake Paalsbufjord. *Det Norske Vidensk. Akad. Oslo, 1, Mat.-Naturv. Kl.* 1931. 4: 1—53.
- FABRICIUS, E. 1953. Aquarium Observations on the Spawning Behaviour of the Char, *Salmo alpinus*. *Rep. Inst. Freshw. Res. Drottningholm* 34: 14—48.
- FOSSEDIREKTØREN. 1932. Nore kraftanlegg. *Medd. Norges Vassdrags- og Elektrisitetsvesen. Foss.* 3. 1: 199.
- FROST, W. E. 1965. Breeding habits of Windermere charr, *Salvelinus willughbii* (GÜNTHER), and their bearing on speciation of these fish. *Proc. Roy. Soc. B.* 163: 232—284.
- GRIMÅS, U. 1964. Studies on the bottom fauna of impounded lakes in southern Norway (Tunnhovdfjord, Paalsbufjord and Rödungen). *Rep. Inst. Freshw. Res. Drottningholm* 45: 94—104.
- 1965. Effects of impoundment on the bottom fauna of high mountain lakes. *Acta Univ. Upsaliensis Abstr. Uppsala Diss. Sci.* 51: 1—24.
- HANELL, L. & R. HOLMBERG 1968. Rödingvandringar i Kultsjön. *Information från Sötvattenslaboratoriet, Drottningholm* (7). 10 pp. (Mimeographed in Swedish.)
- HUITFELDT-KAAS, H. 1935. Der Einfluss der Gewässerregelungen auf den Fischbestand in Binnenseen. Oslo. 105 pp.
- JENSEN, K. W. & P. AASS 1958. Bunnforholdene i regulerte sjøer. *Norges Jeger- og Fiskerforbunds tidskr.* 87: 44—55.
- LINDSTRÖM, T. 1954. Non-reproductive Migrations in the Char, *Salmo alpinus*, L. *Rep. Inst. Freshw. Res. Drottningholm* 35: 118—132.
- LÖTMARKER, T. 1964. Studies on planktonic crustacea in thirteen lakes in northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm.* 45: 113—189.
- NILSSON, N.-A. 1961. The effect of water-level fluctuations on the feeding habits of trout and char in the lakes Blåsjön and Jormsjön, North Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 42: 238—261.
- 1965. Food segregation between salmonoid species in North Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 46: 58—78.
- & G. ANDERSSON 1967. Food and growth of an allopatric brown trout in northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm.* 47: 118—127.
- RUNNSTRÖM, S. 1963. Rödingens lekvanor och vandringar i Borgasjön före och efter sjöns reglering. 12 pp. (Mimeographed in Swedish.)
- 1964. Kontroll av Jormsjöns lekrödingbestånd i Blåsjöälven genom en fiskspärr samt studier över dess vandringar genom märkningsförsök. *Inform. Sötvattenslaboratoriet, Drottningholm* (4). 17 pp. (Mimeographed in Swedish.)

On the ecology of the ide *Idus idus* (L.) in the River Kävlingeån, south Sweden¹

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Contents

I. Introduction	46
II. Techniques	47
III. Study area	47
IV. Physico-chemical environments	49
Water temperature	51
Colour	51
pH	51
Hardness, Ca+Mg	51
Specific conductivity	52
Chloride ion contents	52
Oxygen contents	52
V. Pollution	52
VI. Death of fish	54
VII. Qualitative composition of benthic fauna	55
VIII. Production of plankton organisms	55
IX. Fish fauna and fishery	59
X. Notes on the macrophytic vegetation	61
XI. Migration and spawning season of the ide	61
Spawning time	63
Spawning results	65
XII. Growth and age of the ide	65
Embryonal development	65
Sac-fry growth	66
Growth of young-of-the-year	67
Age and increase in body length	69
Characteristics of the scale annulus	70
Time of annulus formation	70
Regeneration of scales	71
Body-scale relation	75
Length distribution	78

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Growth in length	79
Length-weight relation	81
Calculated growth in weight	86
XIII. Sex ratio on spawning ground	87
XIV. Food habits	88
Composition of the diet in relation to the fish size	89
Food utilization and food abundance	89
Seasonal changes	92
Previous investigations	93
XV. Summary	94
XVI. Acknowledgements	97
XVII. References	97

I. Introduction

Various aspects of the ecology of the ide have been investigated previously. Studies concerning its growth were carried out by BROFELDT (1917), JÄÄSKELÄINEN (1917), ROSÉN (1920), OTTERSTRØM (1930—31), SEGERSTRÅLE (1933, 1950), HOCHMAN (1956), POPESCU *et al.* (1960), PENÁZ (1961), and BALON (1962).

SUNDEWALL (1851, 1855), STANKOVITCH (1921), and SEGERSTRÅLE (1926) reported on the youngest stage of development, BALINSKY (1948) described the development of certain specific characters of the species. LENKIEWICZ (1964) investigated the temperature preferendum. POPESCU *et al.* (1958) treated artificial fertilization, and POPESCU *et al.* (1960) described fecundity, SCHNEIDER (1901, 1920), COLLETT (1905), HUITFELDT-KAAS (1917), JÄÄSKELÄINEN (1917, 1921), OTTERSTRØM (1930—31), and POPESCU *et al.* (1960) worked on the feeding habits. Other papers treating in some way ecological questions of the ide are those by EKSTRØM (1831), SIEBOLD (1863), LILLJEBORG (1891), SMITT (1895), STUXBERG (1895), EKMAN (1922), KOMONEN (1948), BERG (1949), PLISZKA (1953), HOCHMAN (1959), DUNCKER (1960), MANN (1961), ALM (1964), and BOGAN (1964). Further, POPESCU *et al.* (1960) and BALON (1962) reviewed several works dealing with ecological questions of the ide in the U.S.S.R.

LUNDBERG (1899) and BERG (1949) described the geographical distribution of the ide. There are a few more important papers on the life history of the species in the Nordic Countries, *viz.* in Finland, SCHNEIDER (1901), BROFELDT (1917), JÄÄSKELÄINEN (1917, 1921), ROSÉN (1920), SEGERSTRÅLE (1933, 1950), in Denmark, OTTERSTRØM (1914, 1930—31), and in Norway, COLLETT (1905) and HUITFELDT-KAAS (1917).

There are few studies of the ecology of the ide in Sweden. SUNDEWALL (1851, 1855), and SEGERSTRÅLE (1926) studied its early development while EKSTRØM (1831), LILLJEBORG (1891), STUXBERG (1895), and EKMAN (1822) just mentioned spawning and food.

The main purposes of the present investigation were to study the ide population, in the River Kävlingeån in southwestern Sweden with regard to age and size at onset of maturity, age and growth, body and scale relationship, length and weight relation, growth rate in relation to sex and food.

II. Techniques

This study is based on data from ide collected in the River Kävlingeån, in the section Högsmölla to the mouth (Fig. 1). The studies were carried out during a 4-year period (1963—1967). Adult ide were collected mostly by means of seine, bow-nets, and weire-netting used by commercial fishermen in the water course. This sampling gear captured, almost exclusively, fish of age group II or older. Young-of-the-year or fry were collected by electro-fishing.

During electro-fishing, the fish were collected with a hoop-net of a mesh size of ca 1 mm to catch fry and detached bottom fauna at the same time. Fish younger than one year were preserved — like the bottom fauna — in 80 % alcohol.

The total length of the fish (tip of the nose to tip of the tail, lobes compressed) was determined to the nearest millimetre. Representative samples of scales were taken. Fresh weights were determined to the nearest gram (or 0.1 g of some of the fish). Sex was determined by gross inspection of the gonads, or in immature fish by microscope examination. Sex could not be determined of age group 0 or age group I until near the end of the second growth season.

Stomachs of adult ide were removed and fixed in 80 % alcohol for studies of food and feeding habits. In 1964 and 1965 quantitative collections of plankton were made and preserved in formalin. The methods used are described in more detail in the relevant sections.

III. Study area

The River Kävlingeån, which in its lower part is called Löddeå, runs from the Lake Vombsjön and falls out into the Lomma Bay in the straits of Öresund about 15 km north of Malmö (Fig. 1). The length of the river is 46 km.

The river runs through one of the most cultivated parts of the country, and only some of the tributaries run through woodland. The bottom is overlaid with a layer of silt that has been eroded from the fields. Intensive cultivation has caused nearly all the land to be drained, ditched and ploughed. From 1850 to 1900 about 28,000 ha. of bog and lake were drained in the basin of the River Kävlingeån. In addition, large parts of the old

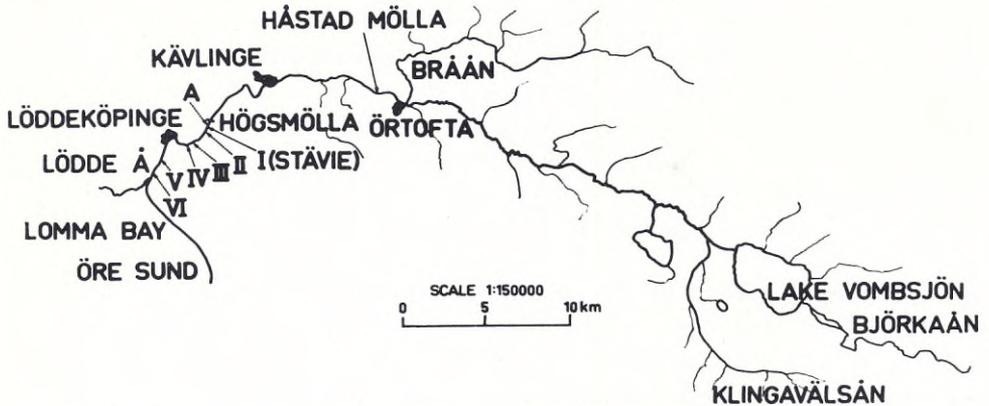


Fig. 1. The water system of River Kävlingeån. Collecting sites I, II, III, IV, V, VI, A.

grazing grounds were put under cultivation, a total of about 19,000 ha. Thus, the rain water, to a large extent, passes into drain-pipes and canals together with much topsoil which is lost out to sea. An analysis of the water of Kävlingeån shows that 1 m³ of water contains about 50 g of humus and 100 g of minerals (WOLF 1960).

The principal tributaries are the streams Bråån, Klingavälsån and Björkaån, the continuation of the river upstreams of the lake Vombsjön (Fig. 1). The tributaries arise between 130 and 170 m above the sea level, while Lake Vombsjön is only 19.5 m above the sea level. The catchment area amounts to about 1,230 km² of which 26.2 km² consist of lake surface. The largest lake, Vombsjön has a surface area of 12.2 km².

Before intensive drainage was carried out during the latter half of the 19th Century the water-holding area amounted to 29 % of the total catchment area. Today this area has decreased to 3.4 %. This has undoubtedly given rise to a greater variation in the water level of the river at different times of the year than in natural conditions (WEIJMAN-HANE 1964). SMHI (Meteorological and Hydrological Institute of Sweden) estimate the water flow at the river mouth as follows:

Highest waterflow	122 m ³ /sec
Normal high water flow	55
Normal water flow	11
Normal low water flow	1.8
Lowest low water flow	0.6

The critical years of 1939 and 1947 a very low water flow was measured at Kävlinge, viz 0.24 m³/sec and 0.39 m³/sec respectively.

Lake Vombsjön and the river downstream of Vombsjön are exploited for water supply, Vombsjön by Malmö city and the river by several industries including Kävlinge community as seen from Table 1.

Table 1. Exploiters of the River Kävlingeån and their future water requirements (after WEIJMAN-HANE 1964).

Exploiter	Future water requirements	
	mean l/sec	maximum l/sec
Furulund Community	15	15
Mab & Mya, Ltd., Furulund	83	200
Swedish sugar factory, Kävlinge	76	100
Kävlinge community	35	35
Kävlinge weaving-mill	7	17
Leather factory, Kävlinge	46	190
Scans' butchery, Krutmöllan	17	17
Swedish sugar factory, Örtofta	55	55
Harlösa milk industry	56	61
Total	390	690

From Table 1 it is seen that the future water need of 0.69 m³/sec considerably exceeds the lowest low water flow. With the present water flow it is not possible to maintain a satisfactory water supply by returning as waste water to the river a lower volume of water than was taken from it. At the same time this means that high demands on the cleanness of the waste water must be set.

The investigation was carried out at six main collecting stations (*vide* Fig. 1), situated at the following distances — as the crow flies — from the mouth of the river: 6.2 km (I), 5.9 km (II), 4.8 km (III), 4.4 km (IV), 2.3 km (V), and 1.2 km (VI). A complementary station was selected at 7.2 km (A).

IV. Physico-chemical environments

Samples of surface water for analysis were collected during June to December, 1965, in the lower reaches of the River Kävlingeån, at six main sites (Fig. 1). The laboratory analysis of the water comprised determination of specific conductivity, pH, oxygen, alkalinity, chloride, Ca + Mg, and colour (Table 2). The methods are based on KARLGREN'S (1962).

During 1963 there occurred several periods of low water flow. At the beginning of June the flow was only 1.6 m³/sec at Kävlinge. This was considerable lower than in the corresponding period in 1961 and 1962 (3.4 and 4.6 m³/sec respectively). At the end of November there was an extreme high flow of 34 m³/sec.

In 1964 the water flow, from the end of May to the end of November, was almost constant, ranging between 2 and 4 m³/sec. The lowest water flow was 1.4 m³/sec at the end of May and beginning of June and 1.6 m³/sec at the end of August. Compared with previous years the flow was lower than

Table 2. Water chemical data from the lower part of the River Kävlingeån, 1965.

Date	Site (vide map 1)	Surface tempera- ture	Colour mg Pt/l	pH	O ₂		≈ 20.10 ⁶	Cl mg/l	Ca+Mg mmol/l	Total alkalinity mequiv./l
					mg/l	per cent				
Jun. 14	I	20.2	50	6.26	9.54	108	504	—	2.7	2.80
" —	II	20.2	50	6.70	6.33	72	473	—	2.6	3.68
" —	III	20.4	40	6.20	4.79	56	483	—	2.6	2.88
" —	IV	20.0	70	6.26	10.38	115	483	—	2.4	2.80
" —	V	21.6	70	5.50	11.12	129	1,239	—	3.2	3.00
" —	VI	21.8	60	6.20	12.08	140	945	—	3.0	2.88
Jul. 1	I	18.1	70	6.00	9.10	99	483	39	2.2	3.00
" —	II	18.4	60	5.80	12.19	133	483	40	2.5	3.40
" —	III	18.0	40	6.36	6.54	71	483	38	2.5	3.04
" —	IV	18.2	50	6.00	9.53	106	473	—	2.5	3.12
" —	V	18.0	40	6.16	8.25	89	1,533	—	3.4	3.16
" —	VI	18.4	40	5.80	11.12	123	2,835	—	4.1	2.80
Jul. 20	I	22.0	70	8.34	13.57	158	462	37	2.4	3.08
" —	II	19.9	60	7.80	8.46	95	483	38	2.6	3.36
" —	III	20.6	60	7.60	5.90	67	483	40	2.5	3.16
" —	IV	20.5	60	7.60	5.27	60	483	33	2.4	3.20
" —	V	20.5	50	7.64	6.76	77	609	120	2.5	3.12
" —	VI	20.7	40	8.04	10.06	112	1,512	550	3.4	2.84
Jul. 30	I	16.0	50	7.20	3.67	38	546	57	2.4	2.92
" —	II	15.8	40	7.36	3.10	32	546	56	2.5	3.04
" —	III	16.2	60	7.46	2.50	26	546	52	2.4	3.20
" —	IV	16.2	70	7.50	3.03	32	546	53	2.4	3.16
" —	V	16.0	60	7.60	5.80	61	588	90	2.5	3.32
" —	VI	16.2	50	7.66	4.09	43	672	120	2.5	3.32
Aug. 6	I	16.2	25	7.30	3.88	41	525	52	2.5	3.16
Aug. 24	I	18.5	40	6.86	3.45	38	536	57	2.3	3.12
Sep. 9	I	14.0	40	6.86	4.63	46	525	55	2.2	2.80
Oct. 20	I	9.6	50	7.50	6.22	56	525	55	2.0	2.80
" —	V	9.8	40	7.50	6.44	58	1,554	480	3.0	2.88
" —	river- mouth	9.8	40	7.00	5.80	53	3,990	2,700	6.1	2.88
Nov. 9	III	7.2	35	7.06	4.73	40	583	52	2.5	3.32
" —	V	7.1	35	7.60	6.44	55	553	54	2.6	3.36
" —	A	7.1	40	7.40	5.27	45	618	51	2.7	3.36
Dec. 7	Lödde- köpinge	0.8	40	7.06	10.38	75	420	23	2.2	2.72
" —	A	0.8	60	7.50	10.91	78	467	40	2.2	2.80

in 1961—63 but considerable more steady. High flow occurred only on a few occasions and had very short duration.

In 1965 the lowest flow was 1.9 m³/sec during some days in June and one day at the end of August. In 1966 the lowest flow, 3.6 m³/sec, was at the beginning of June. During winter and spring there occurred very high flow with a maximum value of 63 m³/sec in late February, which coincided with emptying the ponds from Örtofta sugar factory. During summer and

autumn the water flow was relatively constant (ca 4 m³/sec), and exceptionally low water did not occur. The data on the water flow were taken from WEIJMAN-HANE & ALMESTRAND (1963—1966).

Water temperature

Temperature records are based on the daily measurements at Håstad Mölla by the Salmon and Trout Association (1954—66).

The winter of 1954—55 was very hard: minimum air temperature —24.5°C at the end of February and —14°C in the middle of March. The winters 1956—57 and 1960—61 were mild, and most of the time the air temperature was above zero. As early as 9 March, the water temperature was over 5°C which usually occurs three to four weeks later and above 13°C from the beginning of May until 9 October.

In 1962 the winter was fairly mild but long. The lowest air temperature at Håstad Mölla was —8.2°C in March and most of this month the air temperature was below zero. The water temperature of the river reached 5°C as late as 12 April and was above 13°C from 5 June until 7 September. Thus 1962 differed considerably from 1961. The winter was cold and long in 1963 and very cold in 1966. In 1963 the water temperature at Håstad Mölla reached 5°C on 3 April only for three days, then decreased to about 1°C between 12—19 April; it was 5°C on the 25 April in 1966.

Usually the water of the river reached 5°C at the end of March and beginning of April and was above 13°C from the middle of May to September, *i.e.* there is a long summer without high temperatures. The coldest month is usually February and the highest water temperature occurs in July.

Colour

Colour values vary between 25 (6 Aug.) and 70 (14 June & 1, 20, 30 July) mg Pt/l. No significant differences in the variation between the different sites seem to occur.

pH

The pH varies around 7, as is shown in Table 2. On 1 July the lowest value, 5.50, was recorded. The highest value, 8.34 (one further value, 8.04, is above pH 8) was recorded on 20 July. The latter are probably temporary peaks caused by phytoplankton photosynthesis. The lowest pH values (sometimes below 5) (WEIJMAN-HANE 1964) may be caused by the introduction of acid industrial wastes.

Hardness, Ca+Mg

The hardness varies mainly around 2.5 mmol/l. The highest value, 4.1 mmol/l, was recorded on 1 July. The lowest value, 2.0 mmol/l, was recorded

on 20 October. There is a high value, 6.1 mmol/l from the river-mouth on 20 October connected with influx of sea water.

Specific conductivity

The water of the River Kävlingeån has a κ -value of $473\text{--}945 \times 10^{-6}$ and increases successively downstream (Table 2).

Occasionally there occurs an inflow of sea water giving the lower part of the river the character of an estuary (below Löddeköpinge). Thus the highest specific conductivity of $2,835 \times 10^{-6}$ was measured on 1 July at site VI, and $1,512 \times 10^{-6}$ on 20 July. κ -values of $1,554 \times 10^{-6}$ on 20 October, and $1,533 \times 10^{-6}$ on 1 July were recorded at site V. A κ -value of $3,990 \times 10^{-6}$ was recorded on 20 October at the river mouth which regularly has a mixohaline water.

Chloride ion contents

The Cl^- content varies around 50 mg/l in the upper and central reaches of the river (Table 2). On 9 December the lowest value, 23 mg/l, was recorded at Löddeköpinge. The high values are from the lower reaches of the river where there is an inflow of sea water. There, high values of 550 mg/l, 480 mg/l and 120 mg/l were recorded on 20 July and 30 July. The value of 2,700 mg/l was recorded at the river mouth on 20 October.

Oxygen contents

The oxygen content varies considerably during summer (Table 2). The highest value was 13.57 mg/l measured on 20 July (site I) and the lowest was 2.50 mg/l on 30 July (site III). Low oxygen concentration occurs from late July until September. In spite of the complicated relations in the River Kävlingeån, there is usually a good correlation between the oxygen content and the water flow. Thus, with a water flow of $2.0 \text{ m}^3/\text{sec}$ follows an oxygen content of about 1.0 mg/l (WEIJMAN-HANE 1964).

V. Pollution

River Kävlingeån is severely polluted. The pollution discharged into the river was estimated to about 400,000 Pe (Pe=the equivalent of pollution from one person) (WEIJMAN-HANE 1964). The pollution accumulated downstream Vombsjön was estimated to about 300,000 Pe with the following distribution:

Urban districts	25,000	Pe
Sparsely populated areas . .	105,000	„
Industries	170,000	„

Most of the pollution enters the river near the inflow of the River Bråån (*vide* Fig. 1). Örtofta sugar factory during the working season — October and November — brings heavy pollution to the river which results in large development of the fungi *Sphaerotilus natans* and *Leptomitius lacteus*, which can be found as far downstream as Löddeköpinge. SWENANDER as early as 1910 concluded that the major polluters of the River Kävlingeån were the sugar factories.

Thus, there are two critical periods: from the end of June to September — low water time — and during October to December when the sugar factories are in action. The importance of the latter has changed in the last few years. In 1964 a provisory storage-capacity regulation of the Lake Vombsjön was carried out by the city of Malmö, which guarantees a water flow of at least 1.5 m³/sec at Kävlinge. This condition and storing of the spill water from Örtofta sugar factory in large ponds improved the water quality of the river downstream Kävlinge. The fungi were thereby removed from the river. This was the first autumn since the 1940's that there had been no fungi. But in the following spring when the Örtofta sugar factory started emptying its ponds the development of the fungi began again.

In 1966, the Örtofta sugar factory began to drain the ponds on 18 February and stopped on 7 March as a result of complaint about the development of large quantities of *Leptomitius lacteus* and *Sphaerotilus natans*. The former disappeared almost immediately downstream Örtofta.

During this time 83,700 m³ effluent water were emptied from these ponds into the river. The biochemical oxygen demand was very high: mean BOD₅ = 1,025 mg/l.

Later in the summer the sugar factory emptied the ponds after the water had been treated so that it did not give rise to development of the above mentioned fungi.

Certain bottom sediments are very oxygen consuming and may play an important role in the oxygen cycle of the river. These bottom sediments may be primary, *i.e.* consist of substances which through incomplete purification were released directly into the water course. They may also be secondary, *i.e.* caused by bioflocking or by dead organisms. This phenomenon is very common in the River Kävlingeån and may periodically give rise to oxygen deficiency and mud drift.

Another kind of pollution is the mineral oil that from time to time is emptied into the river.

When the sugar factories are in action, *i.e.* August—November and in the last few years discharge of waste water from dams in spring, the lowest

concentration of oxygen usually occurs at Kvarnvik, some kilometres downstream Örtofta sugar factory. At this time it is often difficult to obtain a correlation between the concentration of oxygen and the water flow. This may partly depend upon the large pollution.

In 1959 at a water flow which for a long time was about 3.0 m³/sec, the concentration of oxygen was 0.42 mg/l at Kvarnvik. In 1961 oxygen concentration was 2.0 mg/l at a flow of 7.2 m³/sec, in 1962 at 5.2 m³/sec 3.6 mg/l, in 1964 0.75 mg/l at 3.4 m³/sec and in 1966 0.7 mg/l at flow of 18 m³/sec.

Much has been done to purify the water of the river, but it seems that the discharge of polluted water tends to increase more rapidly than the measures of purification. With this tendency the present water supply from the Lake Vombsjön is not enough to maintain conditions satisfactory, particularly so at low water flow.

VI. Death of fish

SWENANDER (1910) mentioned that for a long time people have complained about the heavy fish death in the river as soon as the sugar factories began their activities in the autumn. In 1907 at that season, large quantities of fish of different species died in the lower part of the river. He suggested that large quantities of *Sphaerotilus* and *Leptomitus* — occurring downstream of Örtofta sugar factory — indicate strong pollution and scarcity of oxygen, and concluded that the fish death was caused either by poisoning or oxygen deficiency or by both.

Since SWENANDER's report, death of fish has occurred many times in the river. A few more recent cases will be dealt with. In 1947, death of fish occurred in the lower reaches of the river. The rainfall was very low and the water flow at Kävlinge as low as 0.4 m³/sec. In combination with a relatively high water temperature and heavy pollution of the river this was the cause of the death of fish (WEIJMAN-HANE 1964).

The largest mass death of fish in the river occurred in late October 1951 when a pond dam broke down at Örtofta sugar factory discharging stored waste water into the river and causing extensive death of fish downstream as far as the river mouth (WOLF 1965).

In October 1959, the Swedish Salmon and Trout Association (cited from WEIJMAN-HANE & ALMESTRAND 1960) reported death of fish at Krutmöllan as a result of low oxygen content and pollution caused by water coming from the stream Bråån and from Örtofta sugar factory. The same phenomenon occurred at Håstad Mölla in 1960.

On 18 June 1962, upstream Furulund, fish were observed gasping for air at the water surface. The oxygen situation was found to be critical in the river from Kävlinge to Löddeköpinge. In spite of the water flow being

5 m³/sec the pollution from Kävlinge in combination with high water temperature resulted in rapid oxygen consumption which initiated fish death (WEIJMAN-HANE & ALMESTRAND 1962).

In autumn 1962, large quantities of fish died in the lower reaches of the river. WOLF (1965) estimated the dead fish to ca 75 tons. The cause was the low content of oxygen, as low as 0.5 mg/l at Högsmölla, due to pollution by waste water of different kinds (WEIJMAN-HANE & ALMESTRAND 1962).

At the end of August and beginning of September 1964, the situation was very critical between Rinnebäck and Högsmölla. Gasping fish were observed. The oxygen content was slightly over 1 mg/l between Rinnebäck and Kävlinge urban district, but at Högsmölla only 0.8 mg/l (WEIJMAN-HANE & ALMESTRAND 1964). Dead fish were found.

Thus, present conditions are more or less the same as those described by SWENANDER in 1910.

VII. Qualitative composition of benthic fauna

The collections were made when electro-fishing in May to November 1965 and 1966, in the lower reaches of the river. The fauna was collected with a net of ca 1 mm mesh size, and preserved in 80 % alcohol and identified to species or the lowest possible taxon (Table 3).

The samples from each month were added since the organisms in question were found to be distributed through the study area, except such marine or brackish water species as *Neomysis integer* which reach only short distances upstream the river mouth. Most samples were taken near Stävie. The sampling was intended to give a simple survey of bottom-living animals which might be of importance as fish food.

The *Ephemeroptera* were specifically identified by Dr. STAFFAN ULFSTRAND. Fil.kand. L.-E. PERSSON helped with the identification of the *Gastropoda*.

The most important taxa were *Gastropoda*, *Chironomidae*, *Corixidae*, *Ephemeroptera* (especially *Cloëon dipterum*), *Asellus aquaticus*, *Hirudinea* (especially *Piscicola geometra*) and *Oligochaeta* (cf. Table 3).

VIII. Production of plankton organisms

Plankton was collected from April to November in 1964 and 1965. Three samples each of 10 l of water were filtered through a net with a mesh size 100 μ (in 1964) and 145 μ (in 1965). The samples were taken between 10.00 hr and 17.00 hr at the surface (not deeper than 30 cm) and in the same area where fish fry were collected by electro-fishing. The stations are described above (p. 8).

Table 3. The occurrence of bottom and vegetation fauna in the lower part of the River Kävlingeån (xxx = common, xx = less common, x = rare). () * number of samples.

	April	May	June		July		August		Sept.		Oct.	Nov.
	1966 (2) *	1966 (5) *	1966 (7) *	1966 (5) *	1966 (2) *	1966 (7) *	1966 (8) *	1966 (4) *	1965 (4) *	1965 (1) *	1965 (4) *	1965 (2) *
HYDROZA	-	x	x	-	xx	-	x	-	x	x	-	x
TURBELARIA	-	x	-	-	x	xx	x	-	x	-	x	x
NEMATODA	xx	-	-	-	-	-	-	-	-	-	-	-
OLIGOCHAETA	xxx	xx	x	x	xxx	x	xx	-	-	-	xxx	x
TURBELARIA	-	x	-	-	x	xx	x	-	-x	-	x	x
HIRUDINEA												
<i>Piscicola geometra</i> (L.)	-	x	-	-	x	x	x	-	xx	x	xxx	x
Other leeches	xx	x	-	x	xxx	xx	xxx	-	xxx	x	xxx	xx
COPEPODA												
<i>Argulus foliaceus</i> (L.)	-	-	xx	-	xx	xx	-	-	-	-	-	-
MYSIDACEA												
<i>Neomysis integer</i> (LEACH)	-	-	-	-	-	-	-	xxx	-	-	-	-
ISOPODA												
<i>Asellus aquaticus</i> L	-	xx	x	xx	xxx	x	xxx	-	xxx	x	xxx	xxx
AMPHIPODA												
<i>Gammarus pulex</i> L	-	-	-	-	x	x	x	-	xxx	-	xxx	-
HYDRACARINA	x	x	x	x	xxx	x	xx	x	x	-	xx	-
EPHEMEROPTERA												
<i>Baetis rhodani</i> (PICT.)	-	x	-	xxx	-	xx	-	-	-	-	-	-
<i>B. fuscatus</i> (L.)	-	x	-	-	-	x	xx	-	xxx	-	-	x
<i>B. buceratus</i> Etn.	-	-	-	-	-	x	-	-	-	-	-	-
<i>B. vernus</i> Curt.	-	-	-	-	-	-	xx	-	-	-	-	xx
<i>Cloeon dipterus</i> (L.)	-	x	xx	-	xxx	x	xxx	-	xxx	-	xxx	x
<i>Caenis robusta</i> Etn.	-	-	-	-	x	-	-	-	-	-	-	x
<i>Centropilum luteclum</i> (MÜLL.)	-	-	x	-	-	-	-	-	-	-	-	-
ODONATA Larvae	-	x	-	-	x	-	x	-	-	-	xx	xx
HEMPITERA												
Notonectidae	-	-	-	-	x	-	x	-	x	-	-	-
Corixidae	x	xxx	x	xx	xxx	xx	xxx	xxx	xxx	-	xxx	xxx
NEUROPTERA Larva (Sisyridae?)	-	-	-	-	-	-	-	-	-	-	-	x
TRICHOPTERA	-	x	-	-	xx	x	x	x	xxx	xx	xx	xx
COLEOPTERA												
Dytiscidae	-	-	-	-	xxx	-	x	-	-	-	x	-
Other beetles	-	x	-	x	xx	-	x	-	xx	-	x	xx
DIPTERA												
Simuliidae	xx	xx	-	x	-	xx	x	x	xx	-	-	xx
Chironomidae	xxx	xxx	xx	xxx	xxx	xx	xxx	xx	xxx	xx	xxx	xxx
Ceratopogonidae	x	x	-	-	x	-	x	-	-	-	-	-
Other Diptera	x	x	x	-	xx	-	xx	-	xx	-	-	-
GASTROPODA												
<i>Lymnaea auricularia</i> (L.)	-	-	-	-	xx	x	x	-	-	-	-	x
<i>L. stagnalis</i> (L.)	-	-	-	-	x	-	x	-	xx	-	x	-
<i>Physa fontinalis</i> (L.)	-	-	-	x	xx	x	-	-	xx	-	xx	-
<i>Planorbis carinatus</i> Müll.	-	-	-	-	-	-	-	-	-	-	x	-
<i>Anisus vortex</i> (L.)	-	-	-	-	-	-	-	-	x	-	xx	x
<i>Bathymphalus contortus</i> (L.)	-	-	x	x	-	x	-	-	-	-	x	-
<i>Gyraulus</i> spp	-	x	-	-	xx	x	xx	-	xx	-	xxx	xxx
<i>Viviparus fasciatus</i> Leach	-	-	-	-	-	xx	-	-	-	-	-	-
<i>Acroloxus lacustris</i> (L.)	-	x	-	-	-	-	-	-	x	-	x	-

Table 3. (Continued)

	April	May	June		July		August		Sept.		Oct.	Nov.
	1966 (2)*	1966 (5)*	1966 (7)*	1966 (5)*	1966 (2)*	1966 (7)*	1966 (8)*	1966 (4)*	1965 (4)*	1965 (1)*	1965 (4)*	1965 (2)*
<i>Bithynia tentaculata</i> (L.)	-	x	-	-	xx	xx	x	-	-	-	xx	-
<i>B. leachi</i> (SHEPPARD)	-	-	x	-	xx	x	-	-	x	-	x	-
<i>Hydrobia</i> sp	-	-	-	-	-	x	-	-	-	-	-	-
<i>Valvata macrostoma</i> (STEENBUCH)	-	-	-	-	-	-	x	-	-	-	x	-
<i>V. Piscinalis</i> (MÜLL.)	-	x	-	-	xx	-	x	-	x	-	xxx	xx
PELECYPODA												
<i>Anodonta piscinalis</i> NILSSON . .	-	xx	-	-	-	-	-	-	-	-	-	-
<i>Sphaerium corneum</i> (L.)	-	-	-	-	x	-	-	-	-	-	xx	-
<i>Mytilus edulis</i> L.	-	-	-	-	x	-	-	-	-	-	-	-

Rotatoria and nanoplanktonic forms which pass through the meshes of the net, were of subordinate importance for the present study of the diet of the ide fry and its relation to the plankton, since quantities of nanoplanktonic organisms are eaten by fish only during the very early stages of life. The plankton was studied after preservation in formalin. The occurrence of plankton algae was noted only in 1965.

Planktonic organisms in the river were recorded by SWENANDER (1910) and WEIJMAN-HANE & ALMESTRAND (1958—1966). They treated especially those species in some way connected with pollution, e.g. the ciliates *Colpidium colpoda*, *Paramaecium bursaria* EHRENBERG, *Carchesium lachmanni*, *Chilodon cucullulus*, and the flagellates *Euglena viridis* EHRENBERG, and *Chlamydomonas*. They also recorded the rotifer *Rotifer vulgaris*.

The mass development of Protozoa and the rotifers is largely dependent upon the extent of water pollution and they may be used as indicators of pollution.

The lower reaches of Kävlingeån are rich in planktonic organisms typical of an eutrophic environment. Phytoplanktonic organisms of particular importance in Kävlingeån are the green algae *Cladophora* and *Stigeoclonium tenue*. The latter is typical for environments under self-purification. Further, the diatoms *Navicula gregaria* and *Nitzschia palea*, are common.

SWENANDER (1910) lists five crustacean zooplankters from the river, viz. *Bosmina coregoni* BAIRD, *Chydorus ovalis* KURZ, *Daphnia hyalina* LEYDIG and the copepods *Diaptomus graciloides* LILLJEBORG and *Cyclops* sp. *B. coregoni* was the most common species and *Ch. ovalis* the least common of the crustacean zooplankters. In general *Cladocera* were more abundant than *Copepoda*.

My results (Table 4) confirm that *Cladocera* are more common than *Copepoda*, 58.7% compared with 41.3% of the total samples in 1964. 8.8% were *Cladocera* and 13.2% *Copepoda* in 1965.

Table 4. Quantities of crustacean zooplankters in the lower part of the River Kävlingeån with notes on planktic algae in 1965.

Date of collecting	CLADOCERA			COPEPODA		ALGAE xxx = common xx = less common x = rare
	Number of station	Number of specimens per litre of water	% of the total planktic crustaceans per sample	Number of specimens per litre of water	% of the total planktic crustaceans per sample	
9.V.64	Ia	—	—	9	100.00	
"	Ib	—	—	4	100.00	
"	Ic	1	8.33	11	91.67	
28.V.64	Ia	111	25.00	333	75.00	
"	Ib	54	2.95	1,777	97.05	
"	Ic	111	6.45	1,611	93.55	
"	Id	834	37.52	1,389	62.48	
16.VI.64	Ia	142	92.21	12	7.79	
"	Ib	24	92.31	2	7.69	
"	Ic	12	85.71	2	14.29	
"	Id	334	96.53	12	3.47	
"	Ie	6	100.00	—	—	
6.VII.64	Ia	1	50.00	1	50.00	
"	Ib	1	100.00	—	—	
3.IX.64	Ia	2,069	99.28	15	0.72	
"	Ib	430	50.00	430	50.00	
"	Ic	3,846	100.00	—	—	
30.X.64	I	1	50.00	1	50.00	
13.XI.64	Ia	—	—	—	—	
"	Ib	2	75.00	1	25.00	
"	Ic	—	—	1	100.00	
14.VI.65	II	213	84.52	39	15.48	×
"	III	313	73.13	115	26.87	—
"	IV	624	76.28	194	23.72	—
"	V	25	100.00	—	—	×
"	VI	285	96.94	9	3.06	×
1.VII.65	I	159	98.76	2	1.24	×
"	II	296	96.42	11	3.58	×
"	III	415	98.34	7	1.66	—
"	IV	322	97.28	9	2.72	×
"	V	157	96.32	6	3.68	×
"	VI	70	90.90	7	9.10	×
"	A	15	88.24	2	11.76	—
20.VII.65	I	224	82.96	46	17.04	×
"	II	535	90.07	9	9.93	—
"	III	157	74.41	54	25.59	×
"	IV	91	84.26	17	15.74	×
"	V	169	91.85	15	8.15	×
"	VI	33	75.00	11	25.00	×
"	A	13	54.17	11	45.83	—
30.VII.65	I	56	81.16	13	18.84	—
"	II	828	95.50	39	4.50	—
"	III	15	31.25	33	68.75	—
"	IV	9	81.82	2	18.18	×
"	V	217	75.09	72	24.91	×
"	VI	52	89.66	6	10.34	—
"	A	4	66.67	2	33.33	—
6.VIII.65	I	213	75.53	69	24.47	×
15.IX.65	Ia	11	84.62	2	15.38	—
"	Ib	24	58.54	17	41.46	—
18.X.65	Ia	33	45.83	39	54.17	—
"	Ib	—	—	—	—	—
9.XI.65	III	37	100.00	—	—	—
"	A	74	91.36	7	8.64	—

When studying the table we have to remember that although the sampling technique allowed for diurnal variations in the plankton density, no particular regard was taken to possible patchiness of plankton distribution.

IX. Fish fauna and fishery

The fish fauna of the River Kävlingeån is comparatively rich and diverse. In order of frequency the families represented are: *Cyprinidae*, *Percidae*, *Anguillidae*, *Esocidae*, *Gasterosteidae*, *Pleuronectidae*, *Salmonidae*, *Gadidae* and *Petromyzontidae*.

The cyprinids were represented by roach *Rutilus rutilus* (L.), ide *Idus idus* (L.), bream *Abramis brama* (L.), tench *Tinca tinca* (L.), crucian carp *Carassius carassius* (L.), bleak *Alburnus alburnus* (L.), white bream *Blicca bjorkna* (L.), rudd *Scardinius erythrophthalmus* (L.), minnow *Phoxinus phoxinus* (L.), and common carp *Cyprinus carpio* L.

The Percidae were represented by perch *Perca fluviatilis* (L.), pike-perch *Lucioperca lucioperca* (L.) and the ruff *Acerina cernua* (L.). The sticklebacks present were the three-spined stickleback *Gasterosteus aculeatus* L., the ten-spined stickleback *Pungitius pungitius* (L.), and the fifteen-spined *Spinachia spinachia* L.

The salmonids of the river are atlantic salmon *Salmo salar* L. and the sea-trout *Salmo trutta* L. Further species represented are as follows: the eel *Anguilla anguilla* (L.), the pike *Esox lucius* L., the flounder *Pleuronectes flesus* L., the gadids burbot *Lota lota* (L.), the atlantic cod *Gadus morhua* L., and finally the river lamprey *Lampetra fluviatilis* (L.) and the sea lamprey *Petromyzon marinus* L.

All these species were collected by me in the lower part of the river, from Högsmölla to the river-mouth. *Gadus morhua* and *S. spinachia* occurred near the river mouth where also *Cottus scorpius* L., *Labrus berggylta* L. and *Zoarces viviparus* L. were captured by the Swedish Salmon and Trout Association's fishermen. They also captured the cyprinid *Abramis vimba* L. in the lower reaches of the river. I have caught *Pleuronectes flesus* up to Högsmölla, i.e. about 10 km upstream, especially juveniles when electro-fishing. In June 1966, 3 adult specimens of *Petromyzon marinus* were captured.

Rare fish species in the lower part of the river are *Salmo salar*, *S. trutta*, *Lota lota*, *Acerina cernua*, *Alburnus alburnus* and the *Petromyzontidae*.

The river has had no natural stock of salmon during the last hundred years and no stock of sea-trout during the last fifty years, mainly because of the bad pollution. Moreover mill-dams in the lower part of the river during periods of low water flow also formed obstacles preventing the migration of the fish to the spawning ground lying further up.

Table 5. Amount in kg of the most important commercial species of fish captured in the lower reaches of the River Kävlingeån, from Högsmölla to the mouth, during a period of 12 years (data from the *Svenska Lax- och Laxöringsföreningen u.p.a.* 1955—1966).

Year	Pike	Perch	Eel	Bream	Roach & ide	Other fish
1955	175	1,775	—	720	17,400	100
1956	241	1,659	730	645	22,900	127
1957	60	1,191	655	338	9,015	115
1958	90	1,580	1,100	508	10,485	511
1959	209	2,348	1,040	534	16,900	376
1960	178	3,225	540	190	11,220	140
1961	217	1,867	680	398	10,455	202
1962	322	2,158	835	490	14,210	1,132
1963	177	830	875	31	6,615	110
1964	307	1,040	360	310	10,350	165
1965	293	520	785	165	10,750	245
1966	186	350	1,800	175	6,350	400

Up to latter half of the 19th Century there was still good fishing (WOLF 1960). A good supply of perch, pike, eel, roach, ide and crayfish existed. In the lower reaches of the river, about fifty men got a livelihood from fishing. The yield in these parts has been estimated at several hundred tons annually. In the upper parts of the river fish production was also high. Salmon has not been caught since the 1850's. Sea-trout, on the other hand, were caught in small numbers within the lower reaches of the river up to the beginning of the 20th Century. During the present century, the fish yield from the river has steadily decreased.

Between 1945 and 1950 about two million fry of salmon and sea-trout were implanted by the Swedish Salmon and Trout Association in small, unpolluted tributaries of the river. It was found that these small water courses had a considerable productive capacity: brooklets only half a meter to one meter wide yielded more than 300 kg/ha (WOLF 1960).

According to WOLF, a large part of the migrant fish died each year in the seriously polluted lower reaches of the river. A number survived, however, and returned after their growth period in the sea. Returns were first registered in 1949 for *Salmo trutta* and in 1950 for *S. salar*. Since 1950 salmon and trout have been caught every year.

Adult salmonids are taken in a trap at Hållstad Mölla when the fish, after having spawned, migrate to the sea. Some thousand *S. salar* and *S. trutta* have migrated up the river and spawned during the last few years (WOLF 1960). It is not yet certain, however, whether the stock of *S. salar* can be maintained as a naturally reproducing population in the river.

According to WOLF (1965) *S. trutta* fry have not been planted since 1946 in the water system, while between 1962—1964, 18,000—21,000 *S. salar* fry

have been annually implanted in the tributary Bråån. The migration downstream increased from 300 smolts in 1963 to 800 specimens in 1964 (average length 155—160 mm and the largest 198 mm). Some of these salmon were marked and captures were reported from the Norwegian Westcoast and from Dueodde on Bornholm but so far no specimens have been caught in the river. Juvenile *S. trutta* migrate downstream every year, the number fluctuating from 100 to 700 specimens per year. Evidently, a reproducing stock of *S. trutta* exists in the water system.

Table 5 gives the biomass in kg of the most important commercial species captured in the lower reaches of the river, from Högs Mölla to the mouth, during the last 12 years (data from the *Svenska Lax- och Laxöringsföreningen u.p.a.* 1955—1966). The eels were collected at Håstad Mölla.

X. Notes on the macrophytic vegetation

In the lower part of the river there is a rich vegetation of floating and submersed plants, which in the summer develop so that they may cover the entire width of the river (Fig. 2). The vegetation gradually diminishes downstream except for *Phragmites communis*.

Common aquatic plants are *Potamogeton pectinatus*, *P. lucens*, *P. natans*, *Ceratophyllum demersum*, *Lemna minor*, *L. polyrrhiza*, *Scirpus lacustris*, and *Nymphaea alba*, *Nuphar luteum*, and *Phragmites communis*.

XI. Migration and spawning season of the ide

The ide penetrates the River Kävlingeån water system upstream as far as to Lake Vombsjön and the streams Bråån and Klingavälsån (*vide* Fig. 1).

The largest movements of ide occur in the lower reaches of Kävlingeån, between the mouth and Högs Mölla where the migrating fishes encounter the first mill-dam. Upstream of Högs Mölla there are mill-dams and industrial constructions affecting the water flow at Kävlinge, Rinnebäck, Krutmölla, Harriemölla, Besmölla, Kvarnvik and Håstadmölla. Serious obstacles to fish movement occur at Rinnebäck and Kvarnvik where a cement wall across the river diverts all the water except at high flow.

Salmo trutta and *S. salar* pass all these obstacles and reach their spawning places. Ide *en route* downstream are captured at Håstadmölla which shows that the population in the upper reaches is based upon fish migrating upstream for spawning.

Most of the large captures of downstream-migrating ide at Håstadmölla, occur during spring in connection with the large migrations of full-grown ide in the lower reaches, coinciding with spawning movements and high

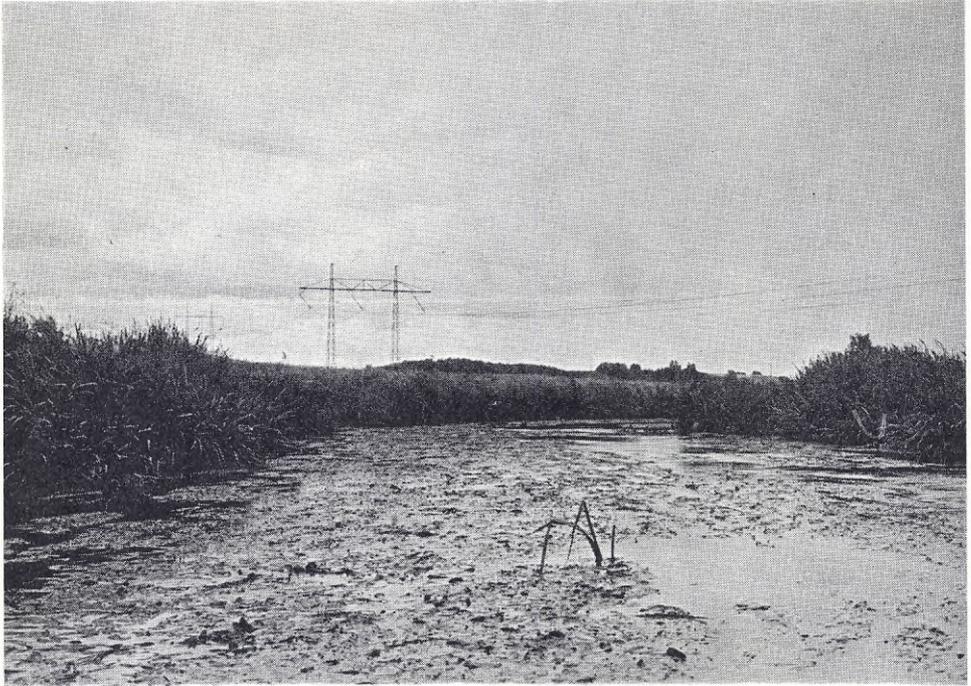


Fig. 2. View of the River Kävingeån (station II). Dense vegetation of *Potamogeton* spp. covering the entire width of the river (9 Aug. 1966).

water flow. Of 57 ide migrating downstream at Håstadmölla 36 were captured in April—June (*Svenska Lax- & Laxöringsföreningen u.p.a.* 1954—1966).

According to EKSTRÖM (1831), SMITT (1895) and ALM (1964) ide may ascend even large rapids, jumping over obstacles like the salmon.

The ide spends the first year of its life in the river and then joins older migrating fish to the sea. During the summer (June—August) ide older than age group 0 disappear almost completely from the river, spending the summer in the sea. However, some specimens not older than group II remain in the lower part of the river and from time to time large ide pass the river mouth and proceed into the lower reaches of the river when weather is rough.

In autumn the ide return to the river, the smallest ones in September and as the autumn advances the schools increase in number and size. Late in November, or before that time depending on water temperature, all age groups are represented in the lower part of the river. The fish remain during winter at the river mouth and in the low reaches (cf. also OTTERSTRÖM 1930—31).

During autumn and spring the fish stay in the lower reaches. At times

large schools are easily observed on the move. The mature fish go to the spawning place. When spawning is complete they leave for the sea, followed by subadult fish and finally by the small individuals.

Generally, the largest ide leave the river earlier (April to May) and return later (October to November). Thus fish larger than 26—30 cm (older than age group IV—V) spend much more of the year in the sea than do the small fish.

Spawning time

The spawning of the ide in the River Kävlingeån during the 4-year study period occurred from 29 March to 17 April. In 1964 it started on 11 April (peak of spawning on 12 and 13). In 1965, spawning began on 1 April (peak of spawning on 2, 3 and 4) and in 1966 on 6 April (peak of spawning on 6 and 7). In 1967 the ide spawned on 29 March (peak of spawning on 30 and 31).

The ide spawns in shallow streams at a depth of 0.5—1.5 m. The eggs adhere to stones, plants, etc. The largest fish spawn first. Spawning began 2 to 3 days after the daily water temperature had reached and remained above 5°C (Table 6). Most ide spawned during 2 to 3 days when the water temperature rose to about 7°C and the weather was fine. This was the case in 1964. But if the water temperature drops after the initial period of spawning, additional spawning takes place when the temperature rises again, as in 1966. Then spawning started on 8 April, on 10 April the water temperature dropped to 2°C and spawning ceased. It recommenced on 25 April when the temperature returned to 5°C (*vide* Table 6).

According to LILLJEBORG (1891) spawning is generally earlier in southern Sweden than further north and varies according to the water temperature.

According to STUXBERG (1895) the spawning period extends from the end of March in South Sweden to June in North Sweden. At a water temperature of 8 to 10°C the spawning is reported to last only 3 to 4 days, occurring day and night.

SMITT (1895) reports spawning of the ide in Central Sweden to occur about the end of April. The males arrive earlier to spawning place than the females, the latter arriving when the water temperature was about 9°C. In Denmark OTTERSTRØM (1914) describes spawning at a water temperature of 8—10°C. Later (1930—31) he reported spawning in March and April, saying that the ide seemed to have begun spawning while the Lake Arresø had a temperature of about 6°C. POPESCU *et al.* (1960) stated that the spawning of the ide starts when the water temperature has risen to 7—9°C and lasts 10 days and that it is interrupted by large changes of temperature or by flooding.

EKSTRÖM (1831) found spawning to occur at the end of April in the islands round Mörkö — Central Sweden — and reports that the peak did not last

Table 6. Daily mean water temperature in °C in the River Kävlingeån at Håstadmölla in relation to the spawning of the ide in 1964—1967.

Date	1964	1965	1966	1967
March				
20	—	3.1	2.8	3.6
21	—	—	3.2	4.2
22	—	2.9	2.8	4.6
23	—	2.9	2.8	5.0
24	—	3.5	2.6	—
25	—	3.8	2.3	3.1
26	—	3.3	2.0	—
27	—	3.2	2.5	5.2
28	—	3.4	3.4	5.7
29	—	4.4	2.6	4.8
30	—	5.5	2.4	5.0*
31	—	6.0	2.4	5.0*
April				
1	—	6.0	3.0	5.1*
2	—	5.8*	3.9	—
3	—	5.9*	5.3	5.1
4	—	5.5*	5.2	5.4
5	—	5.6	5.0	5.8
6	2.8	6.2	4.6*	5.8
7	3.9	6.6	5.0*	5.5
8	3.7	5.9	5.0*	5.3
9	4.6	4.4	4.2	—
10	5.3	3.2	2.0	5.7
11	6.0	3.0	—	6.0
12	—	4.6	—	6.2
13	6.7*	5.2	—	7.2
14	7.0*	5.5	—	8.1
15	7.0	6.1	—	8.2
16	7.7	6.1	—	8.7
17	8.3	6.8	—	8.2
18	9.0	6.8	1.8	6.2
19	10.8	6.5	—	6.3
20	11.5	5.8	—	6.8
21	12.5	7.2	—	8.2
22	11.8	8.2	4.2	6.2
23	11.1	8.5	—	6.4
24	9.8	8.0	4.2	6.8
25	8.9	—	5.1	7.1
26	9.0	7.8	5.9	7.7
27	8.8	8.0	6.4	8.5
28	9.2	7.6	7.3	8.8

* water temperatures at peak of spawning.

more than 3 days and that the males arrived first to the spawning place and that after the spawning males and females return together. STUXBERG (1895), KRÖYER (cited by OTTERSTRØM 1930—31) and DUNCKER (1960) agreed that the males arrived first in the spawning place and that the females are first to leave. MÜHLEN (*cf.* OTTERSTRØM 1930—31) in Estonia (Lake Wirz-Järm) described the spawning of ide above 1 kg from the end of March to the end of April and of the small ide after middle of April.

ÅSTRÖM (1859) reports spawning around 20 March in the River Höljeå in southern Sweden, SIEBOLD (1863) from April to May in middle Europe, and DUNCKER (1960) from March to May in Nordmark (Germany).

Spawning results

Under natural conditions percentage of fertilization is very high. The rate of hatching is usually also rather high (PLISZKA 1953).

The important factors influencing the success of the spawning in the River Kävlingeån are: — 1) hatching is likely to show considerable losses if the water temperature drops after spawning and is below 5°C for some time (*vide* p. 32). Thus, in 1966 the water temperature dropped to about 1°C after the spawning and remained below 5°C for 16 days from April 8 to 24 (see Table 6). — 2) Deficiency in oxygen supply during the early development of the eggs, caused by pollution (*cf. e.g.* p. 13). — 3) Predation: gulls and other birds and certain species of fish feed on the eggs. In 1965 after a very successful spawning gulls were observed taking eggs at the spawning place at Stävie when the water level was rather low.

XII. Growth and age of the ide

The first year of life was divided into three stages, *viz.* 1) embryonic, from time of fertilization to hatching of the eggs, 2) sac-fry, the time during which the young fish obtain their nourishment entirely from the yolk sac, and 3) older fry which stage begins when the fry start to feed actively and continues to the end of the season's growth.

Embryonal development

The length of time required for the eggs to hatch is related to water temperature.

Fertilization of eggs from females with sperm from 2—3 males was carried out in pans at the river side. The eggs were thereafter transported to the laboratory in a pan with 3—5 l of river water and was kept at 4—5°C. Batches of eggs were then distributed in small beakers to aquaria filled with 20—30 l tap water in which the eggs adhered to small branches or to plastic netting.

Material from two spawning periods was examined (Table 7). In 1965 the eggs began to hatch after 5.5 days at a mean temperature of 13.8°C (temperature sum 94): the length of the fry-sac at hatching ranged between 5.8—6.6 mm. In 1967, one batch of eggs began to hatch after 12.8 days at a mean water temperature of 10°C (temperature sum 129), another after

Table 7. Development of embryo and sac-fry stages.

Sample	Embryonic stage (from fertilization to hatching of eggs)				Sac-fry stage during the first week (1965)				
	Σ days to hatch	Temperature °C		Temperature sum	Days	Mean temperature	Σ specimens	Mean length in mm	Growth rate in mm per day
		mean	range						
1965	5.5	13.8	6.5—18.0 (16—18) ¹	94	0	18	10	6.0	—
1967-I	12.7	10.1	8.3—16.8 (8 & 11) ¹	129	1	18	11	7.1	1.1
1967-II	17.0	10.1	4.1—12.6 (11) ¹	172	2	18	12	8.2	1.1
1967-III	23.0	9.3	4.3—10.0 (9—10) ¹	213	3	18	17	8.5	0.3
					4	18	18	8.8	0.3
					6	18	17	9.0	0.2

¹ Modal temperature

17 days at a mean of 10.1°C (172), and a third after 23 days at a mean water temperature of 9.3°C (213). When eggs were kept in water at 4—5°C, they did not hatch.

Thus, low temperatures retard hatching, and below 5°C there is no hatching.

POPESCU *et al.* (1958) gave 9 days as the hatching time of the ide at a mean temperature of 12.6°C (temperature sum 110). According to KRIJANOVSKII (cited by POPESCU *et al.* 1958) the hatching period is longer than 17 days at 10—12°C. SUNDEWALL (1855) and STANKOVITCH (1921) report 14—18 days and SEGERSTRÅLE (1926) 8—12 days, but they do not give the water temperature.

Sac-fry growth

In the laboratory in 1965, the length of the fry at hatching ranged between 5.8 and 6.4 mm (mean, 6 mm) (Table 7).

The growth rate was 1.1 mm per 24 hours during the first 56 hours and than it decreased. On the 6th day it was only 0.2 mm per 24 hours. The mean growth during the first week was 0.5 mm per day, the fry having only the contents of the vitelline sac as source of food.

According to SUNDEWALL (1855) a newly hatched larva measured 5 mm and a three days old larva somewhat above 6 mm. Probably the measurements refer to larvae fixed in alcohol. Stankovitch (1921) gave a length of 7 mm at hatching and 10 mm in 15—20 days old larvae after the vitelline sac was absorbed. Finally, POPESCU *et al.* (1958) give the length as 6.5 mm at hatching, 7 mm after 12 hours and 7.5 mm after 48 hours.

Table 8. Total length in mm of the young-of-the-year ide collected in 1963—1966 in the River Kävlingeån.

Date	Σ fish	Mean	Range
<i>1963</i>			
4.VI	4	16	14—17
19.VI	39	27	20—33
3.VII	229	34	27—45
5.VIII	56	47	35—60
<i>1964</i>			
28.V	42	16	14—17
16.VI	21	25	23—27
30.IX	1	69	—
11.XII	9	66	52—73
<i>1965</i>			
8.I	12	68	59—78
3.II	19	76	57—86
3.VI	26	13	12—15
14.VI	161	18	14—21
1.VII	8	28	26—30
20.VII	3	38	32—44
30.VII	7	59	48—66
15.IX	4	57	55—58
28.IX	20	61	53—71
18.X	6	64	58—73
7.XI	17	68	59—79
9.XI	21	65	57—74
<i>1966</i>			
24.V	56	10	8—11
2.VI	82	11	9—13
5.VII	43	32	26—37
12.VII	10	35	33—38
20.VII	53	40	33—46
9.VIII	47	55	42—64
29.VIII	12	68	54—79
25.IX	32	73	57—87
7.XI	17	67	55—78
24.XI	23	76	54—94

Growth of young-of-the-year

The fry remain in individual broods, usually mixed with roach fry, for a period of about two months after hatching. The length at the end of this period is 2—3 cm.

The total length of 1,081 young-of-the-year, collected at intervals of 2—3 weeks during 1963, 1965 and 1966, was measured to study the early growth (Table 8 and Fig. 3). In 1965 and 1966 samples were taken at seven main sites in the lower part of Kävlingeån covering an distance of about 10 km (*vide* Fig. 1). All the fish collected in one day were treated as a single sample, since there was no significant difference in mean length.

The young-of-the-year were measured after fixation in 80 % alcohol. Total

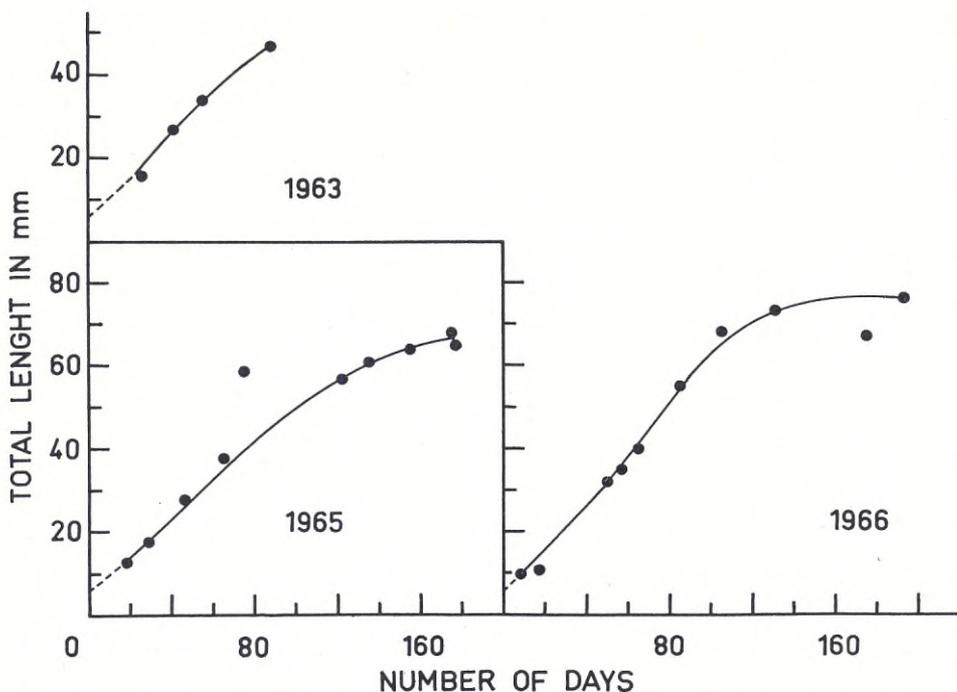


Fig. 3. Increase of total length of young-of-the-year ide, Kävlingeån, 1963, 1965 and 1966. Broken line connects the mean length at hatching with the first sampling each year. The material is listed in Table 8.

body length was measured to the nearest mm. Shrinking due to fixation was corrected for (CALA).

The ide fry were separated from the fry of other cyprinids, mainly that of roach, by means of the pigmentation in the ventral aorta (BALINSKY 1948) or by analysing the pharyngeal teeth (SPILLMANN 1961).

Considerable variation occurred in the growth patterns between the different years. The total length at the end of 2-week intervals after hatching was estimated from Fig. 3 (Table 9). The greatest total increase in one season was observed in 1963 and 1966, while the least growth was observed in 1965. The individual variation in total length was considerable after brood dispersal to deeper water.

The inherent variation is probably increased by the delay and heterogeneity of the spawning conditions.

In order to compare growth in different years, the rate of growth during each 2-week period was calculated from the above material (Table 9). The growth rate was highest during periods 1—3 and then decreased. Growth rates were high for a somewhat longer time in 1966.

It was concluded from the results of the year 1965 and 1966 (*vide* Table 9)

Table 9. Total length in mm of ide fry, calculated for successive 2-week periods, and growth rate during each period, in 1963, 1965 and 1966. The growth rate is expressed as percentage increase of length (in brackets).

The material is based on Fig. 3.

Week no	1963	1965	1966
2	12.0 (100.0)	11.0 (83.3)	13.0 (116.7)
4	19.5 (62.5)	17.5 (59.1)	20.0 (53.8)
6	27.5 (41.0)	24.0 (37.1)	27.0 (35.0)
8	34.5 (25.5)	31.0 (29.2)	35.5 (31.5)
10	40.5 (17.4)	37.5 (21.0)	44.5 (25.4)
12	45.5 (12.4)	43.5 (16.0)	53.5 (20.2)
14	—	49.0 (12.6)	61.0 (14.0)
16	—	53.5 (9.2)	67.5 (10.1)
18	—	58.0 (8.4)	71.5 (5.9)
20	—	61.5 (6.0)	74.0 (3.5)
22	—	64.0 (4.1)	75.5 (2.0)
24	—	65.5 (2.3)	76.0 (0.7)
26	—	—	76.0 (0.0)

that the growth season of the young-of-the-year in Kävlingeån ended in early November. The fry had then attained a mean total length between 6.8 and 7.6 cm for the respective years, and an individual length ranging from 5.5 to 9.5 cm.

STANKOVITCH (1921) gave a total length of 10 mm for 15—20 days old fry and 13.5 mm for 6 week-old fry. SEGERSTRÅLE (1933) reports a mean total length (on 6 October) of 4.4 cm with fry ranging from 3.6 to 5.1 cm.

Age and increase in body length

The age of ide was determined by examination of the scales. Fish were collected from March 17 to April 4, 1966 (294 specimens) and from November 11 to December 5, 1966 (61 specimens). In 1967, 79 ide were captured from February 27 to April 4. Collections were made mostly by seining or by electro-fishing. Some fish were collected in trap nets. Scales were collected from freshly captured fish and the total length and the body weight registered. Sex was determined by gross inspection or, in immature fish, by microscopic examination of the gonads.

Characteristics of the scale annulus

The annulus consists of the usual interrupted ridges or circuli followed by a complete circulus which is laid down as growth resumes in the spring or early summer (Fig. 4). The annuli are easier to recognize in the cranial or anterior part of the scales. The first annuli are easier to recognize than the later ones (Fig. 5), which are especially difficult to recognize in scales from fish older than 10 years (Fig. 6).

A growth field is made up by a series of complete circuli followed by a series of incomplete circuli that gradually shorten as growth slows down (Fig. 4). The first circulus that appears in the following growth season cuts across these shortened circuli. This pattern of growth is most apparent in the cranial part of the scales.

Time of annulus formation

Scanty material was available for the study of annulus formation (Table 10). The data suggest that annulus formation usually occur around early May and is completed about the end of June.

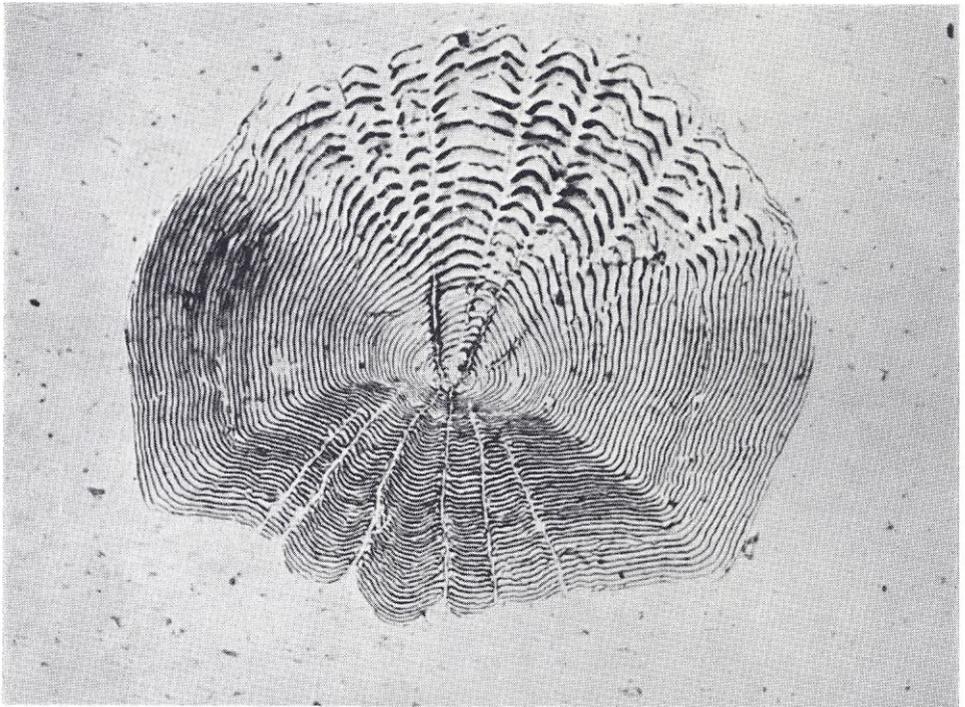


Fig. 4. Scale of ide in age group II (specimen from 18.4. 1966), total length 163 mm, showing the "cutting over" of the circuli at annulus formation.

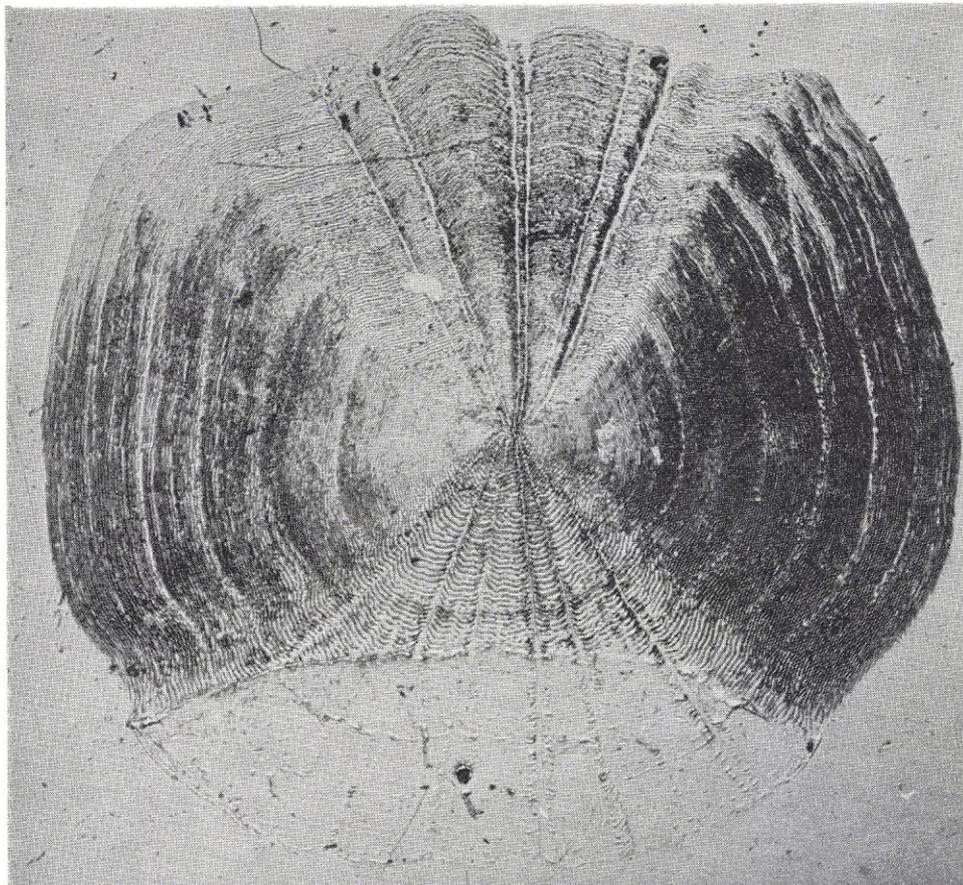


Fig. 5. Scale of ide in age group VII (specimen from 27.4. 1966), total length 440 mm, showing rather easily recognizable annuli.

It seems that older ide, especially mature fish, form annuli earlier than the younger ones. YASUDA (1959) stated that the time of scale ring formation varies considerably. In a single species scale ring formation is influenced by geographical region, age, and degree of maturity. YASUDA concluded that the scale ring generally seems to be formed in an early period of reproductive maturation and/or in connection with spawning. According to BALON (1962) the annulus in scales of the Czech Danube ide may appear in April, but the main formation is in May and June.

Regeneration of scales

The regeneration of scales may be affected by environmental factors such as water temperature and food supply (YAMADA 1961).

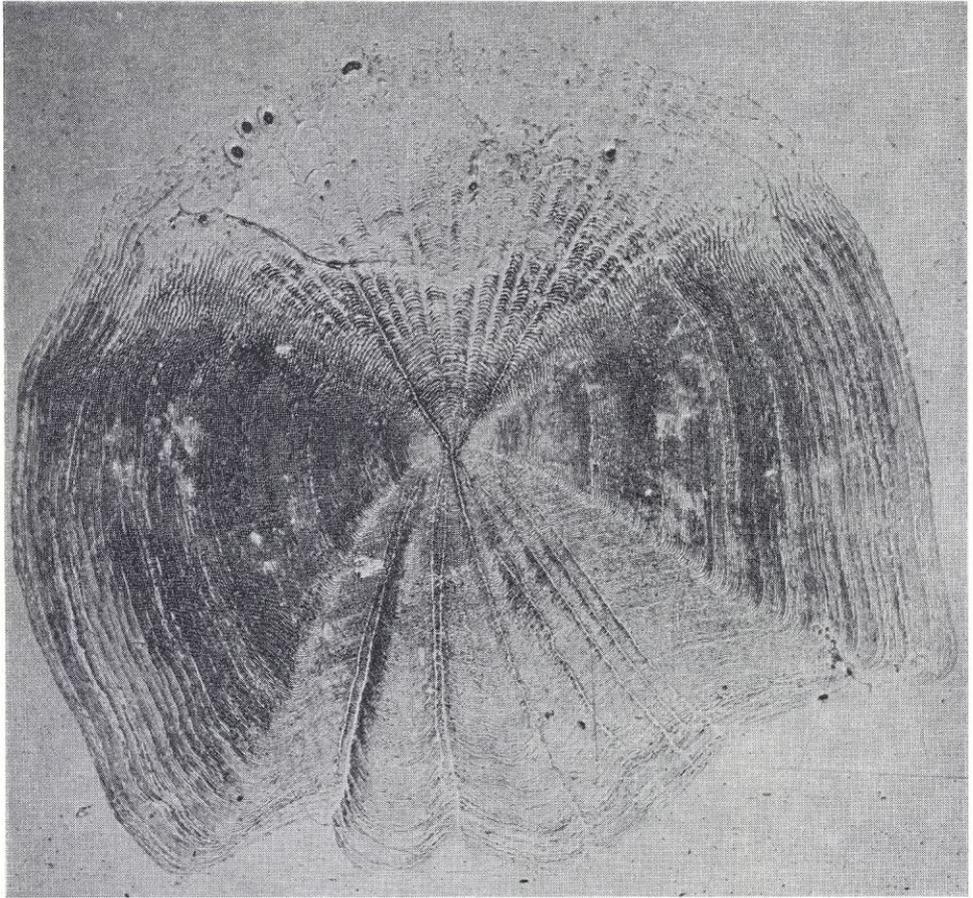


Fig. 6. Scale of ide in age group XII, (specimen from 1.5. 1966), total length 545 mm, showing annuli poorly recognizable in the marginal area.

In 1966 yearlings were captured on 6 May and kept in the laboratory at about 18°C until the start of the experiment on 17 July. Primary scales adjacent to each other were removed from a selected area between the dorsal fin and the lateral line. Five fishes were kept at a mean temperature of about 18°C (warm water), and four fishes at a water temperature constantly changing, by means of a heater, between $4\text{--}11^{\circ}\text{C}$ (cold water). The fish were fed with dry food and *Cladocera*. They were temporarily immobilized with ethyl m-aminobenzoate when measurements and observations were made.

The mean length of the fish in warm water at the beginning of the experiment was 69 mm and the mean weight 2.5 g. The mean length of the fish in cold water was 71 mm and mean weight 2.8 g. On 21 August the values

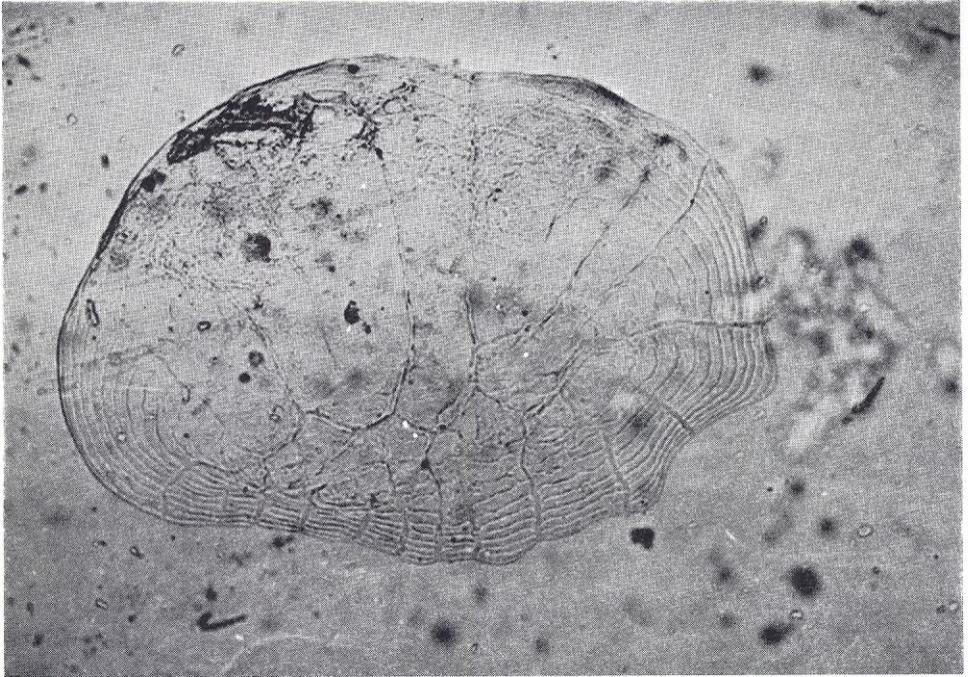


Fig. 7. Regenerated scale, 6 weeks after the removal of the ontogenetic scales, showing circuli in the outer of the central area.

were 72 mm and 2.8 g in warm water and 72 mm and 2.9 g respectively in cold water.

Regenerated scales were observed two weeks after the removal of the primary scales in fish in warm water. The regenerated scales were thin and flexible and had just started the formation of circuli at their margin. Three weeks later 3—5 circuli were present at the scale margin. No regeneration of scales in cold water was observed. On 21 August (after 6 weeks) the regenerated scales in warm water were similar in appearance to primary scales and had about eight circuli in the outer part of the central area (Fig. 7). No regenerated scales were observed in fish maintained in cold water. On 5 September the regenerated scales from fish in warm water was observed to be very similar, even in size, to the primary scales.

Since regeneration of scales in cold water did not occur, one of the fishes from this experiment was transferred to water with a temperature of about 18°C. This fish, like the others kept at the same temperature showed regeneration of scales after 2 weeks. When fish remaining in cold water did not show any regenerated scales on 1 November (about 16 weeks after start of the experiment) the temperature was increased and kept at about 13°C. Two weeks later regenerated scales had developed.

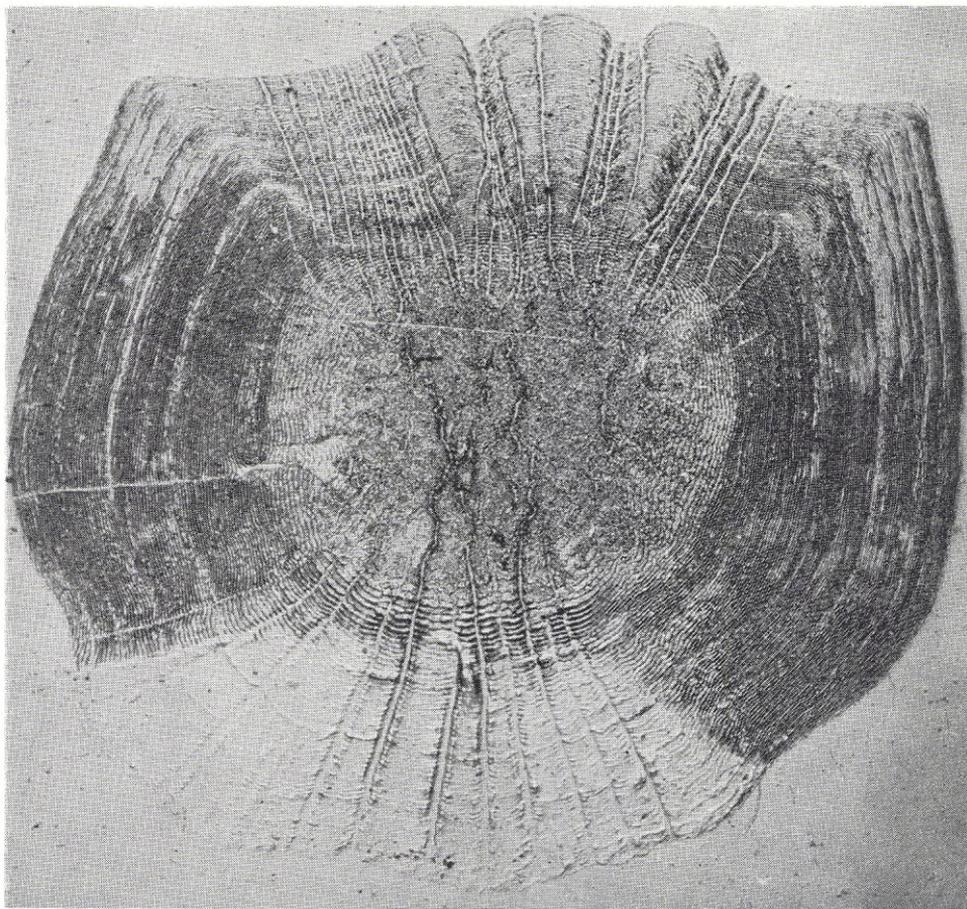


Fig. 8. Regenerated scale from the same fish as in Fig. 4 showing a wide central area and numerous grooves.

The regenerated scales are characterized by 1) a broad central area without circuli but with a grooved network, 2) first circuli were set at broad intervals, and 3) numerous radial grooves in the cranial and caudal area of the scale, connected with the central network (Fig. 8).

Body-scale relation

Scale samples were taken from the side of the fish between the dorsal fin and the lateral line. Scales were impressed on plastic slides by a roller press (SMITH 1954), and were examined with a microprojector at X30. Distance from scale focus to margin, along a selected cranial radius was registered and plotted against the body length (Fig. 9). The body-scale rela-

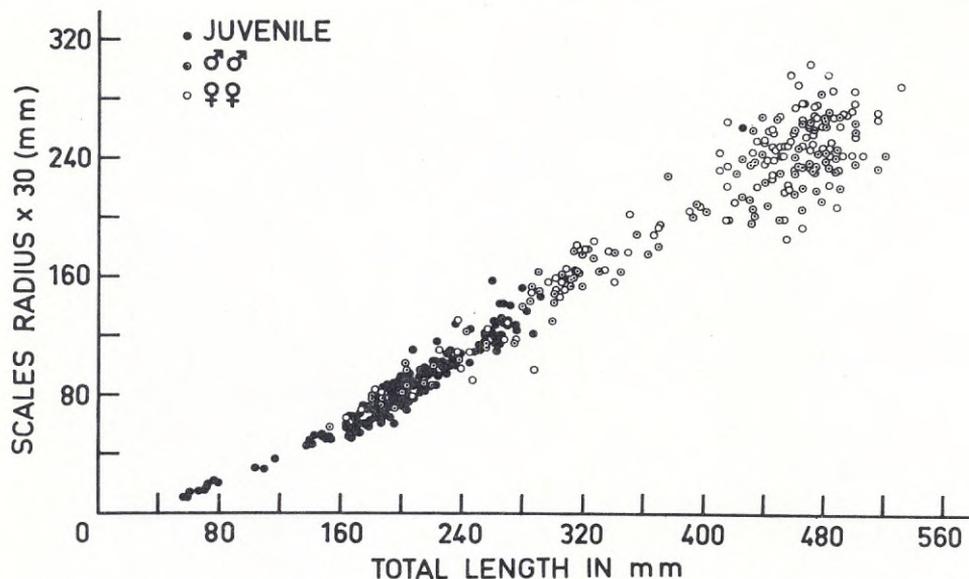


Fig. 9. Relation between scale radius and total body length of material of 433 ide from River Kävlingeån, in 1966—1967.

Table 11. Relation between total body length of fish and scale radius of ide from River Kävlingeån, 1966 and 1967.

Length intervals in mm	Number of fish	Mean total body length in mm	Mean scale radius X30
54—73	8	64	14
74—93	2	77	20
94—113	2	106	29
114—133	1	116	36
134—153	10	140	50
154—173	15	168	59
174—193	58	186	72
194—213	54	201	82
214—233	30	222	95
234—253	17	242	108
254—273	26	263	126
274—293	16	283	135
294—313	13	304	152
314—333	14	320	170
334—353	7	343	173
354—373	4	364	186
374—393	4	383	204
394—413	5	403	219
414—433	17	426	225
434—453	32	445	241
454—473	40	465	248
474—493	35	483	251
494—513	12	499	258
514—433	3	522	267

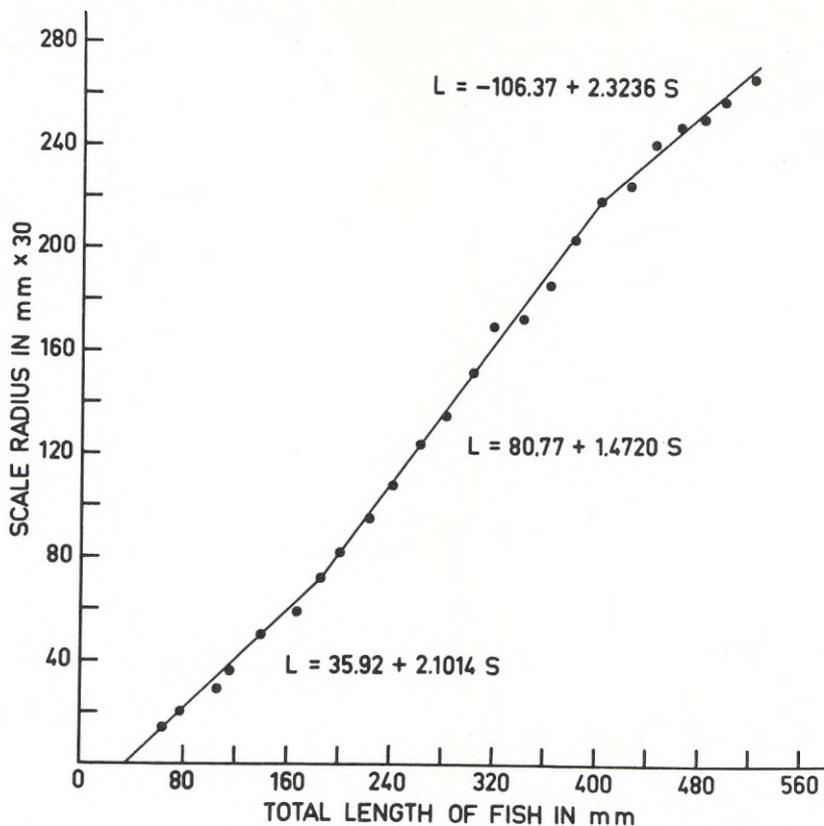


Fig. 10. Relation between total body length and scale radius ($\times 30$) of ide from River Kävlingeån, in 1966 and 1967.

relationship was obtained by plotting the means of total fish lengths (by 2 cm intervals) against the means of the scales measurements (Table 11).

The size-class means (Fig. 10) indicate the body-scale relation to be described adequately by three straight lines intersecting at a length of about 16.6 and 40.3 cm. Thus, the body-scale curve may be subdivided into 3 components: 1) a linear portion representing ide up to 15.3 cm long, 2) a linear portion representing fish between 15.4 and 40.3 cm long, and 3) the linear portion representing larger ide (40.4–53.3 cm). The straight lines fitted by least squares to the means of fish lengths and scale radii had these equations:

$$\begin{array}{ll}
 L = 35.92 + 2.1014S & (L < 15.3 \text{ cm}), \\
 L = 80.77 + 1.4720S & (15.3 < L < 40.3 \text{ cm}), \\
 \text{and } L = -106.37 + 2.3236S & (L > 40.3 \text{ cm}),
 \end{array}$$

Table 12. Length distribution of 433 age-grouped ide from the River Kävlingeån, in 1966—1967.

Total length in mm	Age Group												
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XIII	XIV
56—75	8	—	—	—	—	—	—	—	—	—	—	—	—
76—95	2	—	—	—	—	—	—	—	—	—	—	—	—
96—115	1	1	—	—	—	—	—	—	—	—	—	—	—
116—135	—	1	—	—	—	—	—	—	—	—	—	—	—
136—155	—	8	2	—	—	—	—	—	—	—	—	—	—
156—175	—	3	18	—	—	—	—	—	—	—	—	—	—
176—195	—	—	64	1	—	—	—	—	—	—	—	—	—
196—215	—	—	52	—	—	—	—	—	—	—	—	—	—
216—235	—	—	22	2	—	—	—	—	—	—	—	—	—
236—255	—	—	14	4	—	—	—	—	—	—	—	—	—
256—275	—	—	16	11	—	—	—	—	—	—	—	—	—
276—295	—	—	4	11	—	—	—	—	—	—	—	—	—
296—315	—	—	—	15	1	—	—	—	—	—	—	—	—
316—335	—	—	—	8	3	1	—	—	—	—	—	—	—
336—355	—	—	—	4	6	—	—	—	—	—	—	—	—
356—375	—	—	—	—	—	1	—	—	—	—	—	—	—
376—395	—	—	—	—	2	3	—	—	—	—	—	—	—
396—415	—	—	—	—	—	2	4	1	—	1	—	—	—
416—435	—	—	—	—	—	3	6	2	6	1	—	—	—
436—455	—	—	—	—	—	2	7	13	6	3	—	—	—
456—475	—	—	—	—	—	—	3	18	8	7	4	—	—
476—495	—	—	—	—	—	1	4	11	6	7	4	1	—
496—515	—	—	—	—	—	—	1	2	2	4	1	—	—
516—535	—	—	—	—	—	—	—	—	—	—	—	—	1
Σ fish	11	12	192	56	12	13	25	48	28	24	9	1	1
% of total	2.5	2.8	44.3	12.9	2.8	3.0	6.0	11.1	6.5	5.5	2.1	0.2	0.2
Mean length	70	143	206	288	348	413	443	462	467	472	480	470	530

where L equals total length of fish in mm and S equals length of anterior scale radius (X30) in mm.

Length distribution

The length distribution of the 433 ide whose ages were determined, is shown in Table 12. The values are lengths at capture when the season's growth had not yet started. There was a wide amplitude in length in each age group and extensive overlapping between adjacent age groups. The greatest difference between the longest and the shortest fish in any age group was 17.9 cm (groups IV and VI). Age groups VII, VIII and X had range of 11.9 cm. The well-represented age group III had a range of 15.9 cm. The well-represented size classes contained fish from 2 to 7 age groups. The largest ide (54.5 cm in total length) registered during the four years of study was a male captured on 2 May 1966. It is evident that the body length is a poor indication of age of ide from the River Kävlingeån. Similar conditions were illustrated by BALON (1962) for ide from the Danube.

Table 13. Calculated total lengths of male ide from River Kävlingeån, 1966 and 1967. The last value in each group is the average length at capture.

Age group	Number of fish	Length in mm at the end of the respective year of life										
		1	2	3	4	5	6	7	8	9	10	11
III	15	74	139	200	—	—	—	—	—	—	—	—
IV	21	86	163	227	292	—	—	—	—	—	—	—
V	7	64	154	237	297	351	—	—	—	—	—	—
VI	7	80	171	251	321	370	404	—	—	—	—	—
VII	14	77	181	263	326	374	414	454	—	—	—	—
VIII	19	79	169	245	307	356	397	435	467	—	—	—
IX	11	85	170	250	312	356	390	426	455	477	—	—
X	6	82	167	230	277	319	358	396	424	450	467	—
XI	1	94	176	235	287	337	354	368	402	444	464	480
Grand average calculated length		80	165	237	302	347	386	416	437	457	465	480
Increment of average		80	85	72	65	45	39	30	21	20	8	15
Grand average increment of length		80	85	72	60	48	34	33	31	30	18	16
Sum of average increment		80	165	237	297	345	379	412	443	473	491	507

Growth in length

The growth under previous years of life was calculated from the relation of scale measurements to total length (*vide* Fig. 10). For each fish (433 specimens) the following measurements were made: 1) distance from the focus of the scale to each annulus, 2) length of scale radius, and 3) total length of the fish at the time the scale sample was taken.

The body length at the end of any year of life for a specimen was calculated from Fig. 10. The body length at the time of sampling gives an expected value for the scale radius. The ratio "expected" (R): "observed" (S) value is used as a correction factor ($\frac{R}{S}$) to adjust the radii observed for different years. The corrected scales are referred to the corresponding lengths which are thus the estimated body length of the fish at the end of the respective year of life.

The calculated average lengths for males (101 specimens) and females (132 specimens) showed no significant differences (Tables 13 and 14). Data for males and females of the whole studied ide material (433 specimens) were combined in Table 15.

Calculated lengths exhibited a successive change in growth with increasing age. The discrepancies among calculated growths of the various age groups are approximately randomly distributed. The discrepancies between the older age groups may be attributed to small numbers of fish.

The estimates of the general growth in length at the bottom of Tables 13,

Table 14. Calculated total lengths of female ide from River Kävlingeån, 1966 and 1967. The last value in each group is the average length at capture.

Age group	Number of fish	Length in mm at the end of the respective year of life													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
III	14	82	144	207	—	—	—	—	—	—	—	—	—	—	—
IV	22	87	177	238	297	—	—	—	—	—	—	—	—	—	—
V	5	72	146	221	285	344	—	—	—	—	—	—	—	—	—
VI	6	78	161	240	312	373	423	—	—	—	—	—	—	—	—
VII	12	88	186	256	312	367	401	429	—	—	—	—	—	—	—
VIII	28	86	187	256	315	362	402	434	460	—	—	—	—	—	—
IX	17	81	164	230	290	335	377	411	436	460	—	—	—	—	—
X	18	82	161	232	291	339	378	408	431	454	473	—	—	—	—
XI	8	77	146	211	262	312	358	397	422	443	463	480	—	—	—
XIII	1	68	101	141	173	223	257	300	346	389	420	441	463	470	—
XIV	1	99	188	243	272	302	340	384	418	446	473	495	506	519	530
Grand average calculated length		82	160	225	281	328	367	395	419	438	457	472	484	494	530
Increment of average		82	78	65	56	47	39	28	24	19	19	15	12	10	36
Grand average increment of length		82	78	65	54	49	40	36	30	28	24	20	16	10	11
Sum of average increment		82	160	225	279	328	368	404	434	462	486	506	522	532	543

Table 15. Calculated total lengths of ide from River Kävlingeån, 1966 and 1967. The last value in each group is the average length at capture, as the season's growth had not begun.

Age group	Number of fish	Length in mm at the end of the respective year of life													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
I	11	70	—	—	—	—	—	—	—	—	—	—	—	—	—
II	12	71	143	—	—	—	—	—	—	—	—	—	—	—	—
III	192	79	144	206	—	—	—	—	—	—	—	—	—	—	—
IV	56	83	165	227	288	—	—	—	—	—	—	—	—	—	—
V	12	67	151	231	292	348	—	—	—	—	—	—	—	—	—
VI	13	79	166	246	317	371	413	—	—	—	—	—	—	—	—
VII	26	82	183	260	320	371	408	443	—	—	—	—	—	—	—
VIII	48	83	179	252	312	360	399	434	462	—	—	—	—	—	—
IX	28	83	167	238	300	345	383	417	444	463	—	—	—	—	—
X	24	82	163	231	287	334	373	405	429	453	472	—	—	—	—
XI	9	79	150	213	265	315	357	394	420	443	463	480	—	—	—
XIII	1	68	101	141	173	223	257	300	346	389	420	441	463	470	—
XIV	1	99	188	243	272	302	340	384	418	446	473	495	506	519	530
Grand average calculated length		79	158	226	283	330	366	397	420	439	457	472	484	494	530
Increment of average		79	79	68	57	47	36	31	23	19	18	15	12	10	36
Grand average increment of length		79	79	66	54	48	39	37	31	27	24	20	16	10	11
Sum of average increment		79	158	224	278	326	365	402	433	460	484	504	520	530	541

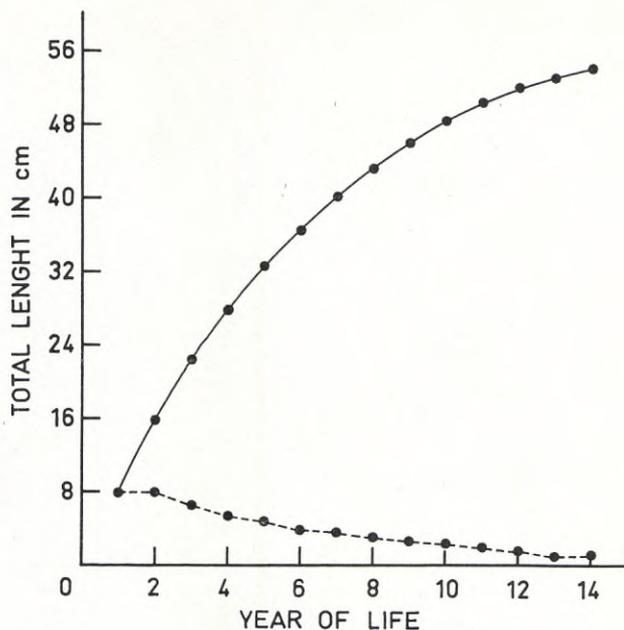


Fig. 11. Increase in length (accumulative) of ide in River Kävlingeån (complete line) and yearly increment (broken line); material (433 specimens) collected in 1966—1967.

14 and 15 are based on the grand average calculated lengths and on the successive summation of the grand average increments of length. Lengths estimated by the two methods were nearly identical for ages 1 through 8 for males and ages 1 through 6 for females.

The sums of the grand average increments were used to demonstrate the growth of the ide in Fig. 11. Male and female ide show their greatest annual increase in length (85 mm and 78 mm respectively) during the second year of life. After the second year the increments decreased to 30 mm (males) and 28 mm (females) in the 9th year and 16 mm (males) and 20 mm (females) in the 11th year.

The low representation of male ide in the older age groups may indicate different mortality of the sexes.

In the present material there is a tendency towards more rapid growth of the ide males in the River Kävlingeån than the females. BALON (1962) stated that the ide males in Little Danube River grew more quickly, but from the 5th year onwards the females grew more rapidly.

Length-weight relation

This study is based on data from 989 young-of-the-year ide collected from May to November during 1963—1966 (*vide* Table 8), and from 428 yearling and older fish collected during the winter months. In 1966, 266 ide

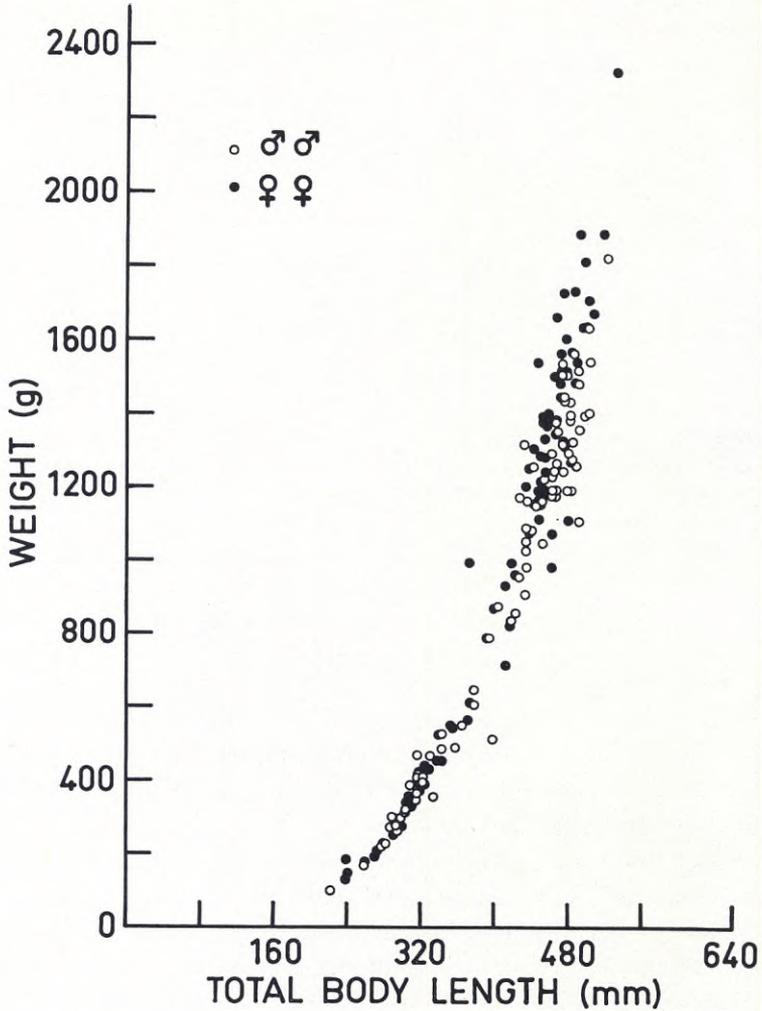


Fig. 12. Length-weight relation for males (○) and females (●) of *ide*.

were caught from March 17 to April 17, and 82 from November 11 to December 5. In 1967, 80 fishes were collected between February 27 to April 4. Collections were made mostly by seining and trap nets, or by electro-fishing especially for young fish. Lengths were measured to the nearest mm and weight of whole fish to the nearest gram, and to the nearest 0.01 g for the young-of-the-year. Measurements of the fish were made as soon as possible after their being collected with exception of the young-of-the-year which were fixed in 80% alcohol. Shrinkage and weight loss, caused by the fixative, was studied and correction made (CALA). Maximum size recorded for females was 53 cm total length and 2.33 kg (one specimen

Fig. 13. Length-weight relation of ide (excepting young-of-the-year) from River Kävlingeån. The curve represents the calculated weights and the dots the empirical weights.

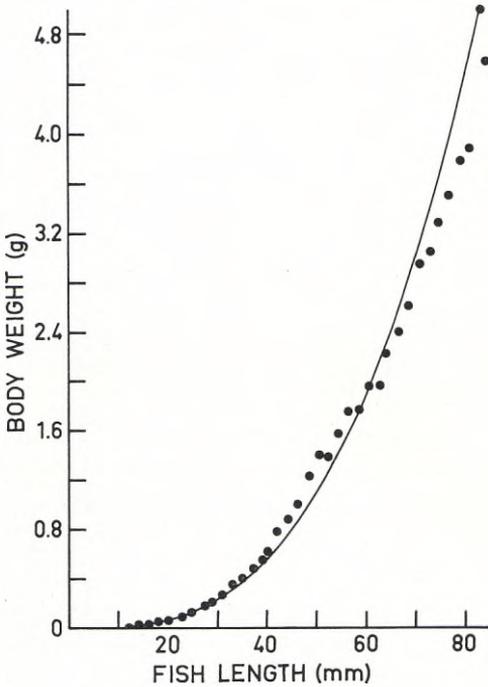
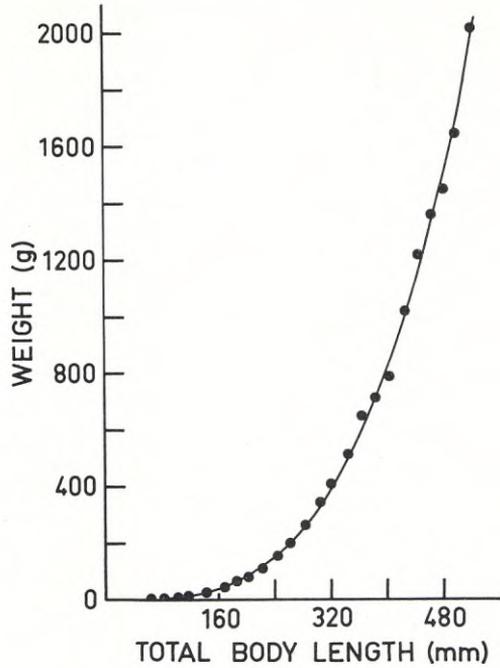


Fig. 14. Length-weight relationship of the young-of-the-year ide from River Kävlingeån, 1963—1966. The curve represents the calculated weights and the dots the empirical weights. The material is listed in Table 16.

Table 16. Length-weight relation of young-of-the-year ide from River Kävlingeån, 1963—1966.

(The lengths and weights are the true means for fish in 2-mm groups).

Total length intervals (mm)	Number of fish	Mean total length (mm)	Mean weight (g)
10—11	98	10.2	0.004
12—13	44	12.1	0.01
14—15	24	14.2	0.03
16—17	98	16.4	0.03
18—19	80	18.2	0.05
20—21	10	20.2	0.06
22—23	5	22.9	0.09
24—25	15	24.7	0.13
26—27	33	27.5	0.18
28—29	27	28.9	0.21
30—31	34	31.1	0.27
32—33	46	33.1	0.35
34—35	65	35.2	0.40
36—37	57	37.4	0.48
38—39	55	39.2	0.55
40—41	29	40.2	0.62
42—43	19	42.3	0.78
44—45	15	44.4	0.88
46—47	13	46.4	1.00
48—49	20	48.7	1.23
50—51	7	50.7	1.40
52—53	13	52.5	1.38
54—55	13	54.5	1.57
56—57	16	56.5	1.75
58—59	19	58.7	1.77
60—61	14	60.6	1.95
62—63	23	62.9	1.96
64—65	10	64.3	2.22
66—67	22	66.8	2.40
68—69	12	68.8	2.61
70—71	11	71.1	2.95
72—73	13	73.2	3.05
74—75	12	74.7	3.28
76—77	4	76.8	3.50
78—79	6	79.2	3.78
80—81	4	80.9	3.88
82—83	1	83.6	5.00
84—85	5	84.6	4.58

captured on 31 March 1967). The largest male measured 52 cm total length and weighed 1.82 kg (one specimen captured on 18 April 1966).

Examination of length-weight data (Fig. 12) in relation to sex, sexual maturity or state of gonads revealed no differences. Determination of the length-weight relation for ide older than age group 0 according to Fig. 13 may be possible only for certain times of the year. Ide of a given length captured during winter — December to March — seem to be consistently heavier than fish taken at other times of the year. Periods of such conditions in advance of spawning have been established for coregonid species (DEASON and HILE; and VAN OOSTEN and HILE, cited by BAILEY 1964).

Table 17. Length-weight relation of ide from River Kävlingeån, 1966—1967. (The lengths and empirical weights are the true means for fish in 2-cm groups; the calculated weights are from the equation shown in Fig. 13).

Total length intervals (mm)	Number of fish	Mean total length (mm)	Weight (g)	
			empirical	calculated
54—73	8	64	2	2
74—93	14	82	4	4
94—113	3	102	8	8
114—133	1	116	13	—
134—153	7	142	25	26
154—173	15	168	44	45
174—193	58	185	62	62
194—213	55	201	77	82
214—233	32	222	108	114
234—253	17	242	153	152
254—273	26	262	197	198
274—293	17	283	257	256
294—313	13	304	341	326
314—333	14	320	405	386
334—353	6	344	405	492
354—373	5	365	446	599
374—393	4	383	707	704
394—413	5	403	785	834
414—433	18	426	1,018	1,004
434—453	29	445	1,217	1,161
454—473	36	465	1,354	1,346
474—493	32	482	1,444	1,516
494—513	10	499	1,641	1,702
514—533	3	522	2,008	1,980

The length-weight relation of ide was linear when both variables were transformed to common logarithms. But it seems that the length-weight relation for ide fry below 13 mm in average length (shortly after hatching to the time of yolk-sac absorption, or beginning of feeding) is different (Fig. 14), although the material does not adequately prove it. For this reason, fish below 12 mm in total length were not included in the following computation of the length-weight relation.

The general parabola, $W=cL^n$, where W =weight, L =total length, and c and n are empirically estimated constants has been used to describe the length-weight relation of numerous species of fish. The least squares regression of the logarithmic transformation ($Y=a+bX$ in which $Y=\log_{10} W$, $a=\log_{10} c$, and $X=\log_{10} L$) was used for estimating values of c and n .

The length-weight equation, determined by fitting a straight line to the logarithms of the lengths and weights listed in Tables 16 and 17, are:

$$\log W = -5.11749 + 3.03175 \log L \text{ (young-of-the-year)}$$

$$\text{and } \log W = -5.77664 + 3.33853 \log L \text{ (yearling and older ide)}$$

Where W =body weight in g and L =total length in mm. The value of n indicates that the body weight increases approximately as the cube of the

Table 18. Calculated weights and annual increments of weight of ide from the River Kävlingeån.

Year of life	Calculated weight (g)	Increment
1	4	4
2	37	33
3	117	80
4	241	124
5	411	170
6	599	180
7	827	228
8	1,060	233
9	1,298	238
10	1,537	239
11	1,760	223
12	1,953	193
13	2,082	129
14	2,229	147

length for young-of-the-year longer than 12 mm in length and more rapidly than the cube of the length for yearling and older ide. The equations make possible the calculation of the unknown weight for a known length and *vice versa*. It becomes evident that the total length of an ide at a weight of 1 g is 52 mm and at a weight of 1 kg 453 mm. These results essentially agree with those of BALON (1962) who found no difference of length-weight relations between the juvenile specimens and males and females. BALON gives the standard length of an ide of 1 g as 39 mm and of 1 kg 361 mm.

Calculated growth in weight

The data of Table 17 indicate a generally good agreement between empirical and calculated weights. The greatest discrepancies (72,61,56 and 49 g) were at 474—493, 494—513, 434—453 and 394—413 mm, respectively, *i.e.* among the larger fish.

The calculated weights of Table 18 were computed by applying the calculated lengths (sum of the average increments) of Table 15 to the length-weight equation.

The annual increments of weight thus increased to a maximum of 239 grams in the 10th year of life, despite the fact that the greatest annual increments of length were attained during the 2nd year. Annual weight increments declined to 129 g in the 13th year. In the River Kävlingeån, ide require 8 years to reach a body weight of about 1 kg.

Table 19. Sex ratio of mature ide taken on the spawning grounds, in the River Kävlingeån, during 1964.

Date	Number of fish		
	♂♂	♀♀	Total
26.III	15	15	30
1.IV	78	90	168
5.IV	5	12	17
6.IV	237	262	499
9.IV	53	60	113
15.IV	31	11	42
16.IV	129	66	195
24.IV	57	61	118
2.V	16	9	25
Σ	621	586	1,207
%	51.4	48.6	

XIII. Sex ratio on spawning ground

A sample of 1207 adult ide taken just before and during the spawning season in 1964 between 1 April and 2 May was composed of 621 (51.4 %) mature males and 586 (48.6 %) mature females (Table 19). These numbers

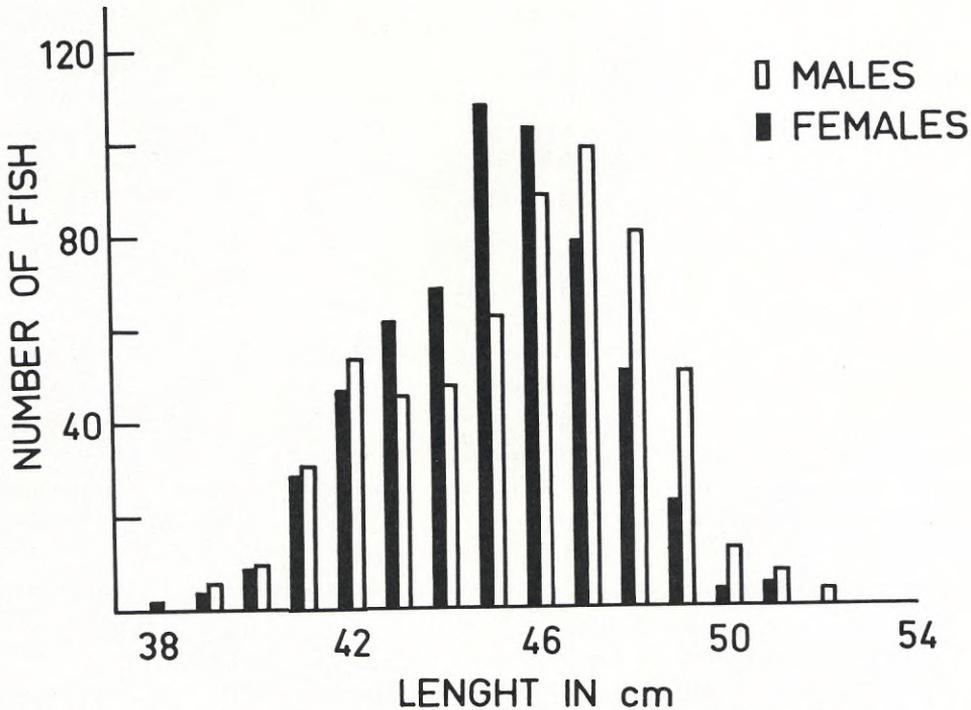


Fig. 15. Sex ratio and length distribution of 1208 mature ide captured in the lower reaches of the River Kävlingeån just before and during spawning in 1964.

Table 24. Food items taken by the ide in the River Kävlingeån, 1963—1967.

ROTATORIA	MOLLUSCA
INVERTEBRATE EGGS	GASTROPODA
ANNELIDA	<i>Lymnaea</i> spp.
OLIGOCHAETA	<i>Physa fontinalis</i> (L.)
HIRUDINEA	<i>Planorbis carinatus</i> MÜLL.
CRUSTACEA	<i>Anisus vortex</i> (L.)
CLADOCERA	<i>Bathynomphalus contortus</i> (L.)
OSTRACODA	<i>Gyraulus</i> spp.
COPEPODA	<i>Viviparus fasciatus</i> LEACH
ISOPODA	<i>Acroloxus lacustris</i> (L.)
<i>Asellus aquaticus</i> L.	<i>Bithynia tentaculata</i> (L.)
AMPHIPODA	<i>B. leachi</i> (SHEPPARD)
<i>Gammarus</i> spp.	<i>Hydrobia</i> sp.
ARACHNIDA	<i>Valvata macrostoma</i> (STEENBUCH)
HYDRACARINA	<i>V. piscinalis</i> (MÜLL.)
INSECTA	PELECIPODA
EPHEMEROPTERA (nymph)	<i>Mytilus edulis</i> L.
ODONATA (nymph)	OSTEICHTHYES
HETEROPTERA	<i>Perca fluviatilis</i> (L.) (young)
CORIXIDAE	<i>Rutilus rutilus</i> (L.) (young)
TRICHOPTERA (larva)	<i>Idus idus</i> (L.) (egg and young)
COLEOPTERA	ALGAE (<i>Cladophora</i> , etc.)
DIPTERA	HIGHER PLANTS
CHIRONOMIDAE (larva, pupa and imago)	PLANT TISSUE
CERATOPOGONIDAE (larva)	<i>Potamogeton</i> spp.
SIMULIIDAE (larva and pupa)	<i>Lemma minor</i>
OTHER DIPTERA	Other higher plants
	SEEDS (<i>Nymphaea alba</i> , <i>Carix</i> , etc.)
	DETRITUS, MINERAL MATTER, ETC.

do not deviate significantly from a 1 : 1 ratio ($\chi^2=0.30$). The male spawning population had a mean length of 45.6 cm, ranging from 39 to 52 cm (mode 47 cm, n=99), and the female 45 cm, ranging between 38—51 cm (mode 45 cm, n=108) (Fig. 15).

XIV. Food habits

1,163 ide from the lower reaches of the River Kävlingeån — collected June 1963 to December 1966 — were examined with regard to the contents of the upper part of the S-shaped digestive tract, from the pharynx to the first loop. The food items in the rest of the intestine are strongly digested with exception of crustacean zooplankters in fry ide which can be easily recognizable in the whole digestive tract. The young-of-the-year were fixed in 80 % alcohol and later dissected for analysis. The intestines of juvenile and adult fish were preserved in 80 % alcohol as soon as possible after capture. Total body length was registered consistently.

The occurrence method was used in assessing the food. After the percentage of the number of fish examined containing the individual food items is found, the number of occurrences of the food items is summed to give the percentage composition of the diet.

Fish such as cyprinids chew their food (HARTLEY 1947, cited from HYNES 1950) and so make counting impossible. The presence of large volumes of mucus prevents accurate measurement of weight or volume. The investigator can therefore only use the occurrence method, which although apparently the least satisfactory was shown to give substantially the same results as theoretically better methods (HYNES 1950). Organisms represented in the intestines are shown in Table 24. The composition of the food based on occurrence, of the different size groups and of the total number of fish are seen from Table 25.

Composition of the diet in relation to the fish size

In the present material there were definite changes in food habits with increase in size which became evident at about 20 mm total length, and at about 140 mm (Table 25). Crustacea were most important in the first group (10 to 20 mm total length), but insects predominated in the second group (20 to 140 mm), especially chironomid larvae. Rotifers were taken by a considerable number of fish, but only by fry below 12 mm.

Cladocera were caught by fish between 10–80 mm and *Copepoda* until 60 mm. If any zooplankton is taken by larger fish it seems to be by mere chance, e.g. when higher plant tissue or algae are eaten.

Medium-sized or large organisms such as *Asellus aquaticus*, molluscs and *Oligochaeta* were rarely found in young-of-the-year ide (less than 80 mm total length). Higher plant tissue and detritus were also rare in this size group. Fish did not appear except in ide larger than 240 mm total length.

In age groups just larger than 140 mm several food items became important such as higher plants, *Asellus aquaticus*, and *Oligochaeta*. *Insecta* continued to be an important group. It seems, however, that some *Insecta* (*Ephemeroptera*, *Coleoptera* and *Ceratopogonidae*) disappeared from the diet and *Chironomidae* become less dominant as the fish grow and at above 260 mm they are replaced by higher plant tissue (Table 25).

Food utilization and food abundance

Simultaneous collections of fry and plankton were made during 1964 and 1965 at the time when the crustacean zooplankters were the main food items of ide fry from about 10 to 25 mm long. Collecting methods and habitats are described above (*vide* pp. 47, 55, and Fig. 1).

Estimated numbers of *Cladocera* and *Copepoda* varied from 6 to 1,834 per litre water (Table 26). Relative numbers of these groups varied considerably, with *Cladocera* being the most abundant (*vide* also Table 4). The occurrence of these groups in the fish intestines (Table 26) shows that the ide in its early life does not specialize on either *Cladocera* or *Copepoda*, but

Table 25. Food of 1,163 ide from River Kävlingeån, 1963—1966, listed containing the various food items. II.

Total length interval in mm	Number of fish	% empty stomachs	Method of assessment	<i>Rotatoria</i>	Vertebrate eggs	<i>Oligochaeta</i>	<i>Hirudinea</i>	<i>Cladocera</i>	<i>Ostracoda</i>	<i>Copepoda</i>	<i>Asellus aquaticus</i> L.	<i>Gammarus</i> spp.	<i>Hydracarina</i>	<i>Ephemeroptera</i> (nymph)
10—20	150	6.0	I	7.3	1.3	—	—	75.3	—	24.7	—	—	—	—
			II	5.8	1.1	—	—	59.8	—	19.6	—	—	—	—
21—40	325	55.1	I	—	—	—	—	7.1	—	1.2	—	—	—	0.9
			II	—	—	—	—	14.1	—	2.4	—	—	—	1.8
41—60	144	31.9	I	—	1.4	1.4	—	4.9	—	2.1	0.7	—	—	2.1
			II	—	1.4	1.4	—	4.9	—	2.1	0.7	—	—	2.1
61—80	117	35.0	I	—	—	8.5	—	0.8	—	—	3.4	—	0.8	0.8
			II	—	—	10.0	—	1.0	—	—	4.1	—	1.0	1.0
81—100	8	62.5	I	—	—	—	—	—	—	—	—	—	—	—
			II	—	—	—	—	—	—	—	—	—	—	—
101—120	6	33.3	I	—	—	—	—	—	—	—	—	—	—	—
			II	—	—	—	—	—	—	—	—	—	—	—
121—140	25	36.0	I	—	—	4.0	—	—	—	—	20.0	—	—	4.0
			II	—	—	2.7	—	—	—	—	13.5	—	—	2.7
141—160	23	26.1	I	—	—	8.7	—	—	—	—	30.4	4.3	—	—
			II	—	—	5.1	—	—	—	—	17.9	2.6	—	—
161—180	45	17.8	I	—	—	13.3	—	2.2	—	—	26.7	—	—	2.2
			II	—	—	7.8	—	1.3	—	—	15.6	—	—	1.3
181—200	56	28.6	I	—	—	5.3	1.8	—	—	—	28.6	—	—	1.8
			II	—	—	3.0	1.0	—	—	—	16.2	—	—	1.0
201—220	40	27.5	I	—	—	5.0	—	—	—	—	12.5	2.5	—	2.5
			II	—	—	3.4	—	—	—	—	8.6	1.7	—	1.7
221—240	29	31.0	I	—	—	6.9	—	3.4	—	—	20.7	—	—	—
			II	—	—	4.3	—	2.1	—	—	12.8	—	—	—
241—260	18	55.5	I	—	—	5.5	—	—	—	—	11.1	—	—	—
			II	—	—	6.7	—	—	—	—	13.3	—	—	—
261—280	49	55.5	I	—	—	8.2	—	—	—	—	10.2	—	—	—
			II	—	—	10.8	—	—	—	—	13.5	—	—	—
281—300	18	50.0	I	—	5.5	16.7	—	—	—	—	16.7	5.5	—	5.5
			II	—	5.3	15.8	—	—	—	—	15.8	5.3	—	5.3
301—320	15	53.3	I	—	6.7	20.0	—	6.7	—	—	6.7	—	—	—
			II	—	6.7	20.0	—	6.7	—	—	6.7	—	—	—
321—340	5	0.0	I	—	—	—	—	—	—	—	—	—	—	—
			II	—	—	—	—	—	—	—	—	—	—	—
341—360	2	—	I	—	—	+	—	—	—	—	+	—	—	+
			II	—	—	+	—	—	—	—	+	—	—	+
361—380	1	—	I	—	—	—	—	—	—	—	—	—	—	—
			II	—	—	—	—	—	—	—	—	—	—	—
381—400	2	—	I	—	—	—	—	—	—	—	—	—	—	—
			II	—	—	—	—	—	—	—	—	—	—	—
401—420	7	28.6	I	—	—	14.3	—	—	—	—	—	—	—	—
			II	—	—	12.5	—	—	—	—	—	—	—	—
421—440	11	45.4	I	—	—	—	—	—	—	—	—	—	—	—
			II	—	—	—	—	—	—	—	—	—	—	—
441—460	18	50.0	I	—	—	11.1	—	—	5.5	—	16.7	—	5.5	—
			II	—	—	8.7	—	—	4.3	—	13.0	—	4.3	—
461—480	29	55.2	I	—	6.9	13.8	—	—	—	—	—	—	—	—
			II	—	10.5	21.0	—	—	—	—	—	—	—	—
481—500	19	63.1	I	—	—	10.5	—	—	—	—	5.3	—	—	—
			II	—	—	11.8	—	—	—	—	5.9	—	—	—
501—520	3	—	I	—	—	—	—	—	—	—	—	+	—	—
			II	—	—	—	—	—	—	—	—	+	—	—
Total			I	0.9	0.7	4.0	0.1	12.6	0.1	3.8	6.2	0.3	0.2	1.1
10—520	1163	37.9	II	1.0	0.7	4.1	0.1	12.8	0.1	3.8	6.3	0.3	0.2	1.1

Table 26. *Crustacea*, *Copepoda* and *Cladocera* in quantitative plankton samples compared with amounts in intestines of fry ide collected at the same time and same place. Length of fry ide 10—20 mm. River Kävlingeån, localities described on p. 49.

Date	Locality	Total number of <i>Crustacea</i>		Per cent			
		water (per litre)	intestine	<i>Cladocera</i>		<i>Copepoda</i>	
				water	intestine	water	intestine
<i>1964</i>							
28.V	Ib	1,831	191	2.95	7.8	97.05	92.2
16.VI	Ia	154	11	91.6	100.0	8.4	0.0
" —	Ib	26	0	92.3	—	7.7	—
" —	Ie	6	1	100.0	100.0	0.0	0.0
<i>1965</i>							
14.VI	II	252	228	84.5	100.0	15.5	0.0
" —	IV	818	228	76.3	100.0	23.7	0.0
" —	V	25	397	100.0	100.0	0.0	0.0
" —	VI	294	198	96.9	100.0	3.1	0.0
1.VII	II	307	22	96.4	100.0	3.6	0.0
20.VII	II	544	18	90.1	100.0	9.9	0.0

there seems to be a tendency for fry to feed more heavily on *Cladocera* when these organisms are abundant.

As stated above (p. 55), collections of benthic fauna were made when electro-fishing, in order to survey bottom-living animals which might be of some interest as fish food. The material is listed in Table 3. The most frequent organisms were *Chironomidae*, *Gastropoda*, *Corixidae*, *Asellus aquaticus*, *Ephemeroptera*, *Hirudinea*, *Oligochaeta*, *Simuliidae*, *Coleoptera* and *Hydracarina*. The importance of the vegetation was discussed on page 61. The major food items of the ide in the lower part of the river (cf. Table 25) were in order of importance *Chironomidae*, higher plant tissues, *A. aquaticus*, *Insecta* (excluding specified groups), detritus, *Simuliidae*, *Oligochaeta*, *Coleoptera*, *Gastropoda*, unidentified animal matter, *Lemna minor*, *Ephemeroptera* and *Corixidae*. There seemed to be no definite preference in the food choice. Some groups, viz. *Corixidae*, *Hirudinea* and *Hydracarina* were well represented in the bottom samples but not in the intestines. The reason seems to be that the *Corixidae* concentrated in shallow marginal water with dense vegetation where ide rarely occur.

Seasonal changes

There are small seasonal variations of the feeding habits of the ide. Plant material as *Lemna minor*, *Potamogeton* and seeds are eaten mainly in summer and early autumn, when the vegetation is luxuriant. *Oligochaeta* seem

to be more frequent in the diet in winter (November to March). It should be noted that large ide spend most of the summer (May to September) in the sea (see pp. 62—63) where their diet consists of marine matter.

Summing up, the ide is almost omnivorous in the River Kävlingeån, taking the most frequent food material that it encounters.

Previous investigations

EKSTRÖM (1831) mentioned that the ide in Lake Mälaren, Central Sweden fed especially on vegetation, but in fish from deeper water he found remains of insects, *Crustacea* and sometimes small fish. SCHNEIDER (1901) concluded that in the Finnish Archipelago, the younger fish feed on insects and molluscs, larger specimens mainly on molluscs. For the west of the Baltic Sea, the diet of the ide was stated to contain *Crustacea*, fish and plant matter, and for the Finnish Bay molluscs and insects and, in freshwater bays plants. COLLETT (1905) recorded that some ide collected in June in brackish water in Norway contained *algae* and *Hydrobia minuta* in large quantities, in larger fish from the same locality where exclusively flower buds of *Potamogeton* spp. In fish from Grue (May) he found only *Odonata* nymphs.

Specimens from Vestfossen (May) had eaten chironomid larvae. Winter specimens from Lundevand in Eidanger had fed on young lumbricids; fish from the same locality in autumn contained only small copepods (*Cyclops*, *Diaptomus*, etc.).

HUITFELDT-KAAS (1916) studied ide from Lake Mjøsen (Norway) and found that fish up to 0.5 kg had taken only *Characeae*. Besides plant matter, medium-sized ide fed on animals, especially insect larvae, while larger fish took much small fish, feeding on pelagic schools of *Osmerus eperlanus* (L.) and *Coregonus albula* L. JÄÄSKELÄINEN (1917, 1921) stated that the Finnish ide fed to a great extent on molluscs but in its mature life regularly was a predatory fish. He summed up the diet as follows: 1) in Ladoga, especially *Mollusca* (*Lymnaea*), insect larvae, fish, (less common food: insects), in older ide fish is the most frequent food item, 2) in the Finnish Bay: mainly *Mollusca* (*Tellina*, *Mytilus*, *Cardium*, *Lymnaea*, *Bythinia*) and *Crustacea* (*Chiridothea*), occasionally *Gammarus*, *Asellus* and insect larvae.

According to OTTERSTRÖM (1930—31) of 18 ide captured in April—June (37—41 cm long) in Arresø (Denmark), 8 specimens had eaten fish and 10 empty intestines. SCHNEIDER (1920) records ide in Lake Wirz-Järm (Estonia) feeding on nymphs of *Ephemera vulgata* L., *Tropicoris rufipes* L., bottom molluscs, remains of plants, *Trichoptera larvae* and chironomid larvae. SMGLIAN (1920) records as food items bottom animals, e.g. insect larvae and molluscs, and plankton. BERG (1949) stated as food insect larvae, mayflies and other adult insects, *Oligochaeta*, fish spawn, small molluscs, diatoms and

filamentous *algae*. SEGERSTRÅLE (1950) concluded that the better growth of larger ide in the Baltic sea at Åland than east of Nyland might be due to the rich source of *Mytilus edulis* L. in Åland water and the lack of this mussel in the Nyland area.

Finally, POPESCU *et al.* (1960) concluded that the ide in the lower Danube River is omnivorous, with tendence to rapacity. It takes insects, *Crustacea*, zooplankton, *Gastropoda*, and plant matter such as diatoms and filamentous *algae*, detritus and higher aquatic plant material. The dominant food items are *Naucoris cimicoides*, *Plea minutissima*, *Corixa* spp., diatoms and remains of plants. In spring (March—April) the predominant food consisted of numerous larvae of *Lepidoptera*, *Chironomidae*, *Coleoptera*, numerous *Lumbricidae*, sporadic molluscs, spawn and fish (*Cyprinidae*, *Pungitius platygaster*). During July and August the dominating items were chironomid larvae, *Gastropoda* (*Lymnaea* sp.), macrophytic plant matter, *Cladocera*, *Copepoda*, *Insecta* and sporadic fishes (*Pungitius platygaster*). They stated that generally young-of-the-year ide between 3—5 cm long, feed on *Cladocera*, larvae of *Chironomidae*, diatoms and filamentous *algae*. From 6—8 cm they take molluscs, adult insects and sporadic larvae of *Chaoborus*. Finally POPESCU *et al.* (1960) mention that the ide start feeding at a water temperature of 1—2°C. According to MANN (1961) plant matter is the main food source of ide in the River Alster (Germany), so fish species which are omnivorous or have an animal diet do not compete with it.

XV Summary

1. This study is based on data from ide *Idus idus* (L.) collected in the lower part of the River Kävlingeån-Högsmölla to the mouth (Fig. 1). The studies were carried out during a 4-year period (1963—67).
2. A list of the literature about the ide's biology in different countries, with especial reference to Scandinavia, has been produced.
3. A physico-chemical analysis (water temperature, colour, pH, hardness: Ca+Mg, specific conductivity, chloride ion contents and oxygen contents) of the study area was realized. Large changes, from time to time, of some of these physical and chemical properties of the river water was noted.
4. Death of fish in the River Kävlingeån have been noted since 1910 (SWENANDER) as a result of low oxygen content, combined with high temperature and pollution caused by discharging of water coming from Örtofta sugar factory and other industries and urban districts.
5. Qualitative notes on the biomass (benthic fauna, plankton, fish and fishery) of the lower part of the River Kävlingeån has been described.
6. The larger movement of the ide occurs in the lower reaches of Kävlinge-

ån. The ide spends the first year of its life in the river and then joins with other migrating fish to the sea. During summer (June—August) ide older than age group 0 disappear almost completely from the river, spending the summer in the sea. In autumn the ide return to the river, the smallest ones in September and as the autumn advances the schools increase in number and size. Generally, the largest ide leave the river earlier (April to May) and return later (October to November).

7. The spawning of the ide in the River Kävlingeån during the 4-year (1964—67) study period occurred from 29 March to 17 April. The ide spawn in shallow streams at a depth of 0.5—1.5 m. The eggs adhere to stones, plants, etc. The largest fish spawn first. Spawning began 2 to 3 days after the daily water temperature reached and remained about 5°C (Table 6). Most ide spawned during 2 to 3 days when the water temperature rose to about 7°C and the weather was fine. But if the water temperature drops after the initial period of spawning, additional spawning takes place when the temperature rises again (Table 6).
8. Eggs from ide, in the laboratory, began to hatch after 5.5 days at a mean temperature of 13.8°C and after 23 days at a mean temperature of 9.3°C. Thus, low temperature retards hatching, and below 5°C there is no hatching (Table 7). The length of the fry-sac at hatching ranged between 5.8—6.6 mm (Table 7).
9. It has been realized a growth analysis of 1081 young-of-the-year (Fig. 3) and 433 ide specimens older than age group 0 of the lower reaches of the River Kävlingeån. It was concluded from the results of the years 1965 and 1966 (Table 9) that the growth season of the young-of-the-year ended in early November. The fry had then attained a mean total length between 6.8 and 7.6 cm for the respective years. The size class means (Fig. 10) indicate the body-scale relation, of ide older than age group 0, to be described by three straight lines. The straight line fitted by least squares to the means of fish lengths and scales radii had these equations:

$$\begin{aligned} L &= 35.92 + 2.1014S && (L < 15.3 \text{ cm}), \\ L &= 80.77 + 1.4720S && (15.3 < L < 40.3 \text{ cm}), \\ \text{and } L &= 106.37 + 2.3236S && (L > 40.3 \text{ cm}), \end{aligned}$$

where L equals total length of fish in mm and S equals length of anterior scales radius (X30) in mm. The body length at the end of any year of life for a specimen was calculated from Fig. 10. The calculated average lengths for males (101 specimens) and females (132 specimens) showed no significant differences (Table 13 and 14). Data for males and females of the whole studied ide material (433 specimens) were combined in Table 15. Males and females ide show their greatest annual increase in length during the second year of life.

10. Annulus formation usually occurs around early May and is completed about the end of June. It seems that older ide, especially mature fish, form annuli earlier than the younger ones. The regulation of scales was affected by the water temperature.
11. Length-weight relation is based on data from 989 young-of-the-year ide, and from 428 yearling and older fish. The length-weight relation in relation to sex, sexual maturity or state of gonads revealed no differences (Fig. 12). The length-weight relation of ide was linear when both variables were transformed to common logarithms, except fry below 13 mm in average length. The general parabola $W=cL^n$, where W =weight, L =total length, and c and n are empirically estimated constants has been used to describe the length-weight relation. Thus, the length-weight equation, determined by fitting a straight line to the logarithms of the lengths and weights listed in Tables 16 and 17 are:

$$\begin{aligned} \log W &= -5.11749 + 3.03175 \log L \text{ (young-of-the-year),} \\ \text{and } \log W &= -5.77664 + 3.33853 \log L \text{ (yearling and older ide),} \end{aligned}$$

where W =body weight in g and L =total length in mm. The value of n indicates that the body weight increases approximately as the cube of the length for young-of-the-year longer than 12 mm in length and more rapidly than the cube of the length for yearling and older ide. The equation makes possible the calculation of the unknown weight for a known length and vice versa. It becomes evident that the total length of an ide at a weight of 1 g is 52 mm and at a weight of 1 kg 453 mm. The greatest annual increment in weight of 239 g occurred in the 10th year of life, despite the fact that the greatest annual increments of length were attained during the 2nd year.

12. A sample of 1207 adult ide taken just before and during the spawning season in 1964 between 1 April and 2 May was composed of 621 (51.4%) mature males and 586 (48.6%) mature females (Table 19). These numbers do not deviate significantly from a 1:1 ratio ($\chi^2=0.30$).
13. 1163 ide from the lower reaches of the River Kävlingeån were examined with regard to the stomachs' contents. In the present material there were definite changes in food habits with increase in size which became evident at about 20 mm total length, and at about 140 mm (Table 25). Crustacea were most important in the first group (10 to 20 mm total length), but insects predominated in the second group (20 to 140 mm), especially chironomid larvae. Rotifers were taken by a considerable number of fish, but only by fry below 12 mm. *Cladocera* were caught by fish between 10—80 mm and *Copepoda* until 60 mm. In age groups just larger than 140 mm several food items became important such as higher plants, *Asellus aquaticus*, and *Oligochaeta*. *Insecta* continued to be an important group. *Chironomidae* become less dominant as the fish

grow and at above 260 mm they are replaced by higher plant tissue (Table 25). Table 26 shows that the ide in its early life does not specialize on either *Cladocera* or *Copepoda*, but there seems to be a tendency for fry to feed more heavily on *Cladocera* when these organisms are abundant. There seemed to be no definite preference in the food choice by ide. There are small seasonal variations of the feeding habits of the ide. Plant material is eaten mainly in summer and early autumn, when the vegetation is luxuriant. It should be noted that large ide spend most of the summer in the sea (see pp. 62—63) where their diet consists of marine matter.

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XVII. References

- ALM, G. 1964. In K. A. Andersson (Ed.). *Fiskar och fiske i Norden*. Vol. II: *Fiskar och fiske i sjöar och floder* (3rd ed. Stockholm): 445—446.
- Årsredogörelse för Svenska Lax- och Laxöringsföreningen u.p.a. Malmö. 1954—62.
- ÅSTRÖM, C. P. 1859. Några iakttagelser rörande de vertebrerade djur, som förekomma i trakten af Lomma. Lund.
- BAILEY, M. 1964. Age, growth, maturity, and sex composition of the American smelt, *Osmerus mordax* (MITCHILL), of Western Lake Superior. *Trans. Amer. Fish. Soc.* 93(4): 382—395.
- BALINSKY, B. I. 1948. On the development of specific characters in cyprinid fishes. *Proc. Zool. Soc. Lond.* 118(II): 335—344.
- BALON, E. K. 1962. The growth's legality of the Danube ide *Leuciscus idus* (L.). *Práce Laboratória Rybárstva* 1: 117—151, 16 photos. (English summary.)
- BERG, L. S. 1949. Freshwater fishes of the U.S.S.R. and adjacent countries. II: 96—99. (Translated from the Russian ed. by Israel Program for Sci. Transl. Jerusalem 1964.)

- BOGAN, F. E. 1964. Expansion of the range and some biological peculiarities of the ide in the upper Pechora. *Zool. Zh.* XLIII(4): 616—619. (English summary.)
- BRÖFELDT, P. 1917. Bidrag till kännedom om fiskbeståndet i våra sjöar. *Finlands Fiskerier* 4: 173—212.
- CALA, P. Effects of alcohol on length and weight of young-of-the-year ide *Idus idus* (L.) and roach *Rutilus rutilus* (L.). *Caldasia* 51 (in press.)
- COLLETT, R. 1905. Meddelelser om Norges fiske i Aarene 1884—1901. *Forh. Vid. Selsk Christiania*, 8: 1—173.
- DUNCKER, G. 1960. Die Fische der Nordmark. Hamburg.
- EKMÁN, S. 1922. Djurvärldens utbredningshistoria på skandinaviska halvön. Stockholm. 612 pp.
- EKSTRÖM, C. U. 1831. Fiskarne i Mörkö skärgård K. *Svenska Vetensk. Akad. Handl.* för år 1930: 149—152.
- HOCHMAN, L. 1956. O rustu jelce jesena (*Leuciscus idus* L.) v rece Dyji. *Zool. Listy* 5(XIX)4: 345—354. (German summary.)
- 1959. Zkusenosti s chovem jesenu v rybnicich. *Čsl. Rybářst.* 14(5): 69.
- HUIFELDT-KAAS, H. 1917. Mjøsens fisker og fiskerier. *K. norske vidensk. Selsk. Skr.* 2: 1—257.
- HYNES, H. B. N. 1950. The food of fresh-water Sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fish. *J. Anim. Ecol.* 19(1): 36—58.
- JÄÄSKELÄINEN, V. 1917. Om fiskarna och fisket i Ladoga. *Finlands Fiskerier* 4: 250—332.
- 1921. Über die Nahrung und die Parasiten der Fische im Ladogasee. *Ann. Acad. Sci. Fenn.*, Serie A, XIV(3): 1—55.
- KARLGREN, L. 1962. Vattenkemiska analysmetoder. Uppsala.
- KOMONEN, A. 1948. Vuoksen pohjoisen suuhaaran kalastosta. *Luonnon Tutkija, Helsinki*, 52: 110—113.
- LENKIEWICZ, Z. 1964. Temperature preferendum of some freshwater fishes. *Folia Biol.* 12(1): 95—140.
- LILLJEBORG, W. 1891. Sveriges och Norges fiskar. Vol. III. Uppsala. 830 pp.
- LUNDBERG, R. 1899. Om svenska insjöfiskarnas utbredning. *Medd. K. Lantbruksstyr.* 58: 1—87.
- MANN, H. 1961. In H. Caspary and H. Mann: Bodenfauna und Fischbestand in der Hamburger Alster. Ein quantitativ-ökologischer Vergleich in einem Stadtgewässer. *Abh. Natur. Ver. Hamburg N. F.* 5: 89—110.
- OTTERSTRÖM, C. V. 1914. Fisk. II. Blödfinnfisk. Danmarks Fauna 15. Copenhagen. 351 pp.
- 1930—31. De danske skallearter (*Leuciscus rutilus* L., *L. grislagine* L., *L. idus* L. og *L. erythrophthalmus* L.). *Vidensk. Medd. Dansk Naturh. Foren.* 90: 85—311.
- PENÁZ, M. 1961. Bemerkungen zum Wachstum des Alands (*Leuciscus idus* L.) im Thaya-Fluss. *Zool. Listy* X(XXIV), 3: 231—241. (German summary.)
- PLISZKA, F. 1953. The effect of spawning conditions in lakes on the survival rate of juveniles. *Polsk. Arch. Hydrobiol.* I(XIV): 165—188. (English summary.)
- POPESCU, E., V. ZIEMANKOWSKI, and A. ROTARU. 1958. Citeva observatii asupra fecundatiei artificiale si dezvoltarii embrionare si postembrionare la vaduvita (*Leuciscus idus* (L)). *Bul. Inst. Cerc. Pisc.* XVII(2): 57—64.
- 1960. Contributii la cunoasterea biologiei vaduvitei (*Leuciscus idus* (L)) din cursul inferior al Dunarii. *Stud. Cercet.* 2(5): 7—33. (French summary.)
- ROSÉN, N. 1920. Om Norrbottens saltsjöområdes fiskar och fiske. *Medd. K. Lantbruksstyr.* 225: 1—94.
- SCHNEIDER, G. 1901. Ichthyologische Beiträge. II. Fortsetzung der Notizen über die an der Südküste Finlands vorkommenden Fische. *Acta Soc. Fauna Flora fenn.* 22(4): 1—57.

- 1920. In M. von zur Mühlen and G. Schneider: Der See Wirzjerw in Livland. Biologie und Fischerei. Dorpat.
- SEGERSTRÅLE, C. 1926. Från en fiskbiologs arbetsfält. I. Idfiske på Sarvfax. *Allas Krönika, Illustrerad Veckoskrift*, 23(27): 685—686.
- 1933. Über scalimetrische Methoden zur Bestimmung des linearen Wachstum bei Fischen. Insbesondere bei *Leuciscus idus* L., *Abramis brama* L. und *Perca fluviatilis* L. *Acta Zool. fenn.* 15: 1—168.
- 1950. Om braxens (*Abramis brama* L.) och idens (*Leuciscus idus* L.) tillväxtart i södra Finlands kustvatten samt i vattnen kring Åland. *Memor. Soc. Fauna Flora fenn.* 25: 156—165.
- SIEBOLD, C. TH. E. v. 1863. Die Süßwasserfische von Mitteleuropa. Leipzig. 430 pp.
- SMITH, S. H. 1954. Method of producing plastic impressions of fish scales without using heat. *Progr. Fish Cult.* 16(2): 75—78.
- SMITT, F. A. 1895. Scandinavian fishes. Vol. II (2nd ed.). Stockholm.
- SMOLIAN, K. 1920. Merkbuch der Binnenfischerei, I—II. Berlin. 1228 pp.
- SPILLMAN, CH. J. 1961. Fauna de France. 65. Poissons d'eau douce Paris. pp. 303.
- STANKOVITCH, S. 1921. Etude sur la morphologie et la nutrition des alevins de poissons cyprinides. *Trav. Lab. Piscicult. Univ. Grenoble XIII*: 1—182.
- STUXBERG, A. 1895. Sveriges och Norges fiskar, deras lefnadssätt, födoämnen, lektid, förekomst och utbredning. Göteborg. 678 pp.
- SUNDEWALL, C. J. 1851. Fisk-ungars utveckling. *Öfversigt K. Svenska Vetensk. Akad. Förh.* 8(6): 161—169.
- 1855. Om fiskyngels utveckling. *K. Svenska Vetensk. Akad. Handl. Ny följd.* 1: 1—24.
- Svenska Lax- & Laxöringsföreningen u.p.a., Malmö. Årsbok. 1963—1966.
- SWENANDER, G. 1910. Biologiska undersökningar i af vissa fabriksanläggningar förorenade vatten. *Södra Sveriges Fisk. Fören. skr.* 6: 7—80.
- WEIJMAN-HANE, G. 1964. Kävlingeån som vattentäkt och recipient. *Skånes Natur* 51: 9—28.
- and A. ALMESTRAND. 1958—1966. Redogörelse för företagna undersökningar beträffande Kävlingeåns förorening. (Mimeographed in Swedish.)
- WOLF, PH. 1950. Fiskeribiologiska undersökningar i Kävlingeån. Lund. 72 pp.
- 1960. Land drainage and its dangers as experienced in Sweden. Altrincham. 73 pp. (See also *Salm. Trout. Mag.* 1960—62.)
- 1965. Kävlingeån — en fråga om ädelfisk eller smutsvatten. *Skånes Natur* 52: 73—80.
- YAMADA, J. 1961. Studies on the structure and growth of the scales in the goldfish. *Mem. Fac. Fish. Hokkaido* 9(2): 181—226.
- YASUDA, H. 1959. Implication of the scale ring-II. Ring formation. *Bull. Jap. sci. Fish.* 25(2): 95—99.

Fishing pressure, growth and recruitment in a small high mountain lake

By T. LINDSTRÖM, Å. FAGERSTRÖM and K.-J. GUSTAFSON

I. Introduction

Lake Långbjörsjön in the Jämtland high mountains has been described in two previous papers (FAGERSTRÖM *et al*, 1969, GUSTAFSON *et al*, 1969) where the methodological aspects of tagging and the distribution of the two existing species — char and trout — over the different habitats in the lake are treated. These studies have been used for the continued analysis in the present paper.

In this small lake, one tenth of a square kilometre in area, a fishing experiment was started in 1958 to investigate whether an increase in the fishing could change the length distribution in the trout population of a small high mountain lake in such a way that the lake would provide the fly fishermen with a more valuable fishing. The immediate effect, that of a reduction of the old and big fish, had been anticipated in, *e.g.*, a memorandum for the management of the sport fishery in the region, written by B. TÄGTSTRÖM (1952). The question was whether the recruitment could also be reduced to a point where the individual growth in the remaining population would increase spectacularly. Consequently the length distribution (Table 11), the growth (Section IV, Fig. 1) and the recruitment of trout (Section VII, Table 8, Fig. 2) have been studied.

The fishing has taken both char and trout, but the growth and recruitment

Table 1. Catch in a full set of gill nets (15 nets, Table 6), fished three nights with a regular distribution over the ten sections and first and second position in gangs. The data have been converted into catch per set.

Date		Mesh-size designation:							Total
		5.00	3.75	3.33	3.00	2.50	2.14	1.67	
1961, Aug. 9—11	a, number of trout . .	0.3	0	2.0	3.0	14.3	16.7	33.3	70
	b, number of char . . .	0	0	0.7	1.0	24.0	22.3	38.3	86
	b:a	—	—	—	0.3	1.7	1.3	1.2	1.2
1965, July 9—11	a, number of trout . .	0	0.3	1.7	2.3	16.0	22.0		42
	b, number of char . . .	0	0.3	0	0.3	7.0	67.0		75
	b:a	—	—	—	0.1	0.4	3.0		1.8
1966, July 1—3	a, number of trout . .	0.3	1.3	2.0	1.7	13.7	7.0	17.0	43
	b, number of char . . .	0	1.0	1.3	1.0	6.3	29.3	47.3	86
	b:a	—	—	—	0.6	0.5	4.2	2.8	2.0

of char has not been investigated, for methodological reasons. As an indication of the char-trout proportion, the proportion in gill nets, set along the shores in a regular manner, is shown in Table 1 (*cf.* also GUSTAFSON *et al.*, 1969). The comparison starts with 1961, the year of the most intense fishing during the experiment.

The density of char in different size categories, like that of trout, is of course related to age distribution and variations in recruitment between years; thus the char-trout ratio was as high as 1.8:1 in 1960 in spite of a distribution of the gill nets over the lake that favoured the catching of trout. A change in the balance between the species would have been a very plausible outcome of a fishing experiment, but nothing definite can as yet be stated in this case; the fishing pressure has unintentionally been directed more against trout.

II. Total Yield from Lake Långbjörsjön

In Table 2 only those fish are included that were not put back into the lake. There may be some illegal fishing that could not be reported, but the known yield is in itself fairly high for a high mountain lake of about 0.1 square kilometre. "Experimental netting" means netting to obtain data on recaptures, etc. "Other fishing" means mainly sport fishing and (1962) seining, but in this group, too, a fair number of the fish have been caught, or checked by the biologists, and scales obtained or tagging noted; this relates specifi-

Table 2. Total yield from Lake Långbjörsjön.

Year	Trout			Char		
	Experi- mental netting, number	Other fishing, number	Total number weight	Experi- mental netting, number	Other fishing, number	Total number weight
1951 ..	—	—	25 4.6	—	—	3 0.4
1952 ..	—	—	186 29.3	—	—	74 7.0
1953 ..	—	—	115 19.6	—	—	105 10.7
1954 ..	—	—	101 18.1	—	—	46 3.5
1955 ..	—	—	89 17.4	—	—	38 4.2
1956 ..	—	—	137 22.1	—	—	3 0.7
1957 ..	—	—	97 16.6	—	—	3 0.4
1958 ..	112	150	262 37.4	79	4	83 6.9
1959 ..	264	60	324 33.2	402	15	417 35.1
1960 ..	176	63	239 —	320	5	325 —
1961 ..	380	176	556 —	441	38	479 —
1962 ..	—	264	264 —	—	255	255 —
1963 ..	65	190	255 33.1	115	36	151 —
1964 ..	46	101	147 20.6	157	25	182 13.5
1965 ..	127	123	250 28.4	224	27	251 20.3
1966 ¹ ..	129	102	231 25.4	267	11	278 20.6

¹ Only part of the season.

Table 3. Mean size of trout in the sport fishermen's catches, kg.

1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966
0.18	0.16	0.16	0.18	0.21	0.16	0.17	0.16	0.13	0.15	0.14	0.13	0.14	0.15	0.10	0.13

cally to 1962 as no gill nets were set in that year, but three-quarters of the yield was caught by the experimental fishing staff.

Dates for the netting are recorded in Table 4 with the exception of the netting October 5—7 in 1961. "Other fishing" was performed in June, July and August.

III. Mean size of trout in catch

The mean size of trout in the sport fishermen's catches decreased in 1959, the second year of the experiment, and did not regain the original level afterwards, Table 3.

Data for fishing places, hook sizes, etc. are not available in full, but the selection through hook size makes mean size in the population — or mean size in the experimental gill nets, too, for that matter — of less relevance for the experience of mean size that a sport fisherman can obtain. Length distribution in the population is not available at all, but in the experimental gill netting the size class above 24 cm could be studied in the size distribution, Table 11, in order to obtain a view of the quality of the water for fly fishing. The number in this size category also drops from 1958 to 1959 and the lowest value is obtained in the last year, 1966, Table 4.

As appears from the table, the date of the gill netting varies from year

Table 4. Number of fish 25 cm or longer in one gill net set of standard composition in 1958—59 and 1961—66 (Table 6). The last row is the minor portion of the trout that was caught in the nets with a knot-to-knot measure from 5.00 to 3.00 cm and gives some suggestion of the correction that should be applied to the 1960 trout values; in 1960 5.00—3.00 mesh size nets were not in use, only nets with 1.67—2.50 cm mesh size.

Year	1958	1959	1960	1961	1963	1964	1965	1966
Date	July 10	July 14—25	July 14 Aug. 14	Aug. 9—11	July 4	June 17	July 9—11	July 1—3
Number of trout	38	17	(11)	16	23	24	22	10
Number of char	16	13	(13)	16	?	7	7	5
Number of above trout caught in nets with 3.0—5.0 cm knot-to-knot mea- sure	7	3	—	3	?	1	3	1

to year, and so does the share of the total catch which preceded the date of gill netting. The gill netting itself, however, takes an important share of the yearly yield, (Table 2). The distribution of the gill nets between the different sections of the lake and between "first" and "second" in each gang (from the shore) is best in 1961, 1965 and 1966. A table of the number of trout 30 cm or longer shows almost the same pattern as Table 4.

IV. Growth of trout

Since 1953 scales from trout have been collected from Lake Långbjörnsjön and the growth rates have been ascertained by "back calculation". The difficulties of achieving an exact result have already been discussed (FAGERSTRÖM *et al*, 1969); nevertheless, although some mistakes are inevitable, the results

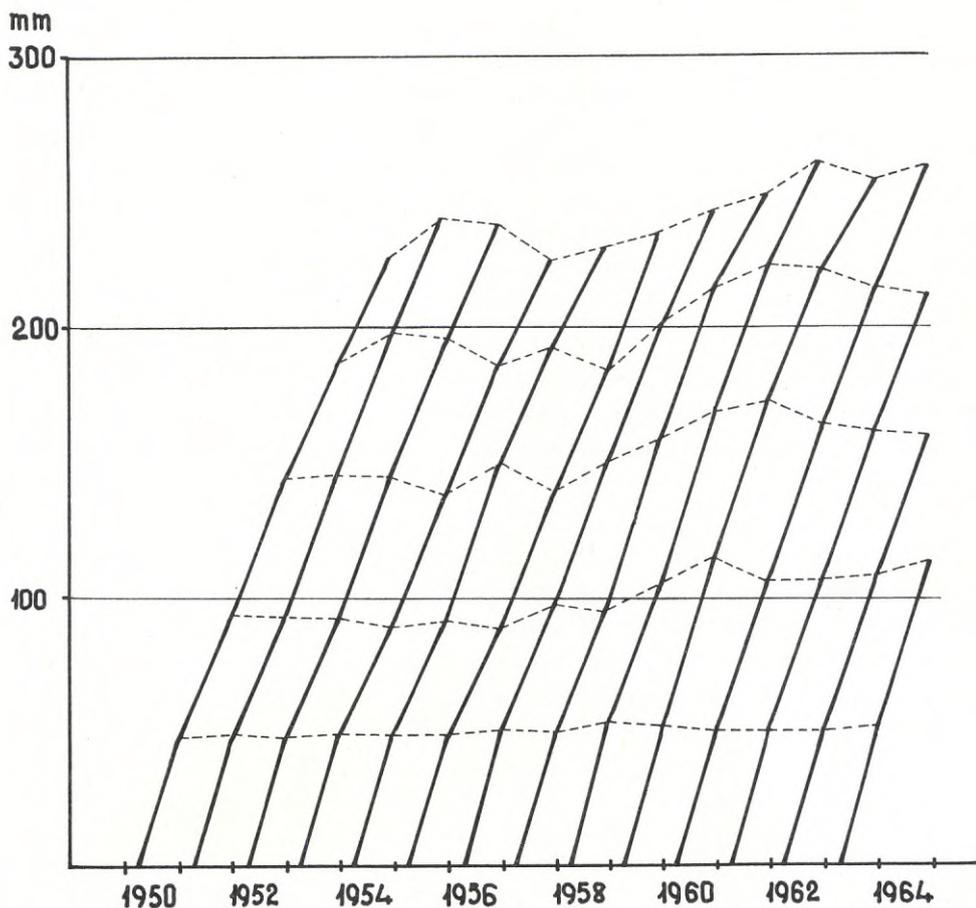


Fig. 1. Growth of trout in Lake Långbjörnsjön.

Table 5. Mean length of trout in Lake Långbjörsjön before and after the beginning of the experiment.

Age	Before	After	Increase in cm	Increase in %
1	4.9 cm (452)	5.1 cm (508)	0.2	4.1
2	9.1 ,, (365)	10.7 ,, (591)	1.6	17.6
3	14.2 ,, (263)	16.2 ,, (561)	2.0	14.1
4	19.1 ,, (180)	20.9 ,, (418)	1.8	9.4
5	23.1 ,, (102)	24.8 ,, (158)	1.7	7.4

(The figures in brackets show the number of trout examined.)

should give a mainly correct view of what has happened regarding the growth rates of trout. Table 5 and Fig. 1 show the growth rate of trout from Lake Långbjörsjön during the years 1950—64, as ascertained from scales collected from 974 fishes.

As early as 1917 DAHL showed what happens when it is attempted to reduce the population of trout in a small lake by removing about 50 per cent of the stock yearly. The old trout were gradually removed and the population then consisted of young fish with a good growth rate. However, a sport fisherman is as a rule not interested in the age of the trout he catches but only in their length and weight. At present it does not seem probable that the better growth rate has neutralized the rejuvenation in Lake Långbjörsjön. The fishing manager is, on the other hand, very interested in what happens to the whole stock.

This table shows that the growth for the trout has increased considerably since the beginning of the experiment. This is especially interesting as regards the trout during their second year. The increase may show that they spend the whole of their second year in the lake. This agrees with the experience of the sport fishermen, who exceptionally catch trout smaller than 10 cm.

There remains another possible explanation for the good growth in the second year: some of the more recent year classes have been rather small, as will be shown in section VII, and the competition within the year class correspondingly reduced on the nursery grounds, wherever they are.

As a matter of fact it has not been possible to ascertain where the trout from the lake spawn. The inlets are very small and look rather unimportant with the exception of the main inlet. This is, however, blocked by a very big flat stone close to the lake and it seems unlikely that the trout can pass this obstacle. The outlet has an impassable rapid at its very beginning. The trout might spawn in Lake Långbjörsjön but the material is not at all conclusive.

V. Variations in growth and fishing; preliminaries for the two following sections

The population structure will be judged by the catch in a gill net set of standard composition. The year classes will be judged mainly by the number in age group 3+ (Table 8), as sport fishing rarely takes such small trout. This age group is generally catchable with the standard set. The increased growth treated in the last section does not interfere seriously even if the falling number of nets in different mesh sizes in a standard set (Table 6) is taken into account; a detailed comparison between Fig. 1 of growth and length distribution in the most fine meshed gill nets shows that it is the year classes 1955 and 1956 at the age of 3+ that may be underestimated by the catch in a standard set as they were not yet fully catchable and this only strengthens the conclusions put forward (*cf.* section VII on recruitment).

Year class 1955. Caught for the first time in 1958 at 3+ years mainly with the 1.67 cm meshed gill nets. All fine-meshed nets closest to the shore and coarse-meshed predominantly as second in the gang; distribution otherwise not specified in 1958.

Year class 1956. Caught for the first time in 1959 at 3+ years with mesh sizes 1.67 and 2.14 cm. Eastern shore less fished than the western, most fine-meshed nets closest to the shore and most coarse-meshed as second in the gang in 1959.

Year class 1957. Caught for the first time in 1960 at 3+ years with mesh sizes 1.67 and 2.50 cm. Gill nets fairly well distributed over the different sections of the lake but twice as many nets in position closest to the shore as in position second net in the gang in 1960. (No coarse-meshed nets.)

Year class 1958. Some eight fish were caught as 2+ already in 1960 by gill nets but in the main this year class, too, was untouched by fishing until the age of 3+, in 1961. In that year, however, much of the sport fishing preceded the gill netting and scale sampling which, as an exception, were performed in August. With the good growth established for this year class some fish may have been caught by sport fishing in July 1961, but on the other hand the year class was certainly fully available to several mesh sizes in the set of gill nets (1.67, 2.14 and 2.50 cm), so the conclusion is that the year class could hardly have been a very good one. Distribution of the gill nets over the different sections was good, and equal numbers on first and second position from the shore in 1961.

Year class 1959. The first that could hypothetically have been influenced by the increased fishing — fewer spawners left in the autumn of 1958. Owing to good growth and late netting in 1961 the year class was caught already in 1961 in fair numbers at 2+ years, mostly in the finest mesh size. In 1962 there was no gill netting, but the year class predominated in the scale samples obtained with hook fishing, etc. In 1963 they were caught at 4+ years, still in good numbers (distribution of the nets not as regular as in 1961). A rough estimate for this year class as 3+ in 1962 would surpass all other 3+ estimates in Table 8.

Year class 1960. Some few may have been caught by the seining and hook fishing by the biologists in 1962; there were 36 trout below 20 cm in the catch but then no 2+ was obtained in the scale sample. Otherwise this year class, too, was unfished until the age of 3+ (in 1963).

Year class 1961. Caught as 3+ in the standard set in June 1964. Fine-meshed gill

nets twice as often in first as in second position from the shore and slightly irregularly distributed over the sections of the lake (in 1964).

Year class 1962. This year class may have been influenced by the heavy fishing in 1961 — fewer spawners left to the autumn of 1961. The fish were caught for the first time in gill nets in 1965, mesh sizes 1.67 and 2.14 cm, and then in an increased number at 4+ years in 1966, mesh sizes 1.67—2.50 cm, both years with good distribution of gill nets over the ten sections of the lake and equal numbers of gill nets in first and second position. Judged by this method it is the smallest year class in the series.

Year class 1963. Some eight caught in gill net 1965 at 2+ years, otherwise caught for the first time in 1966 at 3+ years, mainly in the most fine meshed gill nets (1.67 cm).

VI. Effect of fishing on the population structure of trout

The increased growth in all age groups of trout indicates that recruitment of trout and char has at least not increased to a degree that exploits the whole food production that was "released" when the fishing mortality of the two species increased.

A picture of the population structure of the trout has been obtained from the number of trout in different age groups caught in gill nets in one set of standard composition (Table 6).

Several corrections have to be applied. The first of these are explained in Table 7, *i.e.* a raising factor when all trout in the catch were not aged and a recalculation to catch in one set of standard composition when the fishing was otherwise performed. The corrected density values are listed in Table 8. In 1960 coarse-meshed nets were missing altogether and no correction for this has been applied and the density estimates for different age groups and year classes in Table 8 will be correspondingly low this catch year; the coarse-meshed nets contribute, however, very little to the catch of young age groups.

A third correction relates to the distribution of the gill nets. It is not only catch years 1961, 1965 and 1966, with the best distribution of the gill nets round the lake that are included in this analysis, but particular attention should perhaps be paid to these three catch years. In the catch years 1958, 1959, 1960 and 1964 the fine-meshed nets were more often set close to the shore than as second net in the gangs and the corresponding correction of young-trout values is explained in next section. A correction for old-trout values and the irregular distribution of mesh size 2.50 cm. nets in the catch

Table 6. Composition of a standard set of gill nets.

Mesh size, knot-to-knot measure, cm	5.00	3.75	3.33	3.00	2.50	2.14	1.67
Number of nets in the set	1	1	2	2	3	3	3

Table 8. Density estimates for different year classes and their different age groups. The number caught in a certain mesh size and classified as belonging to a certain age at the scale analysis is multiplied by the factor in Table 7. Corrected values for one age group are then added together from different mesh-size values in one standard set from a certain catch year. The different catch years are shown diagonally in the table with 1958 at the top and 1966 at the bottom and no values for catch year 1962 (no net fishing that year).

Year class	Age group							
	1+	2+	3+	4+	5+	6+	7+	8+
1950	—	—	—	—	—	—	—	3
1951	—	—	—	—	—	—	3	1
1952	—	—	—	—	—	12	1	0
1953	—	—	—	—	42	12	0	0
1954	—	—	—	59	12	1	0	—
1955	—	—	27	12	11	2	—	0
1956	—	2	19	13	6	—	0	0
1957	0	0	10	14	—	3	1	0
1958	0	5	13	—	3	2	0	0
1959	0	35	—	38	22	6	0	—
1960	1	—	17	9	12	1	—	—
1961	—	4	13	14	12	—	—	—
1962	0	0	7	11	—	—	—	—
1963	0	3	14	—	—	—	—	—
1964	0	5	—	—	—	—	—	—
1965	0	—	—	—	—	—	—	—

years 1958, 1959 and 1964 must be a little more uncertain, as the total number caught is less but a maximum reduction by 0.25 (1958) or 0.15 (—59) times the values in Table 8 was tentatively carried out¹. (Catch year 1960 could not be used for the old age groups.) Whichever reduction is made for catch years 1958, and —59, the numbers of old trout (5+ and older) in these years exceed the numbers in 1961, 1965 and 1966 (with regular net distribution), indicating the reducing effect of increased fishing pressure on old age groups. The number of old trout in catch year 1964 occupies an intermediate position, and is highly influenced by the strong year class 1959.

It is theoretically possible that a decreasing natural mortality during the experiment has to some degree masked the effect of increased fishing mortality.

Little information is available on age and length of spawning trout (Table 9). The material suggests that some of the trout are mature at the age of 5+ (Table 9 compared with Fig. 1). Studies of maturity in the gill net catch

¹ The factors were arrived at by studying the catch and the relevant distribution only of nets 2.50 cm knot-to-knot measure. 55 trout ≥ 25 cm were caught by 14 efforts with the nets closest to the shore while 28 such trout were caught by 13 efforts with the nets as second net in the gangs. Due regard to the more coarse-meshed nets and their small catch would tend to reduce the applied corrections.

Table 9. Distribution of spawning (s) and non-spawning (n) trout in a sample, October 1961.

Total length, cm	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	
Mesh size 1.67 s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
n	4	3	4	6	4	—	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.14 s	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
n	—	—	—	1	7	8	2	2	3	1	2	—	1	—	1	—	—	—	—	—	—	—	—
2.50 s	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—	—	1	—	—	—	—	—	—
n	—	—	2	—	—	2	1	2	6	3	7	3	4	4	2	—	1	—	—	—	—	—	—
3.00 s	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	1	—	—	—	—	—
n	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
3.33 s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	2	—	—	—	—	—
n	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Totals, spawners	0	0	0	0	0	0	0	0	0	1	0	1	1	2	2	2	1	3	0	0	0	0	1
Totals, nonspawners	4	3	6	7	11	10	6	5	11	4	9	3	5	4	3	1	1	0	0	1	0	0	0

July 1966 (129 trout) confirm this conclusion. The adult population was large in 1958 and gave rise to the important year class 1959, while the adult population was small in 1961 and gave rise to the small year class 1962. This will be further discussed in the following section.

VII. Trout recruitment estimates

If the density indices for age 3+ from Table 8 are plotted against the mean air temperature in May—June and July—August in the adjacent Storlien, the indices of year classes 1958, 1962 and 1963 (catch years 1961, 1965 and 1966) show a reasonable relation to mean temperatures of either kind of year of hatching, Fig. 2. Using the bottom figures in Table 7, GUSTAFSON *et al.* (1969) for catch in mesh sizes 1.67 and 2.14 cm knot-to-knot, it can be estimated that a net closest to the shore catches 3.4 times the number of trout caught in the second net where the size groups here relevant are concerned. Density indices from Table 8 for year classes 1955, 1956, 1957 and 1961 can then be converted according to the known distribution of the nets between first and second place in the gang (reported in section V) using the conversion factor 0.65 and 0.85 respectively, and these estimates are also introduced in Fig. 2 together with the original values from Table 8 and the rough density estimate 37 for year class 1959 as 3+. The conversion results in a fairly good concurrence between density indices and mean July—August temperature while the year classes 1955 and 1959 do not fit in the relation between year class indices and May—June temperatures. The lake is normally ice-covered from the middle of October up to the end of May.

Some guesses can be made about the year classes 1953 and 1954 though there is no density estimate for these trout in the 3+ age. As is shown by

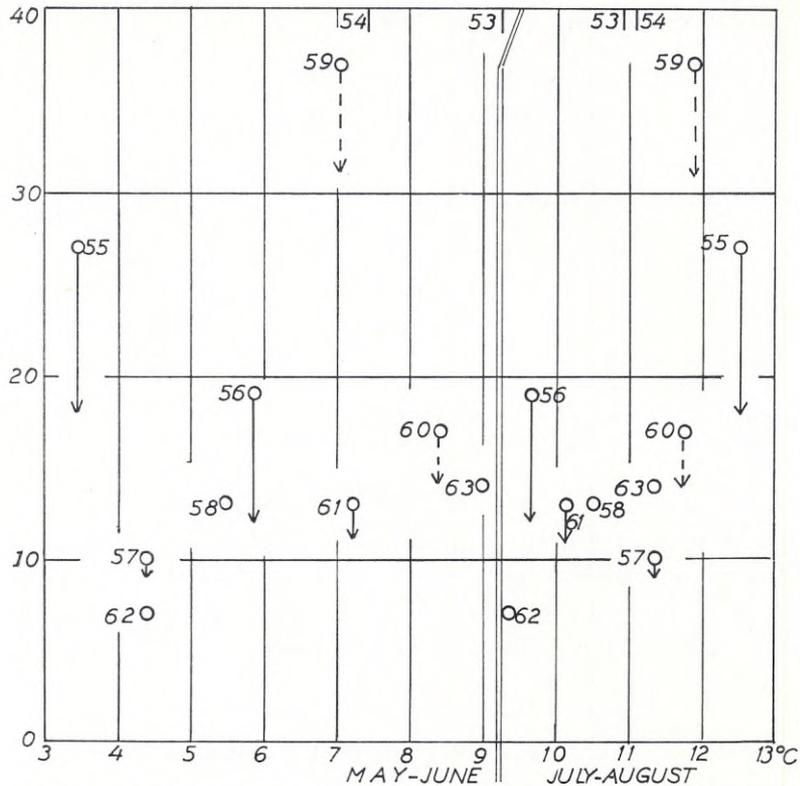


Fig. 2 a. Recruitment estimates for trout and mean air temperature at Storlien during May—June and July—August. The arrows indicate the corrections (reductions) discussed on page 109. 55, 56 etc. indicate year class. Only mean temperatures are inserted for year classes 1953 and 1954.

Table 8 the indices for 3+ and 4+ are generally both on the top of a dome-shaped curve. The indices 42 (age 5+) and 59 (age 4+) from Table 8 should at least not correspond to much lower indices for year classes 1953 and —54 as 3+; the indices would appear very high up in the diagram, Fig. 2. The corresponding mean temperatures are inserted at the top of the diagram. This material does not strengthen the impression of a simple temperature relation.

From the possible composite effects of both temperature and increased fishing mortality, the most promising seems to be a positive correlation between May—June temperatures and recruitment, combined with a reduction of the spawning population in 1959 and subsequent years, due to increased fishing mortality and consequently reduced recruitment level beginning with year class 1960 (*cf.* Tables 3, 4 and 8 and p. 108). The netting during the first year of the experiment (1958) was in any case not enough to bring down the spawning population to a critical level.

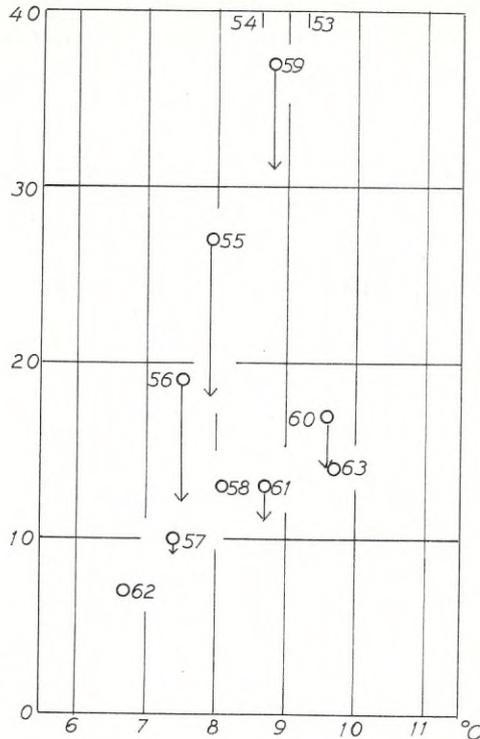


Fig. 2 b. Ditto, mean air temperature during May to September inclusive.

A positive correlation between the size of the spawning population and the size of the resulting year class does conform to the general ideas of population control (*cf.* FROST and BROWN 1967, NORTHCOTE 1969) provided the fishing pressure is high enough to reduce the number of spawners to a point below a critical level where the number of spawners becomes a regulating factor, and perhaps this point is more easily reached for trout than for many other fish. In Sweden their spawning streams are often protected against fishing during spawning time. Once above this critical level, on the other hand, environment or self-regulating processes can make the population size oscillate around a saturation level or even bring the "recruitment curve" downwards at higher population levels (RICKER 1958 p. 237, BEVERTON and HOLT 1957 pp. 55—61).

Within the salmonoid family the parent and progeny fractions of a pink salmon stock seem to be very effectively isolated from each other, the progeny escaping to the sea before the next spawning run (MANZER and SHEPARD 1962, GILHOUSEN 1962). In Lake Jölstervann in Norway where lake spawning is confirmed the different fractions of the trout population co-exist in a very deep lake (JENSEN and SENSTAD, 1962, KLEMETSEN 1967). The self-regulation of the population should be more effective, when the shelter of

Table 10. Population estimates by the Petersen method (within one season). Increased fishing mortality of tagged fish in the recapture period and in-

Species	Trout											
	Fincutting			Tagging			Tagging			Fincutting		
Marking	1959, July 2—11			1960, July 4—10			1961, July 3—16			1961, July 3—16		
Year and date of marking	21—			21—			21—			21—		
Total length, latitude, cm	≤20	25	>25	≤20	25	>25	≤20	25	>25	≤20	25	>25
Number Marked (M)	54	78	45	31	85	46	27	86	55	2	19	3

Recapture period	July 14—25			July 14—24 August 14			August 9—11			August 9—11		
	21—			21—			22—			22—		
Total length, latitude, cm	≤20	25	>25	≤20	25	>25	≤21	26	>26	≤21	26	>26
Number recaptured (R)	11	8	9	2	11	6	5	11	7	0	2	1
Catch, number (C)	151	65	49	69	77	30	126	52	28	126	52	28
Population Estimate	$P = \frac{M \cdot C}{R}$											
	741	634	245	1070	595	230	680	407	220	—	494	84
	1620			1895			1307			—		
Total length, latitude, cm	—	—	—	≤21	26	>26	≤22	27	>27	≤22	27	>27
Number recaptured (R)	—	—	—	4	10	5	5	15	3	0	3	0
Catch, number (C)	—	—	—	83	75	18	134	51	21	134	51	21
Population estimated	$P = \frac{M \cdot C}{R}$											
	—	—	—	643	638	166	724	292	385	—	323	—
	—			1447			1401			—		

the young, pre-recruit stages against interactions from other parts of the population is incomplete. According to our present knowledge a third example, the trout population in the shallow Lake Långbjörsjön, may be a relevant case of strong selfregulation (when the fishing pressure is released), but so far there is not enough material to substantiate this hypothesis.

A permanent influence on the recruitment level of trout should also be exerted by the char population in the lake. This effect is, however, not investigated at all in the present study, and the gap necessitates caution in conclusions about the trout population control.

VIII. Appendix: Population size estimates from marking recapture data

To get a rough impression of the population size in this 0.1 square kilometre lake, where the described population structure changes occurred, the

creased natural mortality of small tagged fish are suspected to operate (FAGERSTRÖM *et al* 1969, Sections III and IV and Tables 4 and 7).

Species	Char											
	Fincutting			Tagging			Tagging			Fincutting		
Marking	1959, July 2—11			1960, July 4—10			1961, July 3—16			1961, July 3—16		
Year and date of marking	1959, July 2—11			1960, July 4—10			1961, July 3—16			1961, July 3—16		
Total length, latitude, cm	21—			21—			21—			21—		
	≤20	25	>25	≤20	25	>25	≤20	25	>25	≤20	25	>25
Number Marked (M) ..	33	35	2	13	38	4	13	107	11	3	19	0

Recapture period	July 14—25			July 14—24 August 14			August 9—11			August 9—11		
	≤20	25	>25	≤20	25	>25	≤20	25	>25	≤20	25	>25
Total length, latitude, cm	21—			21—			21—			21—		
Number recaptured (R)	2	9	2	0	3	3	1	19	4	0	3	0
Catch, number (C)	120	264	17	132	160	28	94	140	25	94	140	25
Population Estimate	$P = \frac{M \cdot C}{R}$			$P = \frac{M \cdot C}{R}$			$P = \frac{M \cdot C}{R}$			$P = \frac{M \cdot C}{R}$		
	1980	1026	17	—	2027	37	1222	788	69	—	887	—
	3023						2079					
Total length, latitude, cm	—			22—			22—			22—		
	≤21	26	>26	≤21	26	>26	≤21	26	>26	≤21	26	>26
Number recaptured (R)	—	—	—	1	4	1	3	19	2	0	3	0
Catch, number (C)	—	—	—	166	144	10	125	122	12	125	122	12
Population estimated	$P = \frac{M \cdot C}{R}$			$P = \frac{M \cdot C}{R}$			$P = \frac{M \cdot C}{R}$			$P = \frac{M \cdot C}{R}$		
	—	—	—	2158	1368	40	542	686	66	—	773	—
				3566			1294					

marking data from FAGERSTRÖM *et al.* (1969) will be used. In the marking analysis it was shown that tags were shed, probably fairly soon after the summer of tagging, and that small fish (below 20 cm) were not recaptured to the same extent as larger ones, not even during the summer of tagging. To use for population estimate tagged fish above 20 cm and recaptures during the first summer — as is carried out in some columns of Table 10 — is, however, not enough to secure a good population estimate, as tagged fish are likely to be somewhat overrepresented in gill-net catches in the present experiment (FAGERSTRÖM *et al.* 1969, p. 31). An attempt to check this population estimate is therefore made in Table 10, using the data of fin-cut and recaptured fish from the marking experiment. Some of those were below 20 cm too, and they have been entered in separate columns in Table 10; different length fractions can be separated but individual recognition is impossible. The number of small, fin-cut fish is low but should not give such a biased estimate of the number of small fish as tagged small fish do. The best population estimate would therefore be obtained by adding the

estimate from those below 20 cm to the estimate from those between 20 and 25 cm and the estimate from those above 25 cm at marking, using the fin-cut series. As stated in GUSTAFSON *et al.* (1969) — corrected by “errata” in that volume — the density falls by something like three or four catchable fish (char plus trout) per ten metres square.

IX. Summary

An experiment was started in a small, high mountain lake to investigate whether the recruitment could be reduced to a point where the individual growth would increase spectacularly. Mean size of trout in the sport fishermen’s catches has decreased and the number of trout and char above 24 cm in a standard set of gill nets has decreased (Tables 3 and 4) although the individual growth of trout has increased (Fig. 1). From the possible composite effects of both temperature and increased fishing mortality on recruitment of trout, the most promising seems to be a positive correlation between May—June temperatures and recruitment, combined with a reduction of the spawning trout population in 1959 and subsequent years (due to increased fishing mortality) and a consequently reduced recruitment level beginning with year class 1960 (Fig. 2). Rough population size estimates are presented in the Appendix.

X. References

- BEVERTON, R. J. H. & S. J. HOLT. 1957. On the dynamics of exploited fish populations. *Fish. Invest. Lond.* (2), 19: 1—533.
- DAHL, K. 1917, 2nd edition 1943. Ørret og ørretvann. Studier o forsøk. Oslo 182 pp. (In Norwegian.)
- FAGERSTRÖM, Å., K. J. GUSTAFSON & T. LINDSTRÖM. 1969. Tag shedding, growth and differential mortality in a marking experiment with trout and char. *Rep. Inst. Freshw. Res. Drottningholm* 49: 27—43.
- FROST, W. E. & M. E. BROWN. 1967. The Trout. London. 286 pp.
- GILLHOUSEN, P. 1962. Marine factors affecting the survival of Fraser River pink salmon. In Symposium on pink salmon, N. J. Wilimovsky (Ed.), MacMillan Lect. Fish., Univ. Brit. Columbia: 105—109.
- GUSTAFSON, K. J., T. LINDSTRÖM & Å. FAGERSTRÖM. 1969. Distribution of trout and char within a small Swedish high mountain lake. *Rep. Inst. Freshw. Res. Drottningholm* 49: 63—75.
- JENSEN, K. & C. SENSTAD. 1962. Ørret som gyter på stille vann. *Jakt-Fiske-Friluft*. 91: 202, 203, 232. (In Norwegian.)
- KLEMETSEN, A. 1967. On the feeding habits of the population of brown trout (*Salmo trutta* L.) in Jölstervann. *Nytt Mag. Zool.* 15: 50—67.
- MANZER, J. & M. P. SHEPARD. 1962. Marine survival, distribution and migration of pink

salmon (*Oncorhynchus gorbuscha*) off the British Columbia coast. In Symposium on pink salmon, N. J. Wilimovsky (Ed.), MacMillan Lect. Fish., Univ. Brit. Columbia: 113—121.

NORTHCOTE, T. G. (Ed.) 1969. Symposium on salmon and trout in streams. MacMillan Lect. Fish., Univ. Brit. Columbia. 388 pp.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.* 119: 1—300.

Period Gear, for gill nets also mesh size designation (cf. Tab. 6)	1960, tagging				1960, recapture period				1961, marking						Total length, cm	
	Seining	Fly fishing	Otter with flies	Totals	2.5	Gill nets		Incomplete standard set		Seining	Fly fishing	Otter with flies	Otter with spoons	Totals, all kinds of gear		Fin cutting all kinds of gear
						1.7	July	Aug.								
Number					12	12	12	1	1							
13	—	—	—	—	1	—	1	0.3	1	—	—	—	—	—	—	13
13.5	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	13.5
14	—	—	—	—	—	—	5	1.8	1	—	—	—	—	—	—	14
14.5	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	14.5
15	—	—	—	—	—	—	6	2.5	2.5	1	—	—	—	1	—	15
15.5	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	15.5
16	1	1	2	4	—	—	1	1.3	1	—	—	—	—	—	—	16
16.5	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	16.5
17	—	1	—	1	—	—	4	1.3	4	2	—	—	—	3	—	17
17.5	—	—	—	—	1	—	4	—	—	—	—	—	—	—	—	17.5
18	4	—	1	5	—	—	6	3.2	0.5	2	2	1	1	6	—	18
18.5	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	18.5
19	10	3	2	15	1	—	6	3.2	2	2	2	1	2	8	1	19
19.5	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	19.5
20	1	2	3	6	2	5	4	3.8	5	4	1	1	2	9	1	20
20.5	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	20.5
21	6	2	4	12	1	7	1	2.8	5.5	7	3	3	2	16	3	21
21.5	—	—	—	—	1	2	2	—	—	—	—	—	—	—	—	21.5
22	12	5	7	24	2	3	—	2	4	2	4	3	1	19	3	22
22.5	—	—	—	—	1	3	1	—	—	—	—	—	—	—	—	22.5
23	7	3	5	15	4	3	—	2	9	1	3	2	3	17	6	23
23.5	—	—	—	—	7	3	1	—	—	—	—	—	—	—	—	23.5

Total length, cm

24	8	4	10	22	5	5	3	5.3	7	4	3	3	5	18	1	24
24.5	2	3	7	12	4	3	2	—	5	—	5	—	2	16	—	24.5
25	2	3	7	12	3	2	1	3.2	5	—	—	—	2	6	—	25
25.5	3	2	2	7	4	4	—	—	4	3	6	—	3	16	1	25.5
26	3	2	2	7	3	3	1	2.5	4	3	—	—	—	—	—	26
26.5	5	—	7	12	4	4	1	—	—	6	3	—	4	15	1	26.5
27	5	—	7	12	—	—	2	—	—	—	—	—	—	—	—	27
27.5	2	2	—	4	2	—	—	—	—	4	—	—	2	8	—	27.5
28	2	2	—	4	—	—	—	—	—	—	—	—	—	—	—	28
28.5	2	1	1	4	—	—	2	—	—	3	—	—	—	4	—	28.5
29	2	1	1	4	—	—	—	—	—	—	—	—	—	—	—	29
29.5	3	1	3	7	1	2	—	—	—	—	—	—	—	—	—	29.5
30	3	1	3	7	2	2	—	—	—	3	—	—	1	6	1	30
30.5	2	1	3	6	2	2	1	—	—	—	—	—	1	—	—	30.5
31	2	1	3	6	2	2	—	—	—	—	—	—	—	2	—	31
31.5	2	1	—	3	—	—	—	—	—	1	—	—	—	—	—	31.5
32	2	1	—	3	—	—	—	—	—	—	—	—	—	2	—	32
32.5	2	1	—	3	—	—	—	—	—	—	—	—	—	—	—	32.5
33	1	1	—	2	—	—	1	—	—	—	—	—	—	—	—	33
33.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33.5
34	—	—	—	—	—	—	—	—	—	1	—	—	—	2	—	34
34.5	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	34.5
35	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	35
35.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35.5
36	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36
36.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36.5
37	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	37
Totals	71	33	58	162	54	50	72	—	—	46	32	19	28	168	24	—
Mean length	23.5	23.8	24.2	23.8	24.5	23.1	18.8	—	—	24.1	23.4	22.6	24.4	23.9	23.5	—

↑ Absence of coarse-meshed
nets most serious in this section
↑ Ditto ↑

Period	1961, recapture period						1961, autumn				1962				1964					
	Gear, for gill nets also mesh size designation (cf. Tab. 6)						Gill nets						Seining				Gill nets			
	Number	5.0— 3.0	2.5	2.1	1.7	stand- ard set	5.0— 3.0	2.5	2.1	1.7	5.0— 3.0	2.5	2.1	1.7	stand- ard set	6	3	3	3	1
11	18	9	9	9	1	18	9	9	9	4	1	—	—	—	—	—	—	—	—	11
11.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11.5
12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12
12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12.5
13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13
13.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13.5
14	1	—	—	—	1/3	—	—	—	—	—	—	—	—	1	—	—	—	—	—	14
14.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14.5
15	—	—	—	11	3 2/3	1	—	—	—	—	—	—	—	—	—	—	—	—	1	1 1/2
15.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15.5
16	1	—	—	17	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16
16.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.5
17	1	2	—	25	9 1/3	—	—	—	3	—	—	—	—	—	—	—	—	—	—	17
17.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17.5
18	—	2	3	14	6 1/3	—	2	—	4	—	—	—	—	—	—	—	—	—	—	18
18.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18.5
19	1	—	5	14	6 2/3	—	—	—	6	—	—	—	—	—	—	—	—	—	—	19
19.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19.5
20	1	3	7	5	5 1/3	—	1	12	4	—	—	—	—	—	—	—	—	—	—	20
20.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20.5
21	—	2	7	4	4 1/3	—	2	10	—	—	—	—	—	—	—	—	—	—	—	21
21.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21.5
22	1	4	1	2	2 2/3	—	2	8	3	—	—	—	—	—	—	—	—	—	—	22
22.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22.5
23	—	4	6	1	3 2/3	—	8	3	1	—	—	—	—	—	—	—	—	—	—	23

Total length, cm

Total length, cm

Period	1965						1966					
	Gill nets						Gill nets					
	5.0— 3.0	2.5	2.1	1.7	standard set		5.0— 3.0	2.5	2.1	1.7	standard set	
Number	18	9	9	9	1		18	9	9	9	1	
Gear, for gill nets also mesh size designation (cf. Tab. 6)												
Total length, cm												
12				1	1/3							
12.5												
13												5/6
13.5								1				
14				4	1 1/3			1		5		2 4/6
14.5										3		
15				3	1					1		1 3/6
15.5										4		
16				3	1 1/3					2		1 5/6
16.5		1								3		
17			1	4	1 2/3					2		2 1/6
17.5							2			4		
18				6	2		1	2	1	2		4 4/6
18.5							3			7		
19			1	2	1		2		3	2		4 3/6
19.5									1	2		
20			1 + 1	1	1			1	3	3		3
20.5			5 + 2	0	2 1/3		1	2	1	2		3 1/6
21							3		1	1		
21.5												

Total length, cm

12
12.5
13
13.5
14
14.5
15
15.5
16
16.5
17
17.5
18
18.5
19
19.5
20
20.5
21
21.5

22	1	—	4	2	21/3	—	—	1	1	1	1	2 4/6	22
22.5	—	—	—	—	—	—	—	—	—	—	—	—	22.5
23	1	5	5 + 1	0	4	—	—	2	3	2 4/6	—	—	23
23.5	—	—	—	—	—	—	—	3	—	—	—	—	23.5
24	1	4	1	1	21/3	1	—	3	2	—	3	—	24
24.5	—	—	—	—	—	—	—	1	1	—	—	—	24.5
25	—	7	3 + 1	1	4	1	—	2	1	1 4/6	—	—	25
25.5	—	—	—	—	—	—	—	2	—	—	—	—	25.5
26	—	10	2	1	41/3	—	—	1	—	1 1/6	—	—	26
26.5	—	—	—	—	—	—	—	2	—	—	—	—	26.5
27	—	4	1 + 1	0	2	1	—	3	—	2 1/6	—	—	27
27.5	—	—	—	—	—	—	—	3	—	—	—	—	27.5
28	2	5	3	—	31/3	—	—	6	—	3	—	—	28
28.5	—	—	—	—	—	—	—	1	—	—	—	—	28.5
29	1	6	2	1	31/3	—	—	1	—	—	—	—	29
29.5	—	—	—	—	—	—	—	—	—	—	—	—	29.5
30	1	—	—	—	—	—	—	1	1	—	—	—	30
30.5	—	1	—	—	2/3	—	—	—	—	—	—	—	30.5
31	2	2	1	—	1 2/3	—	—	2	—	—	—	—	31
31.5	—	—	—	—	—	—	—	—	1	4/6	—	—	31.5
32	4	1	—	—	1 2/3	—	—	—	—	—	—	—	32
32.5	—	—	—	—	—	—	—	—	—	—	—	—	32.5
33	—	2	—	—	2/3	—	—	—	—	—	—	—	33
33.5	—	—	—	—	—	—	—	—	—	—	—	—	33.5
34	—	—	—	—	—	—	—	—	—	—	—	—	34
34.5	—	—	—	—	—	—	—	—	—	—	—	—	34.5
35	—	—	—	—	—	—	—	—	—	—	—	—	35
Totals	13	48	30 + 6 + 30	18.1	—	16	41	22	50	—	—	—	—
Mean length	—	26.5	23.8	—	—	—	25.1	21.7	18.2	—	—	—	—

Table 11 B. Length distribution of char in different kinds of gear. (Mesh size designation 2.1 c=cotton nets, the only nets of this material). Catch in standard set is calculated from the other entered gill net catches. Dates of fishing in Table 4.

Period	1958						1959, marking						1959, Period of recapture					
	Gill nets						Seining	All kinds of gear	Gill nets									
	5.0—3.0	2.5	2.1	1.7	standard set	5.0—3.0			2.5	2.1	(2.1 c)	1.7	standard set					
Number	12	2	2	2	1			30	5	5	(15)	10	1					
12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12			
12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12.5			
13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13			
13.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13.5			
14	—	—	—	—	—	—	—	—	—	—	—	4	—	—	14			
14.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14.5			
15	—	—	—	2	3	1	1	—	—	—	—	14	—	—	15			
15.5	—	—	—	—	—	—	—	—	—	—	—	1	—	—	15.5			
16	—	—	—	4	6	1	1	—	—	—	—	5	—	—	16			
16.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.5			
17	—	—	—	3	4 2/4	3	5	—	—	—	—	2	—	—	17			
17.5	—	—	—	—	—	3	3	—	—	—	—	2	—	—	17.5			
18	—	—	—	6	9	3	3	—	—	—	1	14	—	—	18			
18.5	—	—	—	—	—	—	—	—	—	—	—	3	—	—	18.5			
19	—	—	—	—	12	10	12	—	—	—	—	8	—	—	19			
19.5	—	—	—	—	—	—	—	—	—	—	—	3	—	—	19.5			
20	—	—	1	3	4	7	9	—	—	—	—	17	—	—	20			
20.5	—	—	—	2	—	—	—	—	—	—	6	4	—	—	20.5			

Total length, cm

Total length, cm

21	7	3	10	—	10	6	10.2	3.5	3	—	3	3	9	2	21
21.5	—	5	13	3	9	6	—	—	—	—	—	—	—	—	21.5
22	8	—	—	3	9	6	10.7	4	7	1	—	8	17	1	22
22.5	—	—	—	5	15	4	—	—	—	—	—	—	—	—	22.5
23	6	4	10	6	5	3	10.8	2	6	2	2	8	28	2	23
23.5	—	—	—	14	3	2	—	—	—	—	—	—	—	—	23.5
24	4	—	4	8	6	—	9.3	4.5	4	1	2	4	31	9	24
24.5	—	—	—	8	7	3	—	—	—	—	—	—	—	—	24.5
25	—	1	1	5	5	—	6.3	3.5	1	—	—	5	22	5	25
25.5	—	—	—	4	3	—	—	—	—	—	—	—	—	—	25.5
26	2	1	3	8	3	1	5.5	2.0	—	—	2	—	6	—	26
26.5	—	—	—	5	1	—	—	—	—	—	—	—	—	—	26.5
27	—	—	—	2	1	—	—	—	—	—	—	—	—	—	27
27.5	—	—	—	1	1	—	—	—	—	—	—	—	—	—	27.5
28	—	1	1	—	1	—	—	—	—	—	—	—	—	—	28
28.5	—	—	—	1	—	—	—	—	—	—	—	—	—	—	28.5
29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29
29.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29.5
30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30
30.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30.5
31	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31
31.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31.5
32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32
32.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32.5
33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33
33.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33.5
34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34
34.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34.5
35	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35
35.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35.5
36	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36
36.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36.5
37	—	—	—	—	—	—	—	—	—	—	—	—	—	—	37
Totals	35	20	55	73	90	157	26	6	22.0	21.9	21.9	22.8	131	22	
Mean	length	21.8	22.1	21.9	24.3	18.4	22.0	21.9	21.9	21.9	22.8	23.2	23.1	23.1	

↑ Absence of coarse-meshed nets most serious in this section
 ↓ Ditto ↑

Period	1965						1966					
	Gill nets						Gill nets					
	5.0— 3.0	2.5	2.1	1.7	standard set		5.0— 3.0	2.5	2.1	1.7	standard set	
Number	18	9	9	9	1		18	9	9	9	1	
13	—	—	—	—	—	—	—	—	—	—	—	13
13.5	—	—	—	—	—	—	—	—	—	—	—	13.5
14	—	—	1	—	—	—	—	—	—	—	—	14
14.5	—	—	—	—	1/3	—	—	—	—	—	—	14.5
15	—	—	—	4	1 1/3	—	—	—	—	—	—	15
15.5	—	—	—	—	—	—	—	—	—	—	—	15.5
16	—	—	0 + 3	7	3 1/3	—	—	—	—	—	—	16
16.5	—	—	—	—	—	—	—	—	—	—	—	16.5
17	—	—	—	—	1	—	—	—	—	—	—	17
17.5	—	—	—	3	—	—	—	—	—	—	—	17.5
18	—	—	1	19	6 2/3	—	—	—	—	—	—	18
18.5	—	—	—	—	—	—	—	—	—	—	—	18.5
19	—	—	—	13	4 1/3	—	—	—	—	—	—	19
19.5	—	—	—	—	—	—	1	—	—	—	—	19.5
20	—	—	3 + 3	27	11	—	2	—	—	—	—	20
20.5	—	—	—	—	—	—	1	—	—	—	—	20.5
21	—	1	13 + 4	18	12	—	2	—	—	—	—	21
21.5	—	—	—	—	—	—	—	—	—	—	—	21.5
22	—	—	17 + 4	13	11 1/3	—	2	—	—	—	—	22
22.5	—	—	—	—	—	—	—	—	—	—	—	22.5

Total length, cm

Total length, cm

Table 12. Growth of trout from Lake Långbjörsjön and numbers of examined specimens (figures within brackets).

Year class	Black-calculated length in centimetres at age:				
	1	2	3	4	5
1950	4.7 (10)	—	—	—	—
1951	4.8 (19)	9.2 (10)	—	—	—
1952	4.7 (35)	9.1 (19)	14.3 (10)	—	—
1953	4.8 (52)	9.1 (34)	14.4 (17)	18.6 (10)	—
1954	4.8 (74)	8.8 (52)	14.4 (34)	19.7 (17)	22.6 (10)
1955	4.8 (76)	9.0 (74)	13.7 (52)	19.5 (34)	24.0 (17)
1956	5.0 (100)	8.8 (76)	14.9 (74)	18.5 (51)	23.9 (27)
1957	4.9 (86)	9.6 (100)	13.8 (76)	19.2 (68)	22.5 (48)
1958	5.3 (73)	9.5 (86)	15.0 (99)	18.3 (57)	22.9 (16)
1959	5.2 (189)	10.5 (73)	15.8 (86)	20.0 (69)	23.4 (29)
1960	5.0 (63)	11.4 (189)	16.8 (65)	21.4 (69)	24.2 (16)
1961	5.0 (85)	10.6 (62)	17.2 (120)	22.2 (32)	24.9 (16)
1962	5.0 (48)	10.6 (83)	16.4 (62)	22.1 (78)	26.1 (5)
1963	5.2 (50)	10.8 (48)	16.2 (81)	21.4 (45)	25.5 (40)
1964	—	11.3 (50)	15.9 (48)	21.2 (68)	25.9 (36)

Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren, Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus*¹

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British Columbia Fish and Wildlife Branch, Victoria and
Institute of Freshwater Research, Drottningholm

Contents

I. Introduction	133
II. Methods	134
Physical and chemical limnology	134
Gill net sets	135
Echo sounding	135
Dynamite explosions	135
III. Some limnological features of Lambarfjärden	137
IV. Species and size composition of netted fish	142
V. Seasonal changes in vertical distribution	143
Distribution indicated by netting	143
1. Cisco	143
2. Smelt	143
3. Perch	143
4. Roach	144
Distribution indicated by Echo-sounding	146
1. Interpretation of echo traces	146
2. Results from echo-sounding	148
Distribution indicated by Dynamite Explosions	150
VI. Diel changes in vertical distribution	150
VII. Seasonal and diel changes in horizontal distribution	153
VIII. Discussion and summary	158
IX. Acknowledgements	166
X. References	166

I. Introduction

Interaction between species of fish apparently sharing resources in the environment such as space or food has been the subject of considerable descriptive investigation, of much controversy and of some experimental

¹ The first of a series of papers resulting from a reciprocal research exchange arranged between the British Columbia Fish and Wildlife Branch and the Swedish Institute of Freshwater Research during 1968 and 1969.

research in ecology (see especially NILSSON, 1967). In addition to important basic problems in ecological theory raised by species interaction, there are significant implications for those concerned with management of fish populations utilized for human food, recreation or both. A thorough understanding of the interactive processes between cohabiting species may suggest ways of optimizing production in waters where they already occur or of most effectively utilizing environments into which various species combinations may be introduced.

Although interaction between trout and char has been extensively studied in Swedish lakes (NILSSON, 1965) as has that between various whitefishes (SVÄRDSON, 1949; NILSSON, 1958, 1960; LINDSTRÖM and NILSSON 1962), the relationship between cisco (*Coregonus albula*) and smelt (*Osmerus eperlanus*) has received surprisingly little attention, despite the wide distribution and importance of these species. Both are pelagic, schooling and plankton-eating fishes present in many lakes, particularly in central Sweden (ROSÉN, 1956). General characteristics of the biology and fisheries for cisco and smelt in Mälaren are given in SVÄRDSON (1956, 1966), RUNDBERG (1968) and VALLIN (1969). Of 110 lakes north of Dalälven discussed by SVÄRDSON (1966), 71 contained cisco, 51 smelt but only 13 both species. Their limited coexistence results in part from events and conditions associated with deglaciation, but unsuccessful attempts to introduce cisco into some lakes containing smelt suggest that interaction between the species may also be a factor.

During the summer and early autumn of 1968, observations were made on the spatial distribution of pelagic fishes in Lambarfjärden, a semi-isolated basin of the large, multibasin Lake Mälaren on the eastern coast of central Sweden (Fig. 1). In addition, the vertical distribution of pelagic zooplankton was recorded and the feeding of cisco and smelt examined. Only information relevant to spatial distribution of the common pelagic fishes in Lambarfjärden will be presented here in an attempt to determine if segregation may occur between cisco and smelt in the pelagic region of the lake.

II. Methods

Physical and chemical limnology

Vertical temperature profiles were made at Station A (Fig. 1) with a recently calibrated Freshwater Biological Association (F.B.A.) probe and with an Institute of Freshwater Research (I.F.R.) thermistor TIV using a Tettex AB Bridge 8706. Vertical oxygen profiles were determined with the F.B.A. oxygen probe. Delay in obtaining an extension cable for the probe restricted both temperature and oxygen series to the upper 23 m until later in the summer, however the major changes in these parameters occurred within this depth zone.

Subsurface illumination was measured with a Model 514 M Photovolt photometer modified for underwater use. Combinations of neutral density filters were used to take readings over the wide light range encountered; a scotopic filter (human eye) and opal diffusing glass were also in place for all measurements. The instrument was calibrated using a N.B.S. calibrated lamp and all readings were converted to *approximate* lux units. The photometer response did not fit a cosine function but approximated it reasonably well (Fig. 2).

Gill net sets

Monofilament nylon gangs of nets, each 30 m long and 10 m deep and containing equal lengths of 19 and 27 mm (knot to knot) green mesh, were set at Station A in Lambarfjärden at approximately two week intervals between late June and early September. Net gangs were suspended from the surface and at 10, 20, 30 and 40 m depths usually for 3 hour fishing intervals near midday (about 1030—1330 hours) and midnight (about 2230—0130 hours). Replicate gangs were set at the two depth zones which seemed best to capture cisco and smelt. A supplementary series of day and night sets was made once at selected depths in onshore areas at Station B. All nets were marked by narrow uncoloured portions of the webbing at 2 m depth intervals which facilitated recording the depth distribution of fish in the sets.

Fish were removed from nets on the shore and their depth in the net noted. Usually the entire catch was measured (total length), sexual condition recorded, and stomachs of all cisco and smelt preserved in a 10 % formalin solution. Stomachs of other fish species were sampled to cover the size range of specimens caught. For graphical presentation, all catches have been weighted, where necessary, to represent totals from a 3 hour fishing period by *two* replicate gangs in each 10 m depth zone.

Echo sounding

During most fishing periods echo sounding tracings were made near the net sets at Station A and over a transect from Station A to Lambarudd (Fig. 1). A Furuno F-701 50 Kc/sec sounder was used at Gain 6 to make all tracings; the depth scale was adjusted to compensate for the position of the transducer 0.5 m below the water surface. No objects could be recorded in the upper 2.5—3 m because the zero band on the sounder obscured that depth interval.

Dynamite explosions

One series of fish collections was made at Station A by exploding 100 or 400 gm charges of dynamite (Nitrolit) at various depths. Each charge was suspended from the surface by a small float and detonated electrically from

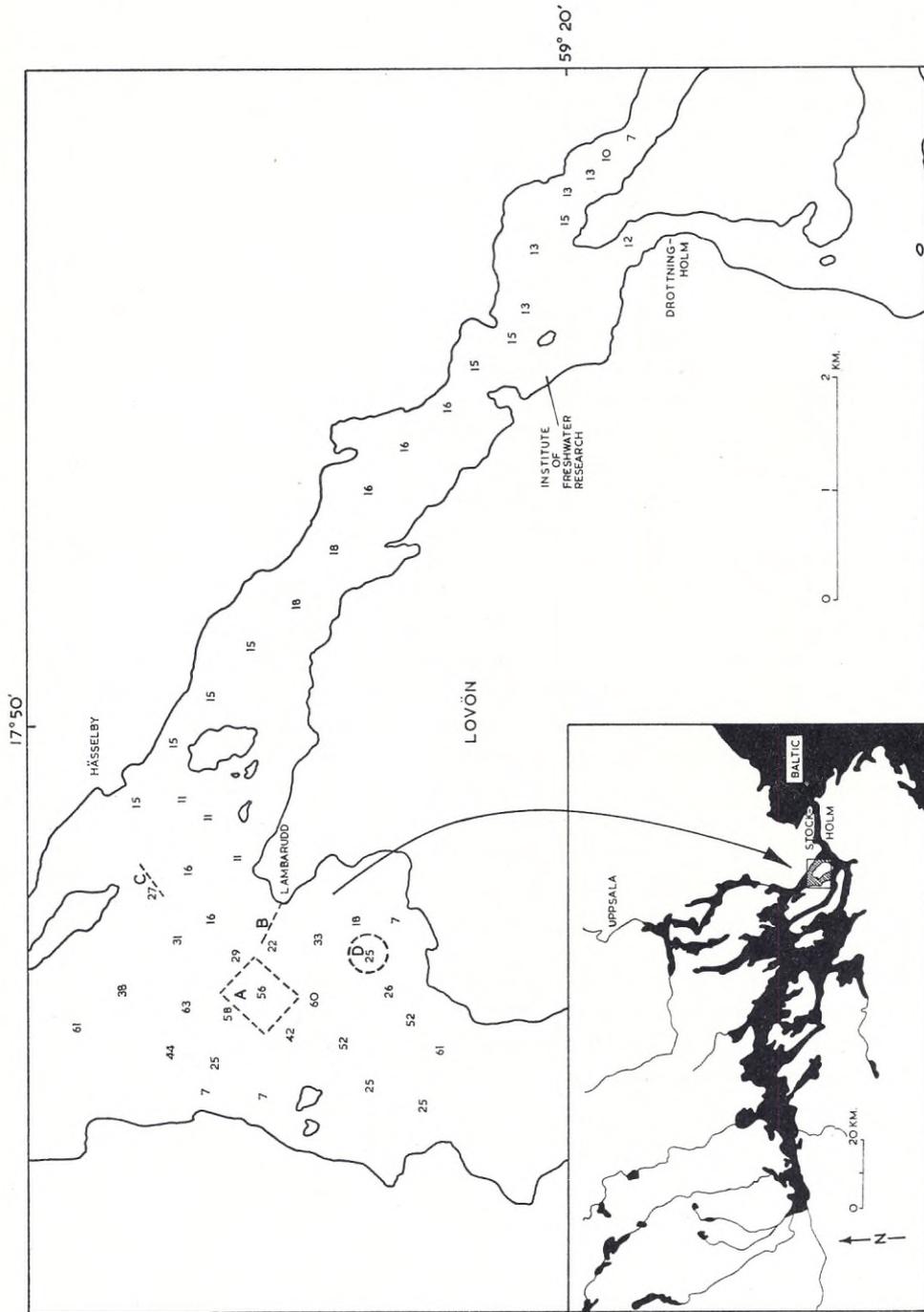


Fig. 1. Lambarfjärden study area showing depths in meters; inset shows location within Lake Mälaren. A — standard midwater netting station; B — Lambarudd, echo sounding and netting area; C — a netting area used for commercial fishing; D — the netting area used by I.F.R. for an annual cisco and smelt sample.

a boat a few meters away. Echo soundings were made as above over each area immediately prior to and following detonation. Charges at each depth were spaced at about 50 m intervals in an easterly direction from Station A. Only the fish which floated to the surface were collected. Seagulls took several large cisco and up to a hundred or more smelt from each of the 400 gm charges; fewer surfacing fish were lost in this manner from the 100 gm charges.

III. Some limnological features of Lambarfjärden

Lambarfjärden, one of the deepest basins in Lake Mälaren, formerly was subject to periodic intrusions of saline water from the Baltic which produced severe oxygen depletion of its bottom water (SVÄRDSON, 1956). Damming of the outlet at Stockholm has prevented further intrusions and rarely now have its deeper layers been subject to serious stagnation. Depths within the main netting area at Station A were close to 50 m; only a few restricted portions of the basin are deeper than 60 m (Fig. 1).

Thermal stratification was well established in the latter part of June (Fig. 3) when the thermocline lay at about 6 m. Thereafter it became progressively deeper, reaching nearly 14 m by early July and ranging be-

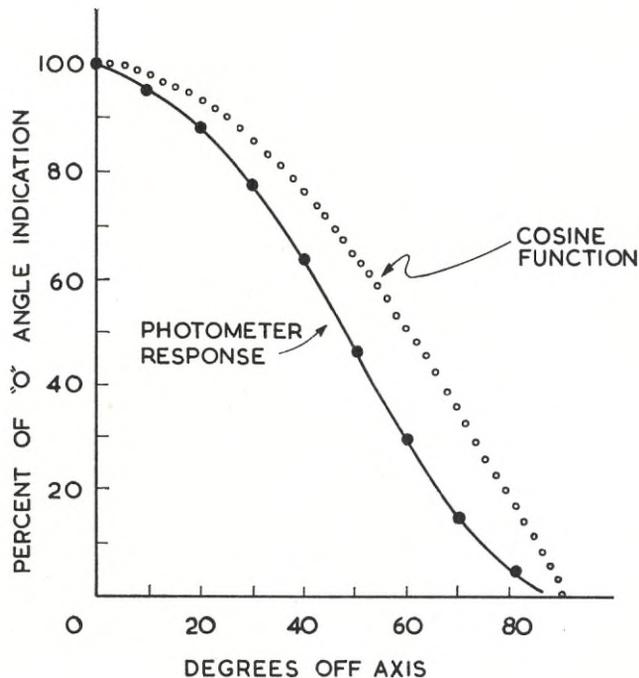


Fig. 2. Approximation of Photovolt Model 514 M photometer response to a cosine function curve (after modification of the instrument for underwater use).

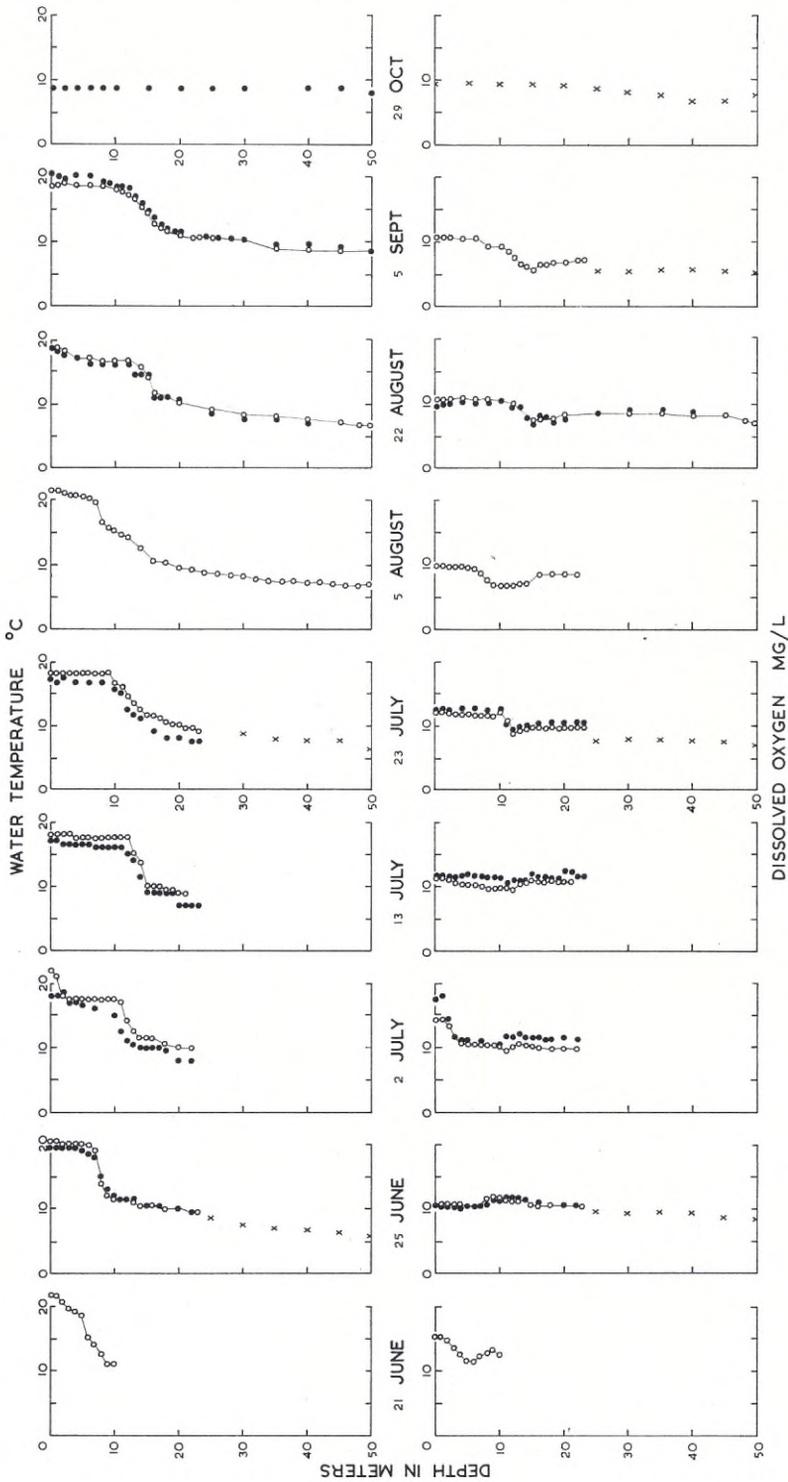


Fig. 3. Midday (joined open points) and midnight (solid points) temperature and oxygen profiles at Station A, Lambarfjärden during summer and autumn, 1968. Crosses give data supplied by Dr. T. Ahl for nearby station on 24 June, 31 July, 12 Sept. and 25 Oct., 1968.

tween 10 and 15 m throughout summer and early autumn. The thermocline had disappeared by late October when the basin was nearly isothermal. Evidence of internal thermal seich action was suggested by changes in mid-day and midnight temperature profiles at Station A, but usually shifts in isotherm levels within 24 hours were only a few meters at most.

No marked oxygen depletion was noted in Lambarfjärden throughout the summer (Fig. 3), and even in near bottom water at 50 m dissolved oxygen concentrations rarely fell below 7 mg/l. Surface layers periodically were supersaturated.

At midday in Lambarfjärden, the lower limit of sensitivity of the photometer (approximately 0.001 lux) was reached at a depth slightly in excess

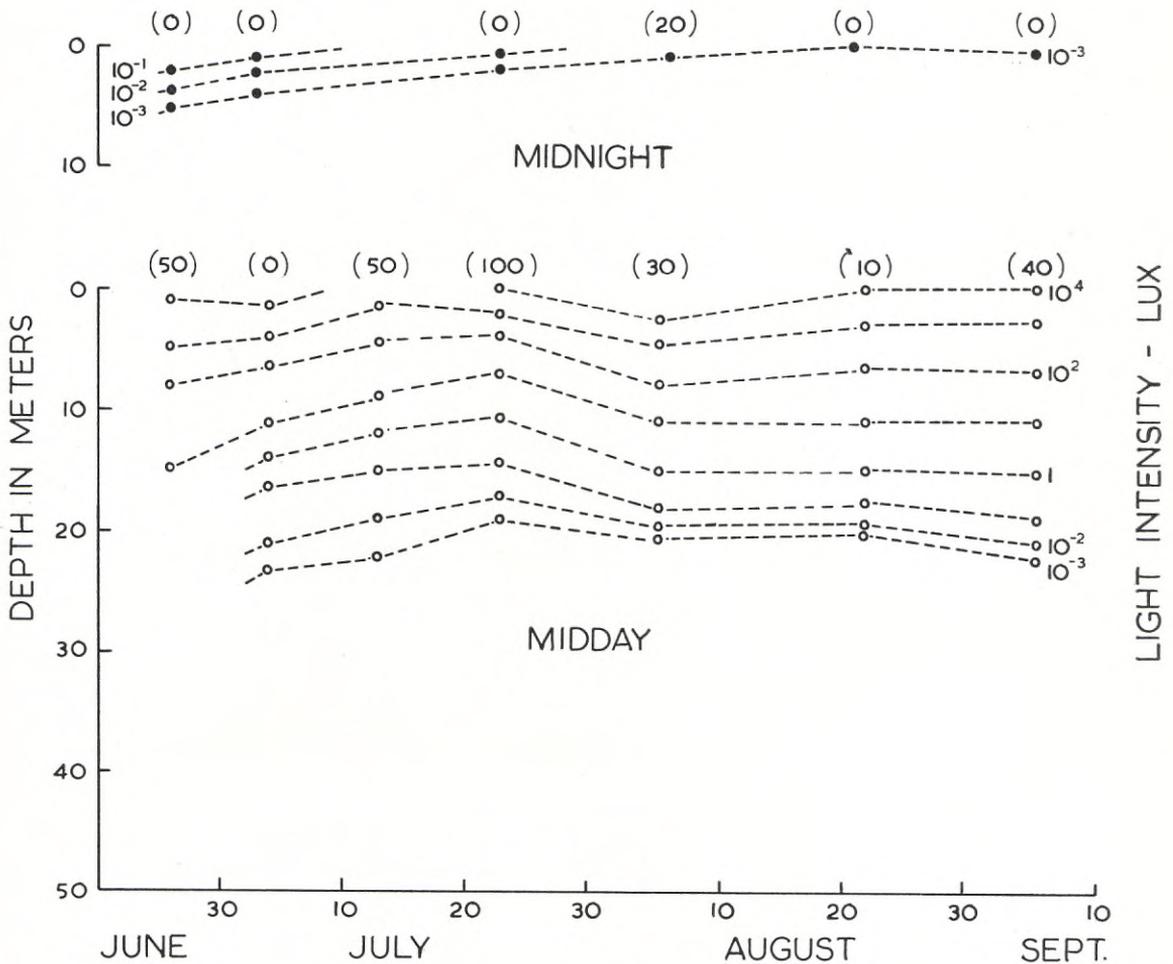
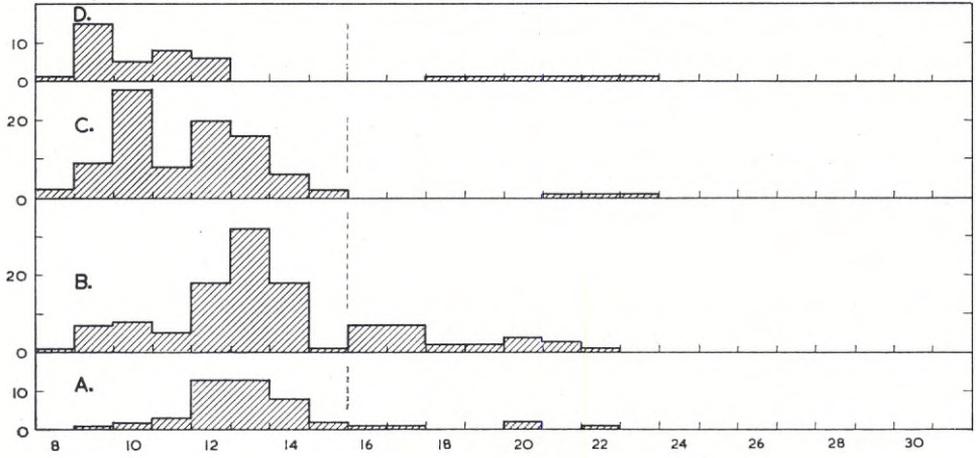


Fig. 4. Midday and midnight levels of subsurface illumination at Lambarfjärden Station A during the summer of 1968. Numbers in parentheses give approximate percent cloud cover.

SMELT



CISCO

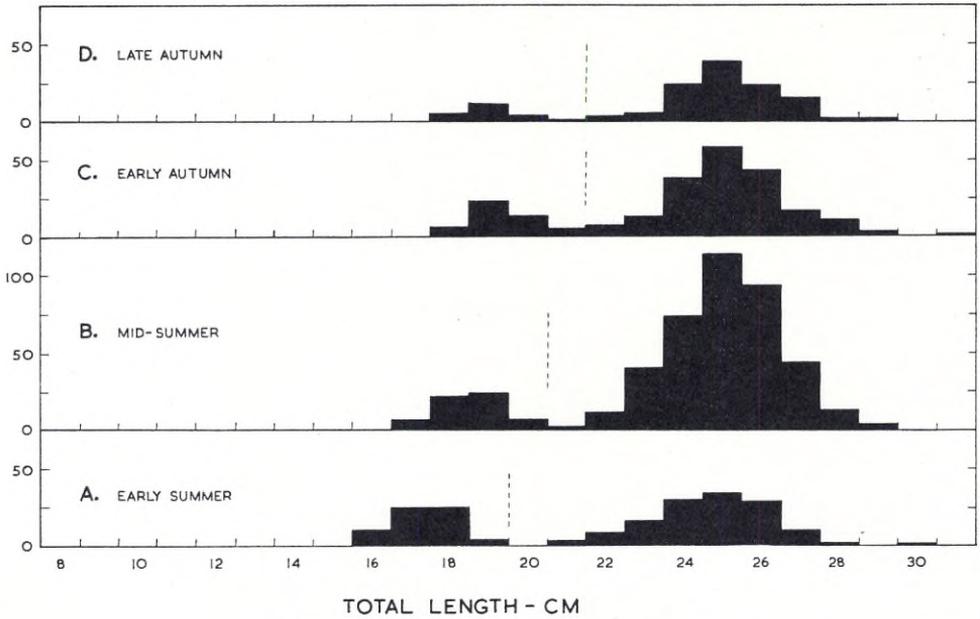
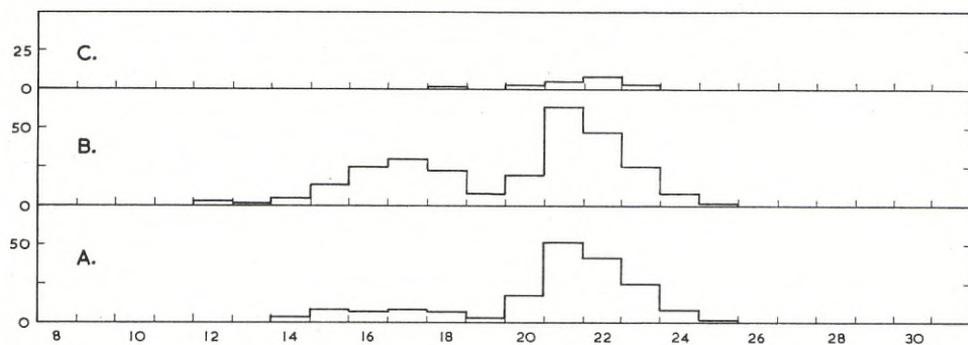
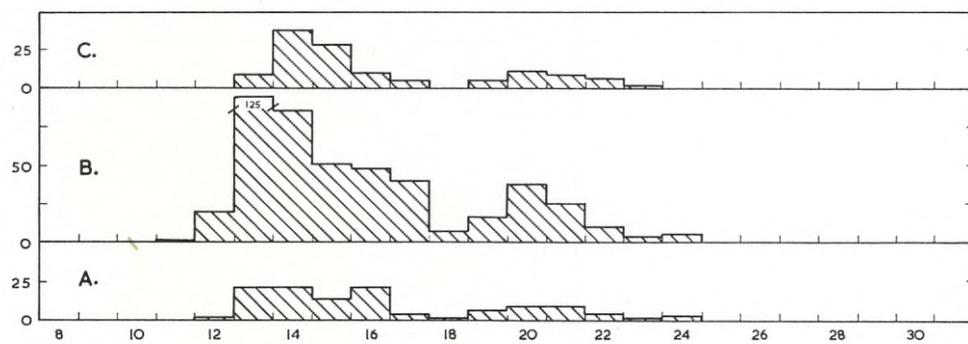


Fig. 5 a and b. Length-frequency distribution of the four species of fishes commonly taken by pelagic netting in Lambarfjärden during summer and autumn, 1968.

ROACH



PERCH



of 20 m (Fig. 4). The rise in isolux levels evident in the mid and late July series probably was a combined result of cloud cover and very dense blue-green algal blooms. Midday surface levels of illumination were close to or slightly above 10,000 lux throughout summer. The 0.001 lux level at midnight occurred near 5 m in midsummer and virtually at the surface later in the summer. Midnight surface readings ranged from about 0.6 lux in June to less than 0.01 lux in late summer.

Extensive studies of the general limnology of Lake Mälaren are carried out by the National Nature Conservancy Office, Limnological Survey (formerly the Lake Mälaren Research Group). Their numerous reports and publications may be consulted for further details.

IV. Species and size composition of netted fish

Of the nine species of fish taken in the netting series at Lambarfjärden Station A, only four were common throughout the season. These were cisco (*Coregonus albula*), smelt (*Osmerus eperlanus*), perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). A few bleak (*Alburnus alburnus*) were netted near the surface in June and a single bream (*Abramis brama*) there in July. Occasionally a burbot (*Lota lota*) or a ruffe (*Acerina cernua*) was captured, usually at night near the bottom. Pike-perch (*Lucioperca lucioperca*) were rarely taken until August when a few were caught at night in the epilimnion; they were more frequently captured in autumn, and at greater depths. Two additional species known to occur in the pelagic region of Lambarfjärden but not taken in the netting series are threespined stickleback (*Gasterosteus aculeatus*) which are abundant and whitefish (*Coregonus lavaretus*) which are rare.

Two size groups of cisco were netted (Fig. 5), the smaller gradually increasing in length from early summer to late autumn while the modal class of the larger group remained between 250—260 mm throughout the season. On the basis of age determinations made from scales of cisco netted at Station D (Fig. 1), most fish in the smaller size class would be 1+ year old, and those in the larger would be 2+ to 4+ years old. Most smelt netted ranged between 80 and 160 mm and would be 1+ to 3+ year old fish. The few larger individuals probably were 4 to 5 years old. Although distinct size classes of perch and roach were evident in the catch (Fig. 5), no attempt was made to estimate their age.

V. Seasonal changes in vertical distribution

Distribution indicated by netting

1. *Cisco*

In June and early July cisco were often taken during midday at depths less than 10 m in nets (Fig. 6). At midnight largest numbers also were caught near the surface, but many more fish were found in deeper layers than during midday. Later in July and in early August very few cisco were caught in the upper 10 m, either during midday or midnight. Most were netted at this period in the 10—25 m depth zone, and many were taken near the bottom (40—50 m). In late August and early September, cisco were again taken near the surface at midday, although they were still abundant in the 10—25 m zone and present in near-bottom levels, particularly during the day. By late October, cisco were broadly distributed over the entire 50 m, being most abundant in the 15—20 m zone during the day and somewhat deeper at night. No close association was evident between seasonal changes in the vertical distribution of cisco and thermal stratification, although their descent into deeper layers before mid July occurred at a time when the thermocline was becoming deeper and when temperatures were relatively high in near-surface layers (Figs. 3, 6).

There appeared to be a considerable difference in vertical distribution of small (chiefly 1+ year old) and large (2+ to 4+ year old) cisco, particularly during mid summer and early autumn (Fig. 7). The former were rarely taken below 20 m while the latter were often caught in deeper layers, some near the bottom.

2. *Smelt*

In contrast to the cisco, at no time during the summer were many adult smelt caught in the upper 5 m (Fig. 6). During July and August, most smelt were caught at night between 10 and 20 m. A gradual spread and deepening in their midday vertical distribution was suggested, since they were rarely taken in the 30—50 m zone in June or July but more frequently so in late summer and autumn.

3. *Perch*

Large numbers of perch were taken in near-surface waters (above 15 m) throughout July and August (Fig. 8), particularly in midday sets. For most of the summer relatively few perch were caught at the surface (0—4 m) during midday, and most were concentrated between 6—10 m. In early and mid July many small perch were netted at night near the surface. Later in the summer they either were not present in the pelagic region at night or were not moving so as to be caught there. By autumn very few small or large perch were captured in the pelagic area at any time.

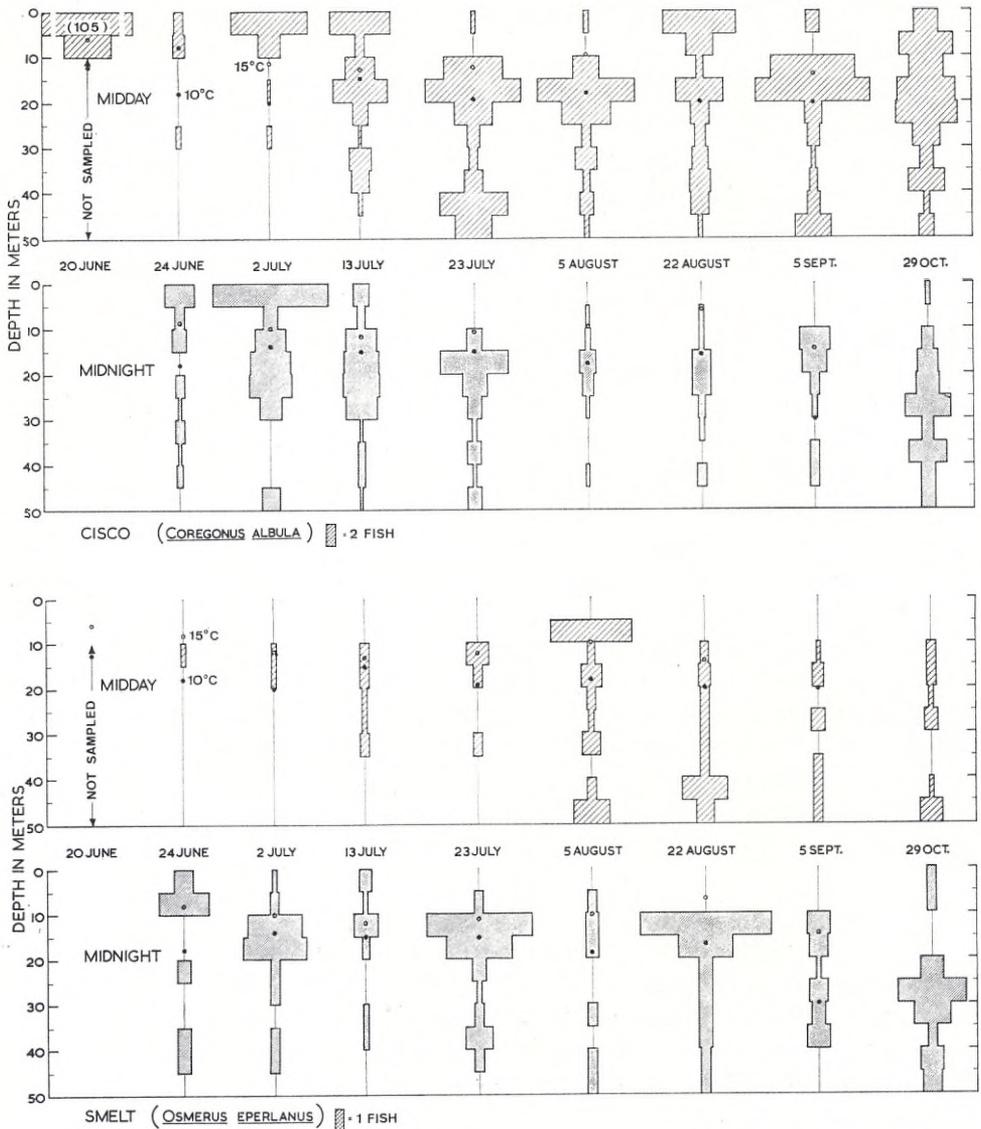


Fig. 6. Seasonal changes in midday and midnight vertical distribution of cisco and smelt taken in gill nets set at Station A, Lambarfjärden (catch combined for each 5 m depth interval). Open and solid circles show depth of the 15 and 10°C isotherms, respectively.

4. Roach

Only recently have roach become abundant in the pelagic region of Lake Mälaren according to reports from commercial fishermen and others (RUNDBERG, 1968). In 1968 they were present in near surface waters there by

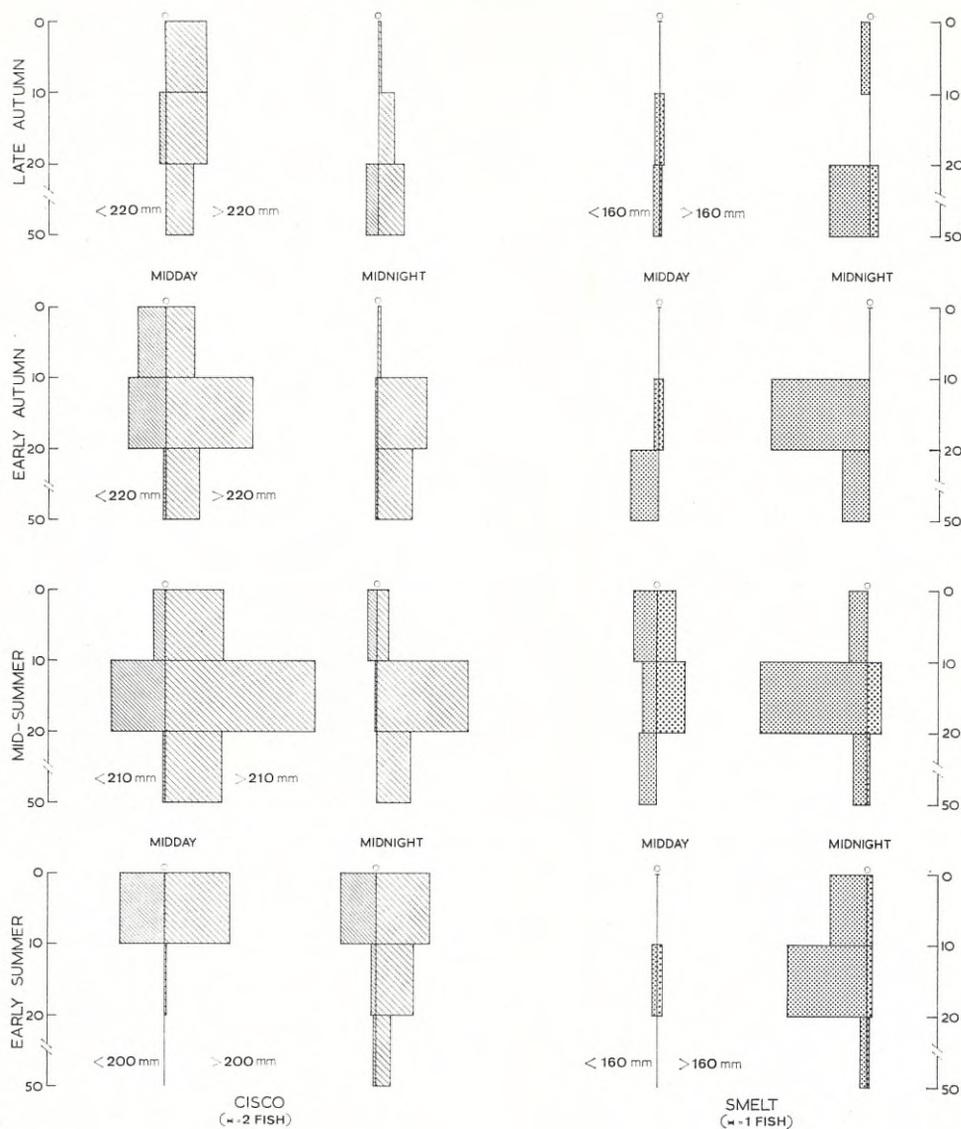


Fig. 7. Seasonal changes in the vertical distribution of small and large size classes of cisco and smelt taken in pelagic netting at Station A, Lambarfjärden, 1968.

early June and many were caught in midday and midnight sets from late June to early August (Fig. 8). Unlike the perch, they were usually most abundant at the immediate surface (0–2 m) and rarely were taken below 6 m. In late summer and autumn very few were caught at Station A.

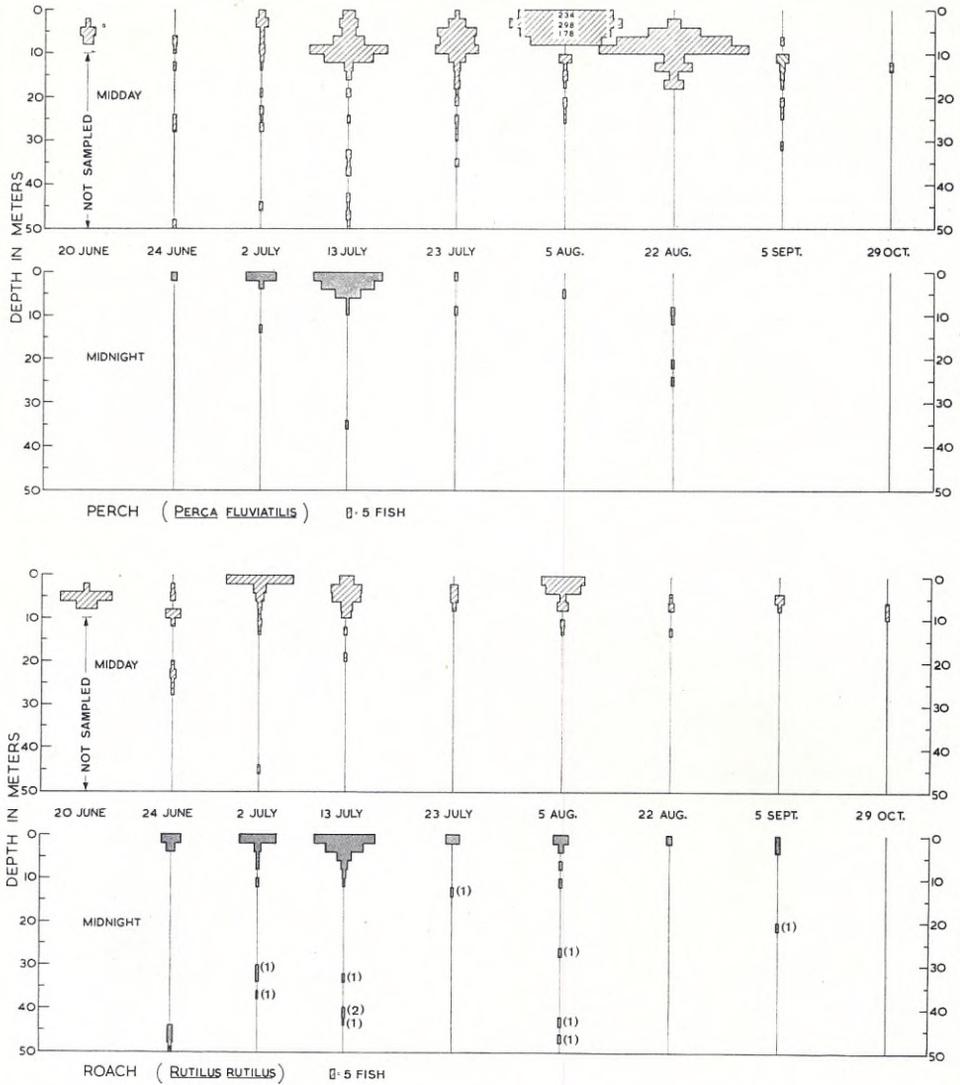


Fig. 8. Seasonal changes in midday and midnight vertical distribution of perch and roach taken in gill nets set at Station A, Lambarfjärden (catch combined for each 2 m depth interval).

Distribution indicated by echo-sounding

1. Interpretation of echo traces

The discrete inverted v marks evident on the echo traces in Figure 9 are most probably fish. They undergo rapid vertical changes in depth distribution (as will be shown later) and appear very similar to those strongly

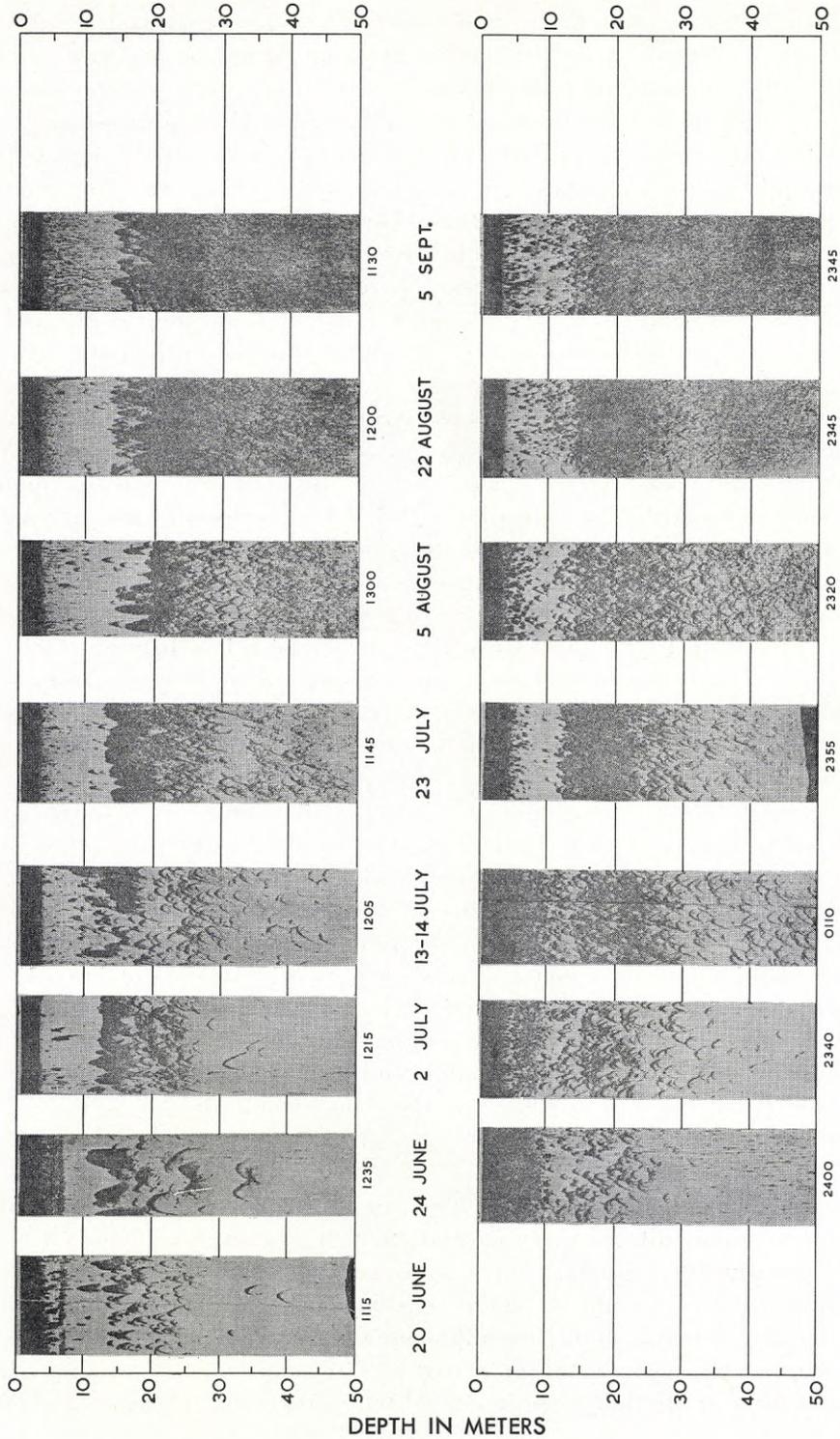


Fig. 9. Midday (upper) and midnight (lower) echo traces at Station A, Lambarfjärden adjacent to gill net sets shown in Figures 6 and 8.

implicated as fish in other lakes (NORTHCOTE *et. al.*, 1964; MAITLAND, 1968; DEMBINSKI, MS 1969). Even if all these markings could be ascribed solely to fish, it still would be difficult to determine with any certainty the species indicated. Nevertheless some progress can be made in this direction.

Obviously the density of marks shown on the traces would suggest, if they are indeed fish, that they are quite numerous. Therefore, unless most are of a size too small to be taken in the extensive netting series, then only 4 species would seem to be primarily involved — *i.e.* cisco, smelt, perch and roach. Because perch and roach are largely restricted to the upper 10—15 m throughout the summer (Fig. 8), most of the marks below that depth probably represent cisco or smelt, both of which are known to be abundant in deeper layers of Lambarfjärden.

Additional evidence that many of the marks below 15 m indicate cisco and smelt comes from echo tracings made adjacent to commercial and I.F.R. standard netting areas for these species (Fig. 10). On echo tracings made over a commercial fishing area for cisco (Fig. 10 A) a concentration of broad inverted v marks can be seen near the bottom at depths between 15 and 25 m. The total catch in sets made there was comprised largely of cisco and a few smelt. Similarly at the I.F.R. netting area, a somewhat less distinct layer of broad inverted v marks can be seen on the traces between 15 and 30 m (Fig. 10 B). Unfortunately the marks are obscured by static from the sounder which was malfunctioning at the time. Catches from gill nets set along the bottom in the region of the layer of marks again were dominated by cisco and smelt.

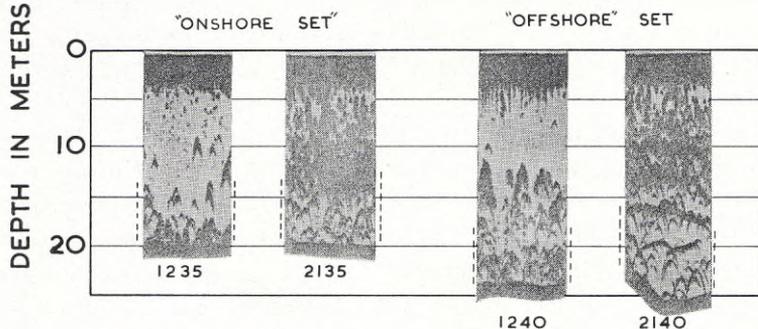
Furthermore, the concentration of marks on the midday echo tracings at depths between 15 and 25 m suggesting schools of fish are very similar in appearance to the midwater layers recorded by Schärfe (1951) in Grosser Plöner See, by LIEDER (1962) in Schweriner Aussensee, by MAITLAND (1968) in Lochmaben and by DEMBINSKI (MS, 1969) in several Polish lakes. All interpreted these layers as being largely composed of schools of cisco or a similar species.

Collections of fish from experimental dynamite charges (Figs. 11, 12) show that cisco are present and smelt abundant in the 15—30 m depth zone where the characteristic marks are evident on the echo tracings.

2. Results from echo-sounding

Obvious seasonal changes are evident in the distribution of marks on midday and midnight traces from Station A, Lambarfjärden (Fig. 9). In June and early July, midday traces show concentrations of marks in two depth zones, above 7 m and 12—25 m. The upper zone probably results from cisco, perch and roach which are abundant then in that region (Figs. 6, 8), while the lower zone may be comprised of cisco and smelt, although only small numbers of the latter species were taken there by netting. Very few

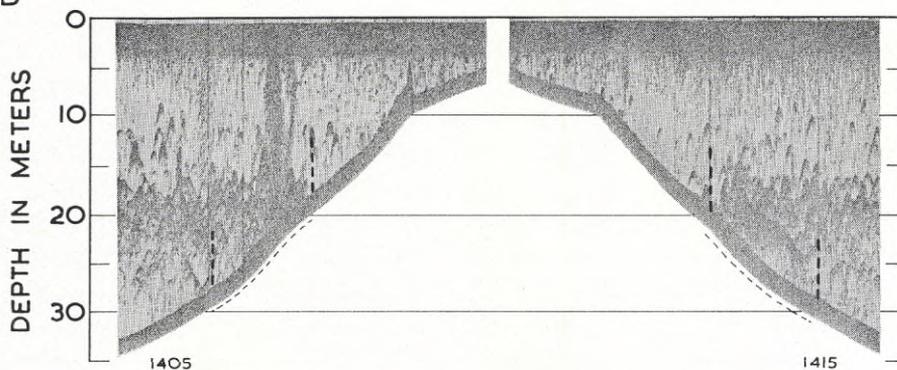
A



TOTAL CATCH (0800 JULY 2 — 0030 JULY 3)

<u>COREGONUS ALBULA</u>	ca 1500 (150 kg)
<u>OSMERUS EPERLANUS</u>	75
<u>PERCA FLUVIATILIS</u>	1
<u>RUTILUS RUTILUS</u>	0

B



TOTAL CATCH (1400 JULY 10 — ca 1000 JULY 12)

<u>COREGONUS ALBULA</u>	-----	317
<u>OSMERUS EPERLANUS</u>	-----	108
<u>PERCA FLUVIATILIS</u>	-----	very few, if any
<u>RUTILUS RUTILUS</u>	-----	" " " "

Fig. 10. A — Echo tracings adjacent to commercial cisco netting area (Station C, Fig. 1) and associated net catch. Broken lines show approximate depth of nets. B. — Echo tracings adjacent to I. F. R. standard cisco and smelt netting area (Station D, Fig. 1) and associated net catch. Broken lines show approximate location of 6 m deep nets fished on bottom.

marks were recorded in the 30—50 m zone and virtually no fish were taken in June and early July net sets there during midday. At night, particularly in early July there was an increase in marks recorded in the deeper layers which seemed to be reflected in catches of cisco and smelt (Fig. 6). High densities of marks in near-surface layers (above 10 m) at night, especially from June to mid July may be caused by small smelt and perch.

From mid July to early August there is a progressive concentration of marks within the 12—25 m zone at midday as well as a marked increase in those recorded from 30—50 m. This fits reasonably well with seasonal changes noted previously (Fig. 6) in vertical distribution of cisco and smelt, particularly the former. Evidence of dense schools of fish, probably cisco and smelt, can be seen in many of the midday traces from July and August. These "schools" seem to disperse in the midnight traces which suggest a more scattered distribution of large numbers of individuals. General darkening of the traces in August below 20 m may be caused by concentrations of smelt. Some evidence for this possibility will be given in the following section.

Distribution indicated by dynamic explosions

Cisco were not taken in the series of daytime explosions at near-surface depths (5, 10 m) but were collected from deeper charges (15, 20, 30 m) set at Station A (Figs. 11, 12). Results of the 100 gm series (Fig. 11) suggest that small smelt (40—65 mm) were concentrated in the 10—20 m zone whereas larger smelt (> 80 mm) were more abundant in deeper layers. Relative proportions of the two size classes taken by 400 gm charges at 20 and 30 m also indicated such a trend (Fig. 12).

Large numbers of smelt were collected from the 400 gm charges. Echo traces made several minutes after the explosions showed that much of the fine scattering evident at depths near the charges prior to detonation had disappeared (Fig. 12) but within an hour was re-established. Possibly the fine scattering shown on the echo traces at depths below 15 m was primarily caused by smelt, whereas the broad, heavy inverted v marks were chiefly cisco.

If the above interpretation is valid, then one might infer from the tracings in Fig. 9 that in addition to the gradual deepening of cisco distribution throughout the summer there was a similar deepening and increase in abundance of smelt in 20—50 m layer.

VI. Diel changes in vertical distribution

Attempts were made in early June, 1968 to follow diel changes in vertical distribution of fishes by gill netting at Station A, Lambarfjärden. This did

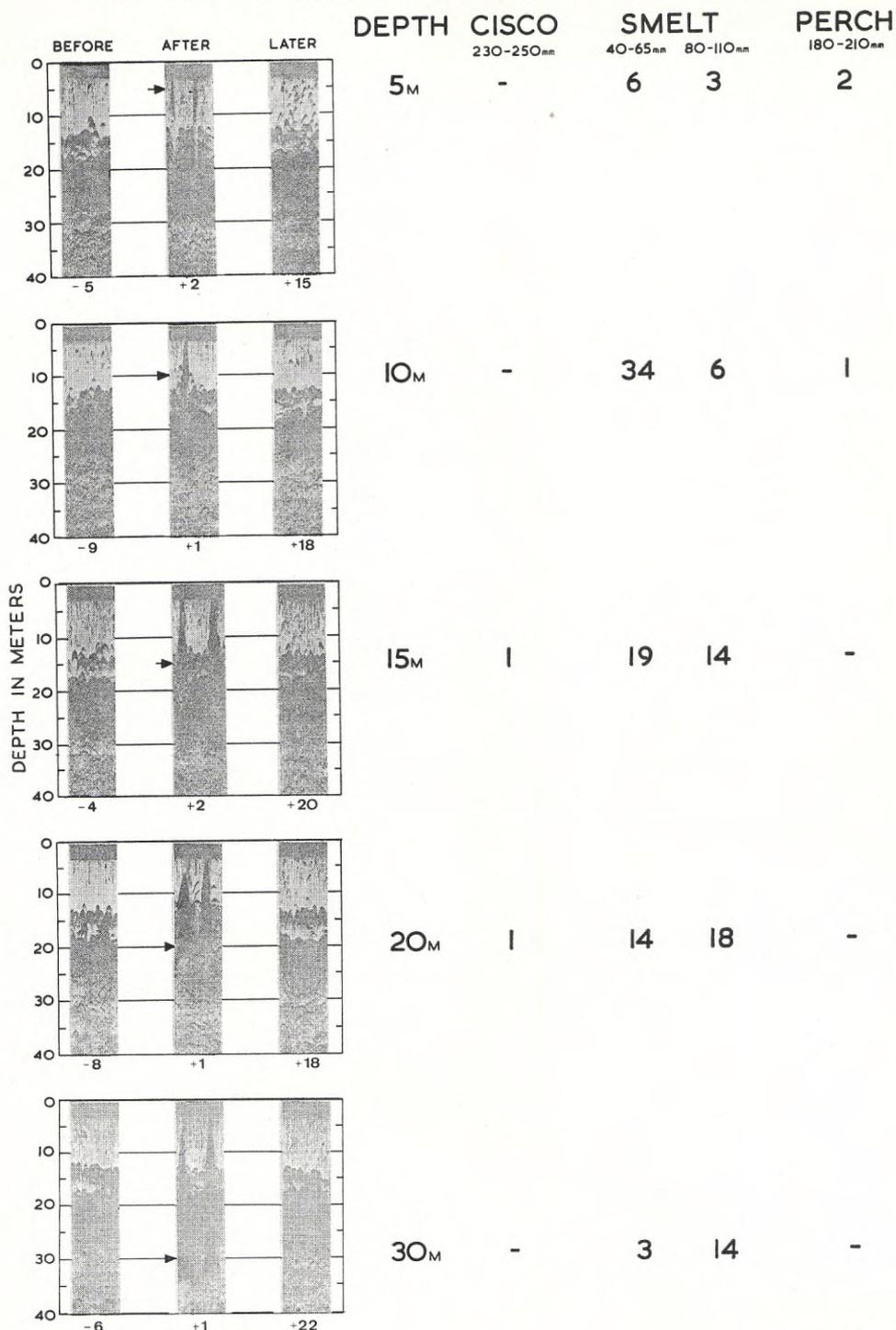


Fig. 11. Echo tracings associated with surface collections of fish rising from submerged explosions of 100 gm dynamite charges at Station A, Lambarfjärden, 0900—1200 hours, August 30, 1968. Minutes relative to detonation (time zero) given beneath each trace.

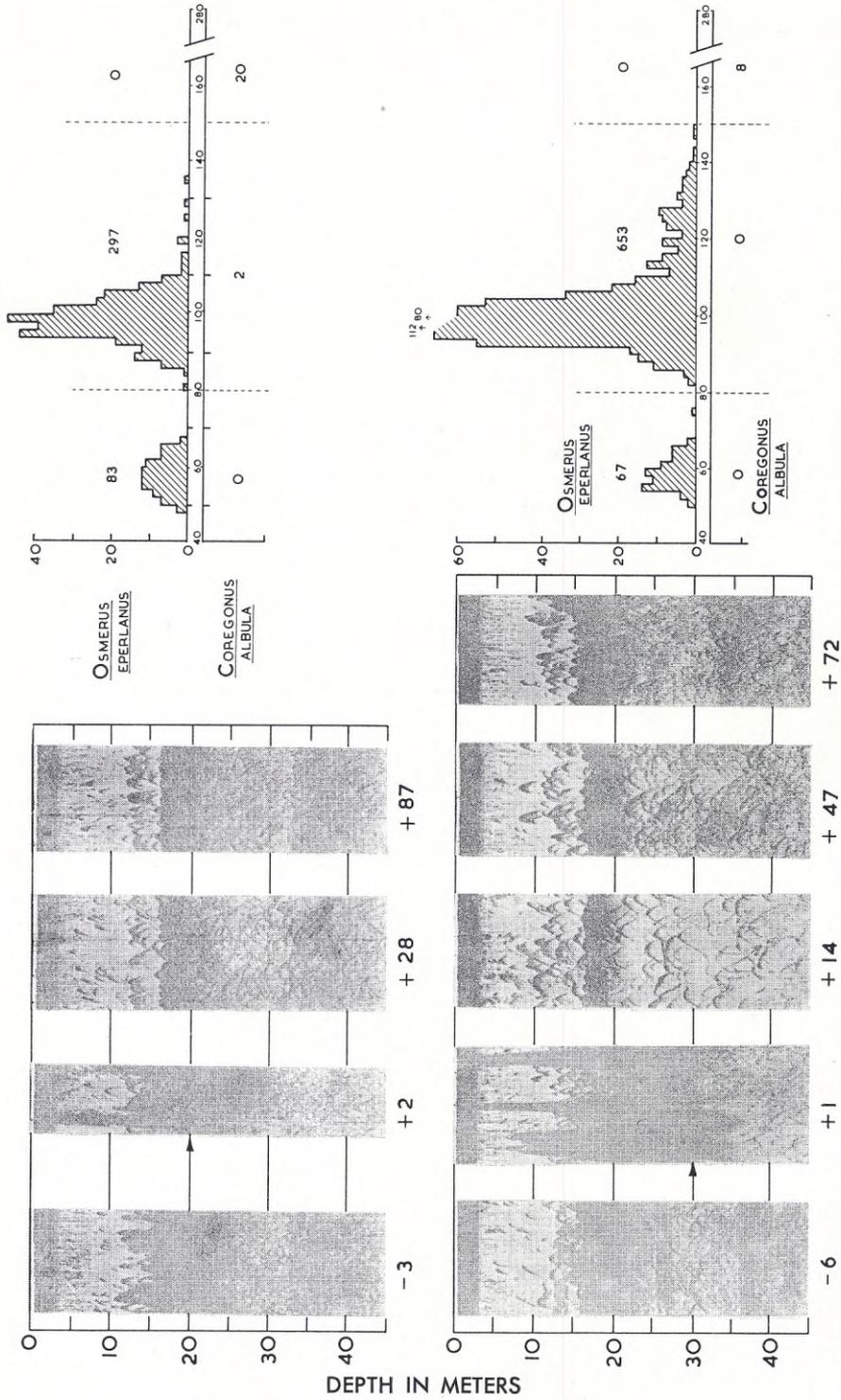


Fig. 12. Echo tracings associated with surface collections of fish rising from submerged explosions of 400 gm dynamite charges at Station A, Lambarfjärden, 1400-1600 hrs, August 30, 1968. Minutes relative to detonation (time zero) given beneath each trace; total numbers of each size class of cisco and smelt given at right of traces, length-frequency distribution shown for smelt only; upper and lower series show results from explosions at 20 and 30 m respectively.

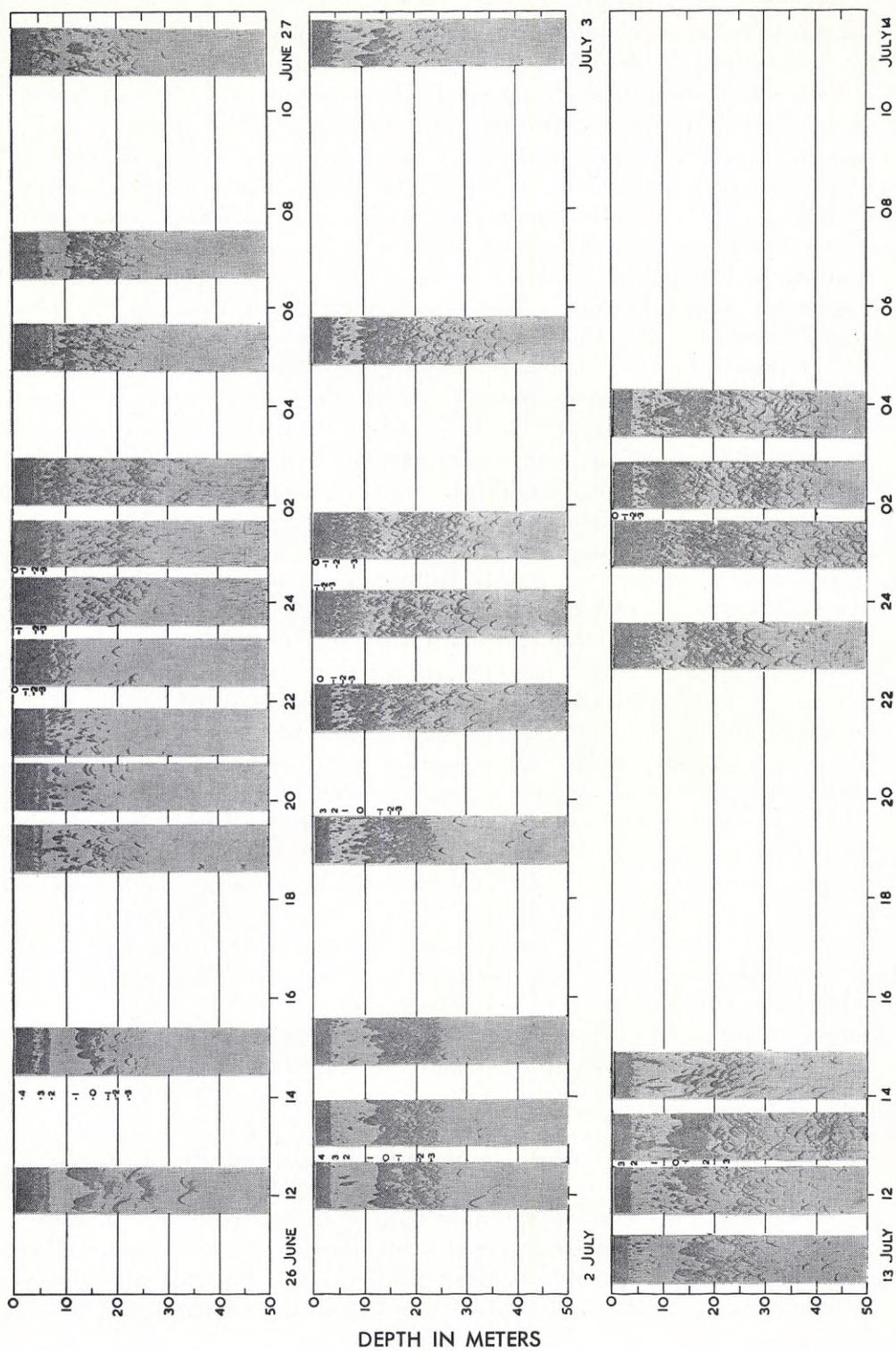
not prove feasible with equipment and staff available. Evidence of diel vertical fish migration may be inferred from echo sounder tracings (Fig. 13), although they are difficult to interpret because marks of individual species cannot be recognized. Nevertheless most series from early to late summer indicated an evening ascent of fish from midwater layers (10—30 m) towards the surface, a concentration there prior to midnight and a dispersal and deepening of vertical distribution after midnight. By morning, a midwater concentration layer was reformed. Because perch and roach were largely confined to depths above 10 m, cisco and smelt were the species most likely responsible for the daytime midwater concentration layer and its apparent vertical nocturnal migration to and from the surface as indicated in the echo sounder traces. Throughout summer the concentration zone during midday was usually found from 15—20 m, where light readings ranged from 0.1 to 0.001 lux (Fig. 13). Midnight levels of illumination near the surface were about 0.1 lux in June but dropped to less than 0.01 by late August. Suggestions of a dusk rise, a midnight dispersal, and a morning descent of fish are evident in several of the series (Fig. 13).

More complete echo sounding traces were made in September (Fig. 14). Movement of marks (assumed to be fish) from the midwater concentration layer had started by 1830 hours on September 6 (Fig. 14 A), coincident with a rise in the illumination isopleths towards the surface. Dusk occurred somewhat earlier on September 9 due to cloud conditions; onset of fish movement towards the surface and rise of light isopleths also occurred earlier than on the evening of September 6 (cf. Fig. 14 A and B). Early evening rise of fish from a 15—25 m concentration layer is clearly indicated in the series of closely spaced tracings made on September 16 (Fig. 14 C). "Surfacing" schools of fish thought to be adult and sub-adult cisco were first seen at 1635 hours and many groups were noted between then and dusk. Concurrent catches in nets suggest that cisco were present in the concentration layer and that they moved towards the surface at dusk, however, the pattern is confounded by the numbers of roach caught near the surface then. Additional netting in the autumn of 1969 confirmed that the surfacing schools of fish which appear in late afternoon are indeed cisco.

Descent of fish to the concentration layer was indicated at dawn (Fig. 14 A) when light isopleths were also moving downwards.

VII. Seasonal and diel changes in horizontal distribution

Although the investigation was primarily concerned with vertical distribution of fishes in the pelagic region of Lambarfjärden, some information was obtained on their distribution between Station A and a prominent onshore point (Lambarudd), shown as Station B in Figure 1. One netting series was



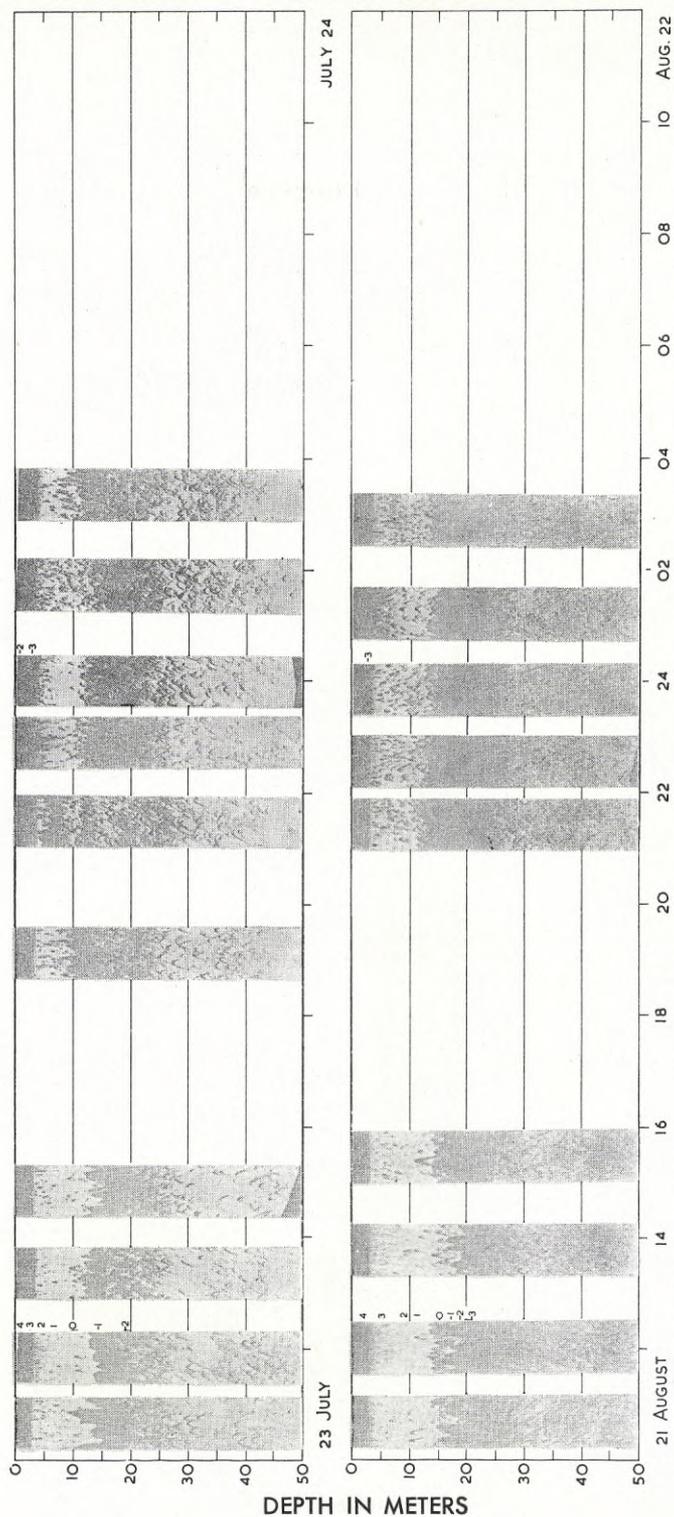
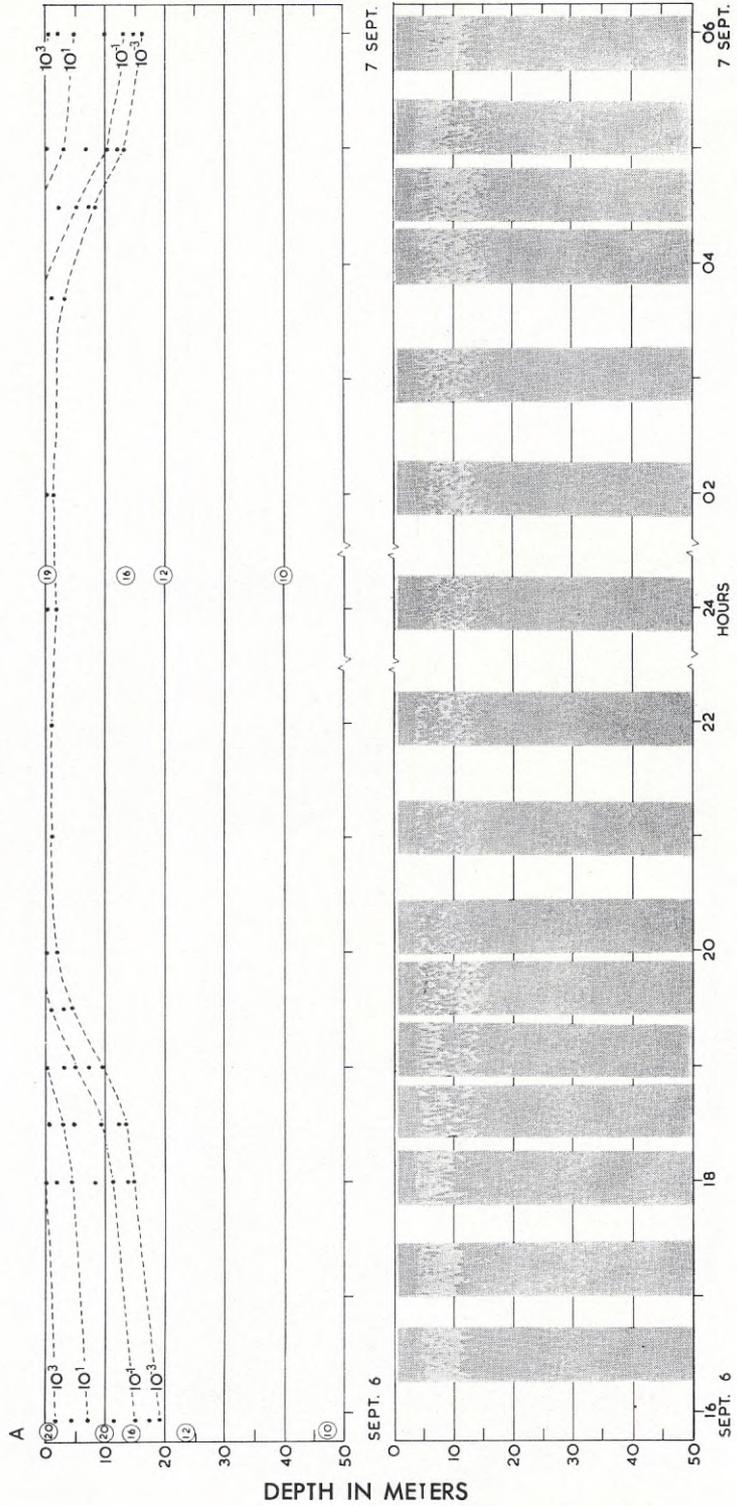


Fig. 13 a and b. Diel series of tracings from echo soundings made at Station A, Lambarfjärden during the summer, 1968. Light intensity in lux ($1 \times$ power to base 10) given at right of some traces.



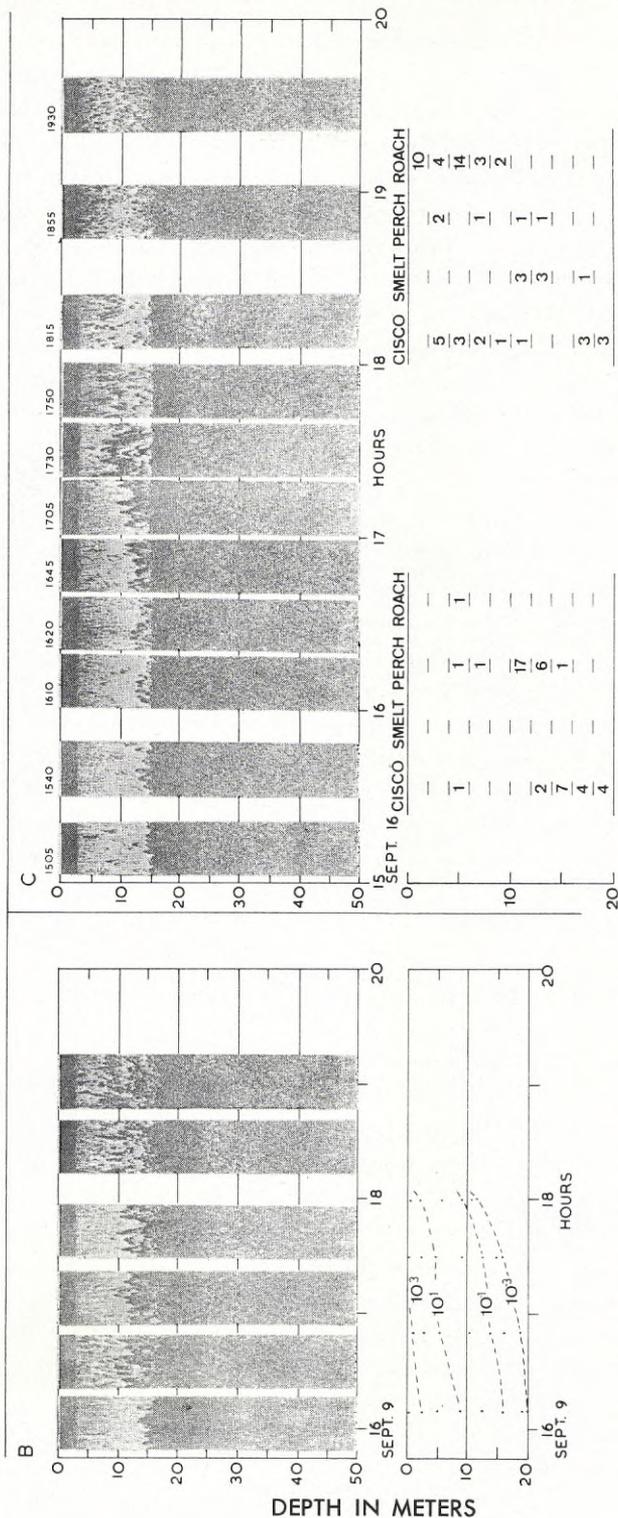


Fig. 14 a, b and c. Diel series of tracings from echo soundings made at Station A, Lambarfjärden during autumn, 1968. Light intensity in lux ($1 \times$ power to base 10) shown for September 6-7 (A series) and 9 (B series); numbers in circles (A series) indicate isotherm depths. Fish catch in 1 hour gill net sets at Station A (1530-1630; 1815-1915) shown for 2 m depth intervals (0-20 m) on September 16 (C series).

made in midsummer in this area (Fig. 15). During midday, cisco (plus a few smelt and perch) were taken in the 20—30 m bottom set, a depth zone corresponding to the most dense portion of the concentration layer shown on the echo sounder traces. A few perch and pike-perch were taken in the 10—20 m bottom set, which may be represented by the scattered marks shown on traces in that region. Perch and roach were abundant in the onshore set at 10 m. Between evening and midnight the concentration zone on the echo traces had moved upward and onshore; at the same time cisco and smelt were netted in considerable numbers in the 10—20 m depth zone, a region where they were not captured during the day. Few perch were caught in any area whereas roach were confined to the onshore set. Results from this combined netting and echo sounding series would indicate shoreward movement of cisco and smelt in the evening associated with their concomitant vertical migration.

Seasonal changes in horizontal distribution of fish at Station B may be interpreted from echo sounding series (Fig. 16). As shown in traces at Station A, the midday concentration layer (probably largely cisco and smelt) gradually deepens and becomes denser throughout the summer. The concentration layer evident in the pelagic region at Station A extends to the corresponding depth onshore, and during ascent of the layer at dusk an onshore movement of fish forming the layer must occur. Although early morning traces are not shown for the summer period, those taken indicate that a corresponding offshore horizontal movement also occurs at dawn. An onshore-offshore pattern of movement associated with diel vertical migration of fish forming the midday concentration layer is evident in the more complete autumn echo sounding series (Fig. 17).

VIII. Discussion and summary

The inability of nets to adequately record distribution and abundance of smelt, the problems encountered in interpreting and distinguishing species on echo-sounding traces, and the limited use of dynamite explosions for fish collection all make it difficult to determine the extent to which cisco and smelt may be spatially segregated in the pelagic region of Lambarfjärden. Nevertheless differences were evident in the vertical distribution of these and other fishes there, and it would seem possible to indicate roughly the depth zones utilized by each species during summer and early autumn. Information obtained by netting, echo-sounding and dynamite collections will be used to develop a generalized picture of spatial distribution of the fishes. Because of obvious limitations of the data, the following outline can only be considered a tentative one and several features require much more detailed study.

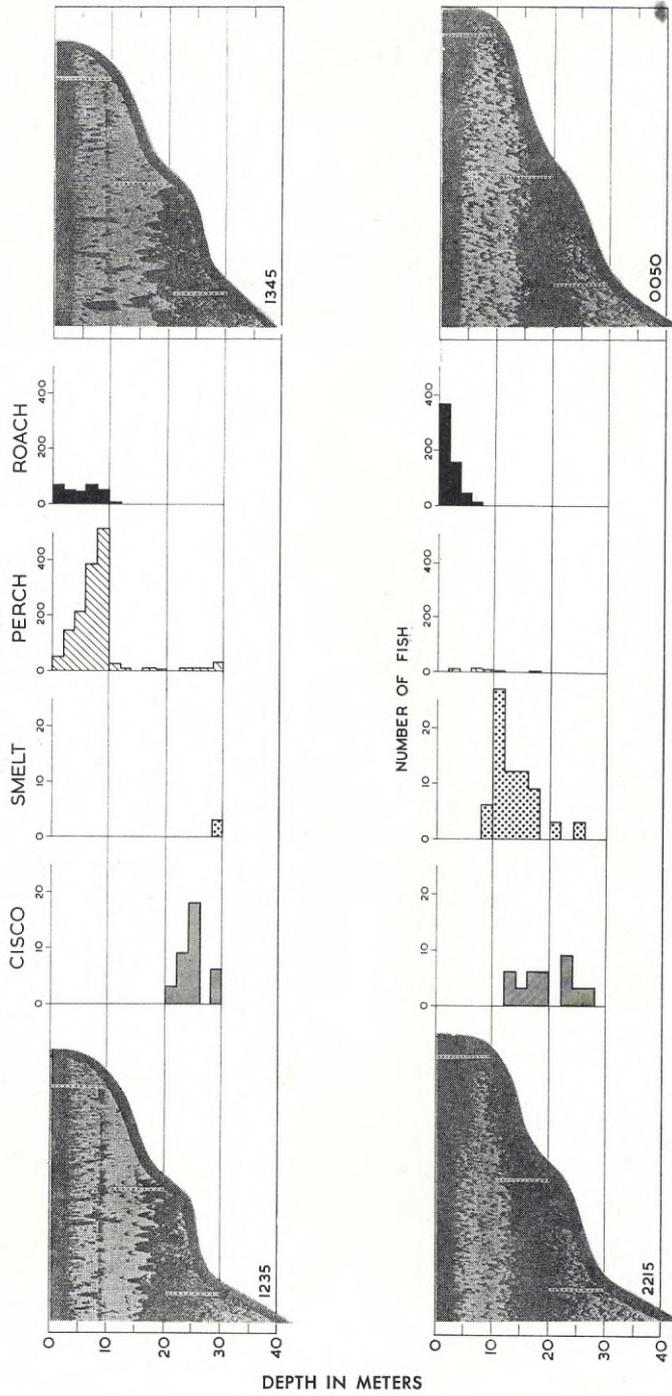


Fig. 15. Midday (upper) and midnight (lower) catches of fish (weighted 3 hour periods) in 10 m deep gill nets set August 1—2 on bottom at three locations (indicated on echo traces) along transect between Station A, Lambarfjärden and Lambarudd; echo traces taken along transect near beginning and end of netting periods.

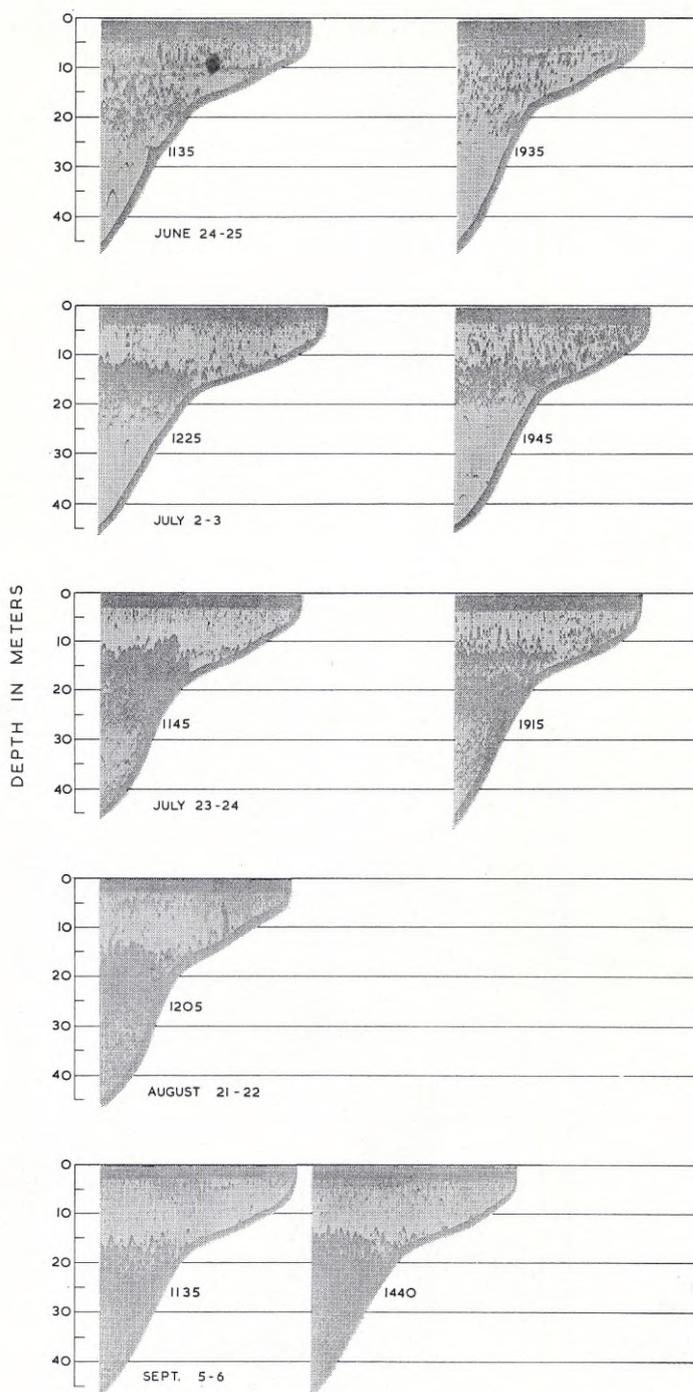
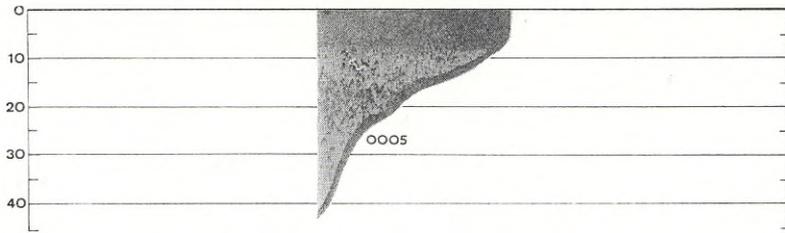
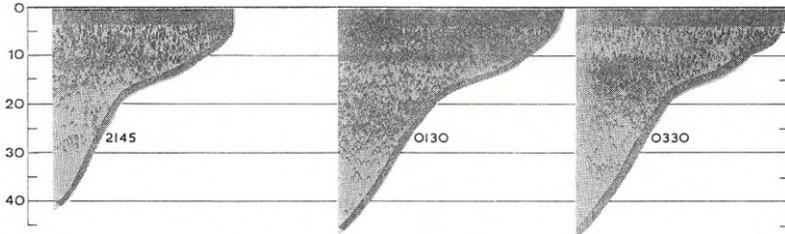


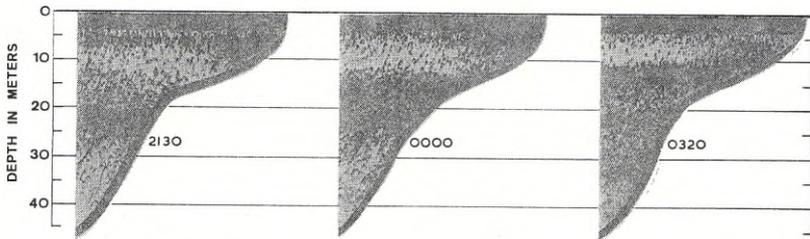
Fig. 16 a and b. Off-shore to onshore echo sounding traces made at Station B, Lambarfjärden during summer and early autumn, 1968.



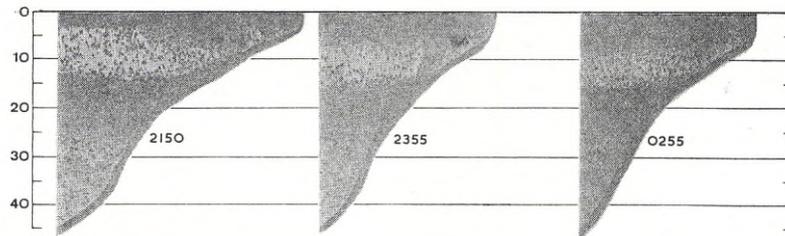
JUNE 24-25



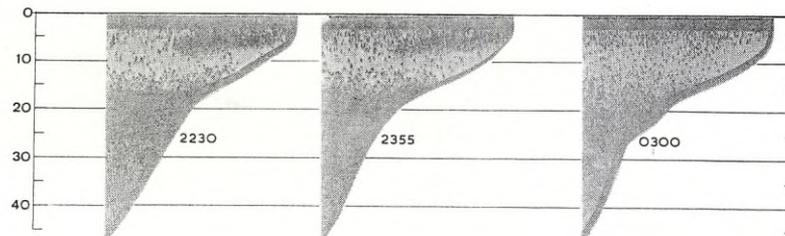
JULY 2-3



JULY 23-24



AUGUST 21-22



SEPT. 5-6

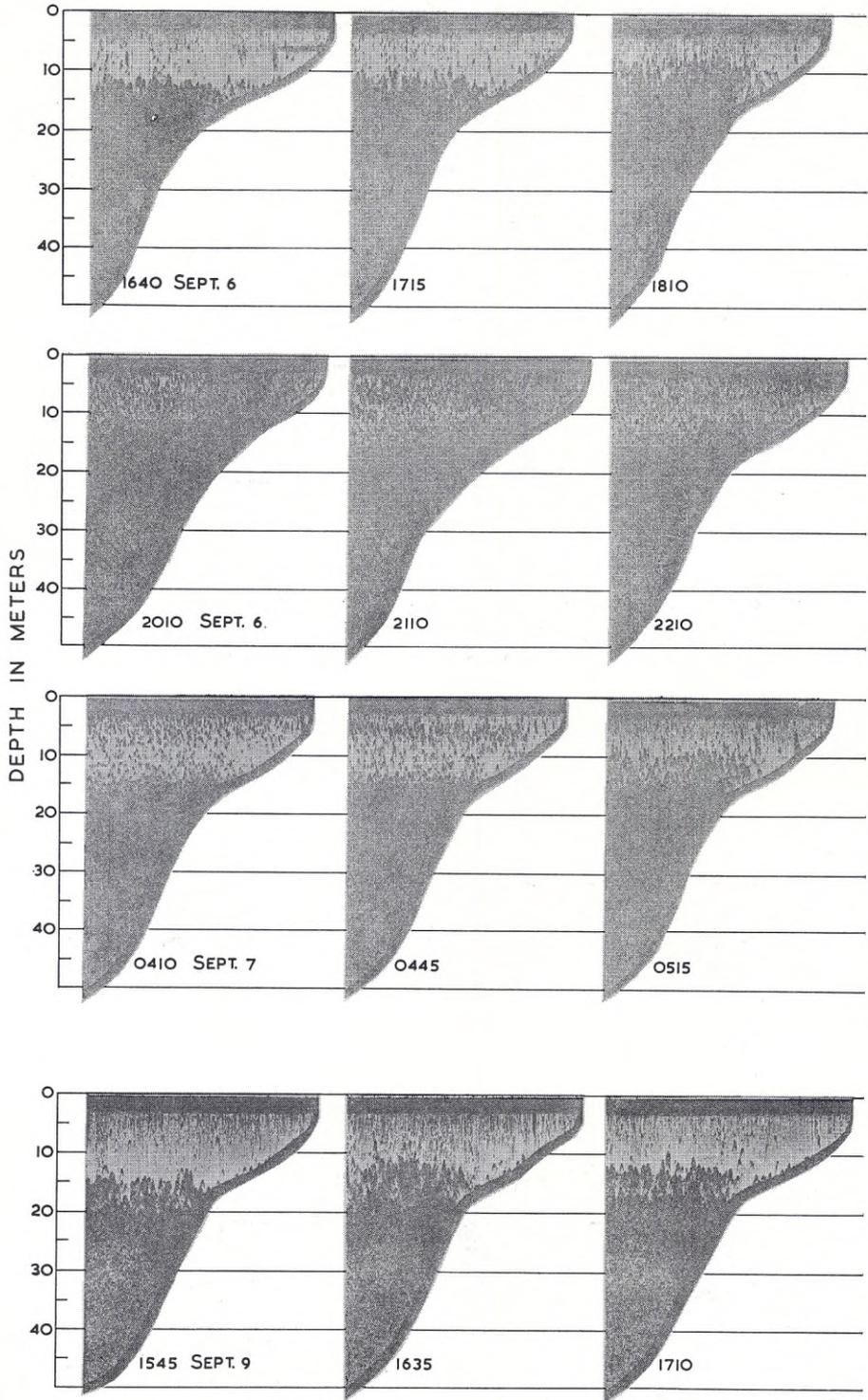
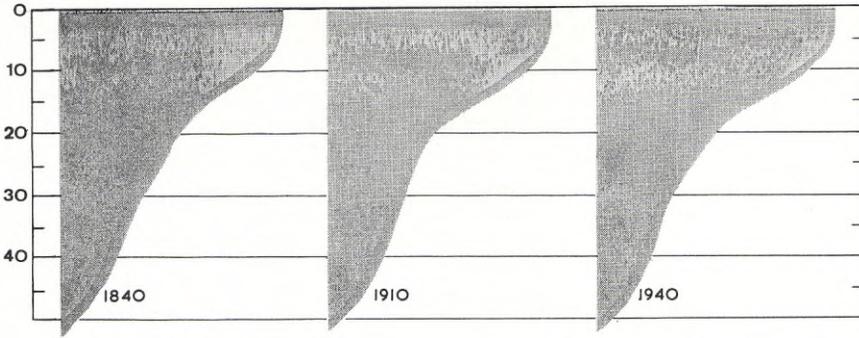
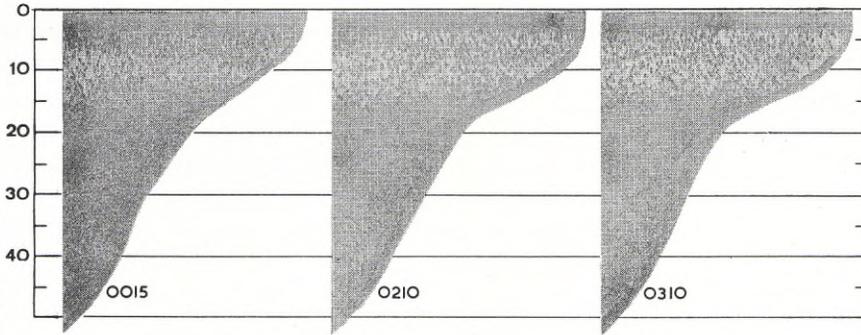


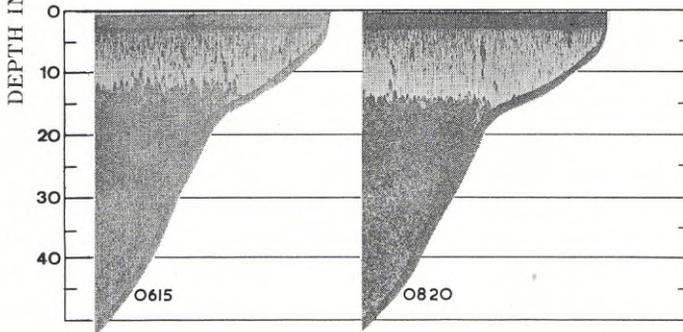
Fig. 17 a and b. Offshore to onshore echo sounding traces made at Station B, Lambarfjärden. Upper three rows — afternoon, September 6 to morning, September 7. Lower row — afternoon to early evening, September 9.



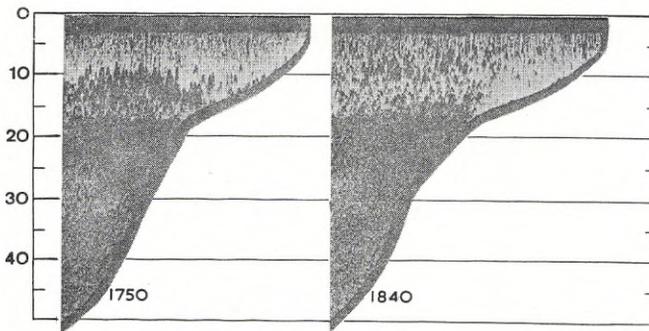
SEPT. 6



SEPT. 6



SEPT. 7



SEPT. 9

DEPTH IN METERS

In June cisco are present in the epilimnion and upper metalimnion of Lambarfjärden, both during day and at night. Many probably undergo some diel vertical migration then, moving closer to the surface at dusk and later dispersing into deeper regions. In July and early August, cisco move away from the surface, concentrating in schools during the day between 10—25 m, with larger individuals descending into near-bottom water. Diel changes in vertical distribution probably continue with a rise towards but not to the surface at dusk. Concomitantly, horizontal movement and dispersion of schools in the concentration layer takes place up the slope of the lake basin. A gradually deepening in distribution apparently occurs near midnight and reformation of schools in the concentration layer near dawn. Such a pattern of movement would result in passage of individuals or groups forming the lateral margins of the concentration layer at least twice every 24 hours along the lake bottom between 10—25 m and may account for the success of commercial nets fishing that depth zone. Later in the summer schools of cisco appear near the surface again during the afternoon and at dusk, although many are still found in a midwater layer and some in deeper regions. Onset of the rise of cisco towards the surface is earlier then, apparently regulated by the earlier approach of dusk.

Small schools of adult cisco were seen at the surface near sunset on several occasions in early September. Members of a school frequently leapt clear of the surface, all moving rapidly in one direction, but with no common orientation apparent between schools. Such behaviour has been reported for cisco in Swedish lakes (ROSÉN, 1956) and similar surface activity noted at dusk in Lochmaben vendace (MAITLAND, 1968).

By late October, cisco were present at all depths in the pelagic region, although midwater concentrations still were evident.

The pattern of distribution and migration suggested above for cisco in the pelagic region of Lambarfjärden seems in general similar to that observed in other lakes. In Grosser Plöner See (SCHÄRFE, 1951; MOHR, 1964) and in Lake Pluszne as well as other deep Polish lakes (DEMBINSKI, MS 1969) cisco schools form midday concentration layers in the metalimnion or upper hypolimnion during the summer, undergo vertical migrations towards and away from the surface at dusk and dawn respectively, and disperse or broaden their distribution during the night. Contrary to their autumn behaviour in Lambarfjärden, in Lake Pluszne the cisco apparently do not migrate towards the surface at dusk in September but instead the schools break up and disperse at their daytime depth. However, by autumn circulation in November the cisco are widely distributed at all depths. LIEDER (1962) describes nocturnal dispersion in mid November of cisco schools concentrated between 20—30 m in Schweriner Aussensee. In Finland, NISSINEN (1966) notes that cisco commonly descend into deeper regions of lakes in midsummer, a phenomenon affecting the localities and depths where fisher-

men set nets as for example in Puruvesi Lake. VALTONEN (1970) shows a summer increase in depth distribution of cisco in the Bothnian Bay. MAITLAND (1968, 1969) describes the vertical distribution and diel migratory behaviour of vendace in Lochmaben and of powan in Loch Lomond and in Loch Eck, Scotland. Both forms have some features of summer distribution and diel migration similar to those described for Lake Mälaren cisco.

Throughout summer adult smelt were rarely caught in near-surface waters but frequently in midwater regions. Later in the season their distribution, like the cisco, deepened and extended into the hypolimnion. Although net catches did not suggest any marked size stratification vertically, results from dynamite collections in late August did, the smaller size class (40–65 mm) being relatively more abundant above 20 m while large smelt were predominantly below that depth. Evidence for an evening vertical migration of smelt towards the surface was not as strong as that for cisco, although small fish (<10 cm) which appeared to be smelt were occasionally seen "jumping" in schools at the surface at dusk and dawn in late August and early September.

Smelt are known to be abundant in middle or near-bottom waters of Swedish and Polish lakes in summer (ROSÉN, 1956; ANDERSON, 1968; DEMBINSKI, MS, 1969) and undergo nocturnal vertical migrations towards the surface in at least some of these (DEMBINSKI, MS, 1969). Similar distributions and migrations have been recorded in the Great Lakes for the American smelt, *Osmerus mordax* (FERGUSON, 1965; GORDON and LARSEN, 1965).

Marked vertical segregation was evident between four common pelagic fishes in Lambarfjärden during the summer. Perch and roach were most abundant in the upper 10 m, although some individuals (especially large perch) did appear at greater depths. Stratification between these latter two species occurred at least during the day in near-surface waters; perch usually being most abundant between 6 and 10 m, roach between 0 and 6 m. Numbers of both perch and roach caught in the pelagic area decreased sharply in autumn. Cisco were found in epilimnial waters early in the summer, but later in the season concentrated in the upper hypolimnion, and extended into profundal regions (40–50 m). They were again common in upper layers in autumn and exhibited an evening rise to the surface. The vertical distribution of cisco and smelt overlapped considerably during the summer, although adult smelt were not often taken near the surface.

The possibility of horizontal segregation between the four common pelagic species was suggested with both seasonal and diel differences in distribution and movement patterns.

Of the common pelagic fishes studied in Lambarfjärden, cisco and smelt would appear to have the greatest opportunity for competitive interaction since both are plankton feeders occupying similar depths. They may segregate, however, by stratification within the general zone occupied or by short

term (diel) differences in distribution. Neither of these possibilities could be effectively examined in this study. On the other hand their segregation, if existent, may not primarily involve space at all but instead food, and be brought about by utilization of different forms or size in the array of plankton ostensibly available.

IX. Acknowledgements

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X. References

- ANDERSON, T. 1968. Undersökningar av fiskbeståndet i Erken med hjälp av ekolod och trål. *Information från Sötvattenslaboratoriet, Drottningholm*, 1968 (12), 24 pp. (Mimeographed in Swedish.)
- DEMBINSKI, W. 1969. Vertical distribution of *Coregonus albula* and other pelagic fish species in some Polish lakes. Manuscript, Inland Fisheries Institute, Olsztyn, Poland.
- FERGUSON, R. G. 1965. Bathymetric distribution of American smelt *Osmerus modax* in Lake Erie. *Publ. Gr. Lakes Res. Div. Univ. Mich.* 13: 47—60.
- GORDON, W. G., and LARSEN, A. 1965. Application of the echo sounder to Great Lakes fishery research. *Publ. Gr. Lakes Res. Div. Univ. Mich.* 13: 61—68.
- LIEDER, U. 1962. Ergebnisse und Perspektiven der Fischortung in der Binnenfischerei. 1. Die Echo-Ortung von Kleinmaränenschwärmen in Schweriner Aussensee kurz vor dem Beginn der Laichzeit. *Dtsch. Fish. Ztg.* 9 (1): 8—17.

- LINDSTRÖM, T. and NILSSON, N.-A. 1962. On the competition between whitefish species, p. 326—340. In Le Cren, E. D. and Holdgate, M. W. (Eds.) *The Exploitation of Natural Animal Populations*. Oxford, Blackwell Scientific Publications.
- MAITLAND, P. S. 1968. Echo sounding observations on the Lochmaben vendace, *Coregonus vandesius* Richardson. *Trans. J. Proc. Dumfries. Galloway Nat. Hist. Antiq. Soc.*, 44: 29—46.
- 1969. The reproduction and fecundity of the powan, *Coregonus clupeoides* Lacépède, in Loch Lomond, Scotland. *Proc. Roy. Soc. Edinb. (B)* 70 (12): 233—264.
- MOHR, H. 1964. Netzfarbe und Fängigkeit bei Kiemennetzen. *Arch. Fisch. Wiss.*, 14 (3): 153—161.
- NILSSON, N.-A. 1958. On the food competition between two species of *Coregonus* in a north-Swedish lake. *Rep. Inst. Freshw. Res. Drottningholm*, 39: 146—161.
- 1960. Seasonal fluctuations in the food segregation of trout, char and whitefish in 14 north-Swedish lakes. *Rep. Inst. Freshw. Res. Drottningholm*, 41: 185—205.
- 1965. Food segregation between salmonoid species in north Sweden. *Rep. Inst. Freshw. Res. Drottningholm*, 46: 58—78.
- 1967. Interactive segregation between fish species, p. 295—313. In Gerking, S. D. (Ed.) *The Biological Basis of Freshwater Fish Production*. Oxford and Edinburgh, Blackwell Scientific Publications.
- NISSINEN, T. 1966. Miksi muikku "menee hautaan"? *Kalataloudellisen tutkimustoimiston tiedonantoja*. 1: 5—9, 17—20.
- NORTHCOTE, T. G., H. W. LORZ and J. C. MACLEOD. 1964. Studies on diel vertical movements of fishes in a British Columbia lake. *Verh. int. Ver. Limnol.*, 15: 940—946.
- ROSÉN, N. 1956. [Ed.]. *Svenskt Fiskelexikon*. Stockholm, 704 pp.
- RUNDBERG, H. 1968. Fisket i Mälaren. Intervjuundersökning angående det yrkesmässiga fisket 1964—1966. *Information från Sötvattenslaboratoriet, Drottningholm*, (13), 49 pp. (Mimeographed in Swedish.)
- SCHÄRFE, J. 1951. Fischwanderungen im Grossen Plöner See während einer Tagesperiode dargestellt an Echogrammen. *Arch. Fisch. Wiss.*, 3: 135—146.
- SVÄRDSON, G. 1949. The coregonid problem. Some general aspects of the problem. *Rep. Inst. Freshw. Res. Drottningholm*, 29: 89—101.
- 1956. Lambarfjärdens siklöja. *Svensk Fisk. Tidskr.*, 65 (5): 73—80.
- 1966. Siklöjans tillväxt och utbredningsgränser. *Information från Sötvattenslaboratoriet, Drottningholm*, 1966 (4), 24 p. (Mimeographed in Swedish.)
- VALLIN, S. 1969. Siklöjans näringsbiologi i Lambarfjärden i Mälaren. *Information från Sötvattenslaboratoriet, Drottningholm*, (7). 57 pp. (Mimeographed in Swedish.)
- VALTONEN, T. 1970. The selected temperature of *Coregonus nasus* (Pallas), sensu SVÄRDSON, in natural waters compared with some other fish, p. 341—362. In Lindsey, C. C. and Woods, C. S. (Eds.) *Biology of Coregonid Fishes*. Univ. of Manitoba Press.

The food ecology and the annual food cycle in the Baltic population of fourhorn sculpin, *Myoxocephalus quadricornis* (L.). Pisces

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Contents

I. Introduction	169
II. Material	170
III. The site of the investigation	170
IV. Methods	170
V. Results	172
1. Sex ratio	172
2. Length-weight ratio	173
3. The stomach fullness	173
4. The frequency of empty stomachs	174
5. The food components in the stomachs of fourhorn sculpin	174
(a) Priapulids	174
(b) Mysids	174
(c) Isopods	178
(d) Amphipods	178
(e) Molluscs	186
(f) Fish	186
(g) Fish roe	186
(h) Miscellaneous	186
6. Other fish species trapped in gill nets at the investigation site	193
7. Parasitic nematods	194
VI. Discussion	194
1. General remarks	194
(a) The method of collection	194
(b) Remarks on the methods of studying the food consumed	196
2. Sex ratio	197
3. Abiotic factors	198
(a) Salinity	198
(b) Temperature	199
(c) Oxygen	199
(d) Light	199
(e) Pressure	200
4. General remarks on the prey fauna	200
5. The annual life cycle of the fourhorn sculpin	202
6. The food habits of inland-water and brackish-water populations of fourhorn sculpin of Palearctic and Nearctic origin	202

7. Factors possibly limiting the distribution of fourhorn sculpin in the Baltic ...	204
8. Trophic relationships	206
VII. Acknowledgements	207
VIII. Summary	207
IX. References	208

I. Introduction

The fourhorn sculpin, *Myoxocephalus quadricornis* (L.), is of common occurrence along the east coast of Sweden from the middle of the Baltic to the innermost part of the Gulf of Bothnia. The fish is also present in about twenty Swedish lakes, among them the three largest: Mälaren, Vänern and Vättern.

The sculpin is nowadays of no importance as human food, in contrast to what was the case at the turn of the century and earlier. Such importance as it possesses is thus of an indirect nature and is positive in that the sculpin furnishes food for economically more valuable species and negative in that it competes with these species for the available food. In this competition the fourhorn sculpin would seem, owing to its density, to be in a favourable position.

So common a species as the fourhorn sculpin might be expected to be the subject of numerous investigations, but in fact, owing to the present lack of interest nowadays in this fish as human food, few studies have been made.

For this reason, over a period of two years a fairly large series was collected in order to enable a deeper knowledge to be obtained of the sculpin's food and of the problems involved.

Some information exists, of course, regarding the type of food consumed (EKSTRÖM 1831, LÖNNBERG 1900, JÄÄSKELÄINEN 1917, LAMPE 1969), but this information deals with the food consumed during only a very limited part of the year. No information is available for the rest of the year, particularly from the time when the water becomes ice-covered. This is serious in regard to a species, which has been proved to be active and feeding throughout the year. This lack of information from the winter period does not apply only to species belonging to the group "no economic value" or of "indirect importance" only, it is the rule rather than the exception for most species in the subarctic area.

The present investigation was at first designed to cover one year with sampling of material once a week in order to obtain information from the stomach contents, about the annual variation in food volume and about variation in prey. Information regarding the annual differences in the composition of the food between different size groups of sculpins and the fre-

quency of empty stomachs was to be obtained together with the sex ratio. After a year, however, a prolongation of the period was decided, but now with sampling twice a month. This second year could give information as to whether the tendencies found in the first year of investigation were repeated.

II. Material

The present investigation was started in March 1966 and concluded in March 1968, with sampling once a week during the first year and twice a month during the second year. The samplings were always performed by using gill nets with a knot-to-knot mesh size of 2.5 centimetres. During the period of investigation 1916 fourhorn sculpins measuring from 11.5 to 28.5 centimetres were examined. Owing to ice conditions no sampling could be performed in the last half of December 1967.

III. The site of the investigation

Tyresö—Brevik, situated in the archipelago of Stockholm in Erstaviken, a bay of the Baltic, was selected as the place of investigation and during the period of two years all samplings were performed at that locality.

The fourhorn sculpin is known to be a very cold stenothermal species (WESTIN 1968 b) and migrates from deeper strata in the autumn after the turnover to regions with a total depth of a few metres.

When the water was covered by ice and the water temperature was low the fish was caught at a depth of 11 metres about 40 metres off the shoreline. During spring and autumn, when a stratification was either in formation or in retrogression, capture took place at a depth of 15—17 metres about 75 metres from the shoreline, and during the period of highest water temperature the sculpins were trapped at a depth of 20—25 metres. The first 5 metres of the bottom was covered by a belt of *Fucus vesiculosus*. Down to a depth of around 10 metres a belt of red algae was to be found. After this depth the soft bottom began, and a rather slight downward slope occurred, interrupted by rocks and stones at a depth of about 20 metres. In holes and crevices there were often large amounts of loose algae, particularly red algae. These algae masses seems to be largest in the autumn. These observations were carried out by diving at the investigation site. The salinity of this part of the Baltic is about 5—6 ‰ S.

IV. Methods

The fish were killed as soon as possible after capture. This was done in order to prevent the continued digestion or decomposition that might other-

wise take place, especially if the fish were exposed to warm air temperatures. The sculpins were measured and weighed fresh, and remaining basic data were recorded. The stomachs were removed from the body cavity. Only the stomachs were investigated, as the contents of the intestines were so fully digested that practically no items could be recognized. Alcohol was used as preservative. Several methods for the enumeration of stomach contents of fish have been reviewed by HYNES (1950). The following two were employed in the present study.

The first method was that of frequency of occurrence. The stomach contents were examined and the individual food organisms sorted and identified. The number of stomachs in which a certain item occurred was recorded and expressed as a percentage of the total number of stomachs examined, empty stomachs being excluded. This method demonstrates what organisms are being fed upon, but gives no information on quantities or numbers.

The other method used was the volumetric one, which is a very simple and accurate method when large volumes of food are present and the number of items to be segregated is small.

The stomach content was measured by its displacement, which was divided by the weight of the fish. This figure (food in pro mille of fish weight)

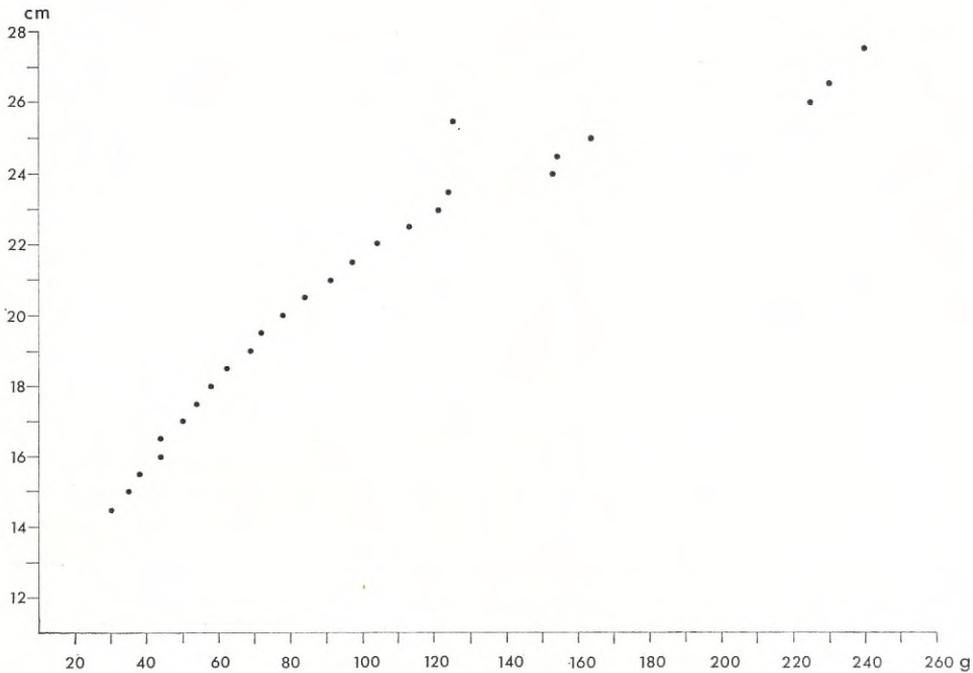


Fig. 1. The length-weight ratios in fourhorn sculpin during two years of investigation, Tyresö—Brevik.

Table 1. Percentage frequency of males trapped during the consecutive months. Altogether 1,916 fourhorn sculpin and 39.1 per cent males.

	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1966/67	36.5	21.7	43.3	57.9	34.6	45.5	36.5	31.9	39.6	39.3	42.4	33.3	37.5
1967/68	37.5	17.9	23.1	37.0	42.1	44.6	40.3	48.9	47.4	58.5	35.5	30.1	49.3

was divided into units in accordance with the present volume of the different food items in this particular stomach. The value of each of the various food items from the stomachs of all fourhorn sculpins from a sampling was added and finally expressed as a percentage.

When dividing the volume of food by the weight of fish to obtain the food in pro mille of fish weight, the real weight was not applied but the weight, which a sculpin of a particular length has according to the length-weight ratio drawn in Fig. 1. The two sexes were at first kept separate as were also the two years but as no significant difference could be detected the method described was chosen.

Thus in the figures which present different food items, the dots and lines, represent percentage of those sculpins examined that had eaten the food type in question at the time of the year (the occurrence method), while the histograms give information about the average volume per cent (the volumetric method). The first year when sampling was performed once a week the mean value of these is drawn in Figs. 2—18. All food items were classified by species with the exception of Gammarids, where the genus *Gammarus* was employed.

V. Results

1. Sex ratio

In Table 1 the percentage of males captured is presented. In only 2 of 25 months do the males exceed the females in number. Three hypotheses were tested statistically. These hypotheses, expressed in question form, were as follows. (1) Is there any significant difference between the sex ratios for the two years? (2) Are there any significant differences between the sex ratios for the months? (3) Is the chance, that a captured fourhorn sculpin is a male 50 per cent? The answers derived from the statistical analysis were: (1) there is no difference between the two years, nor (2) is there any significant difference between the months. (3) The chance that the captured sculpin is a male is not 50 per cent.

Table 2. Percentage frequency of fourhorn sculpin in the different size groups during the two years of investigation.

Year	Length in cm				
	10,0—13,9	14,0—17,9	18,0—19,9	20,0—22,9	23,0—
1966/67	0,3	9,1	44,7	42,9	3,0
1967/68	0,1	7,2	32,7	54,9	5,1
1966/68	0,2	8,4	40,4	47,2	3,8

2. Length-weight ratio

In calculating the length-weight ratio the sexes and the two years were kept separate. A comparison of the four curves obtained revealed only small differences. The values were without trends and were often overlapping. This was the reason why the length-weight ratio was calculated on the basis of all fourhorn sculpins captured during the two years. The mode of procedure adopted was that all fish captured during a quarter of a year were kept separate, and the mean weight values of every half-centimetre-of-body-length class were calculated. Then eight half-centimetre classes from the eight quarters of the years were put together and their mean value were calculated. Such final values for each half-centimetre class are shown in Fig. 1.

The object of establishing the length-weight ratio in such a complicated manner was to obtain an annual mean value which is only slightly influenced by the increase and sudden decrease in body weight in connection with maturing of gonads and the release of eggs and sperms during the spawning time, because the curve obtained was the basis for the estimation of stomach fullness and volumetric method instead of the real weight at this particular moment.

From Table 2, where the captured fourhorn sculpins are divided into size groups, it is obvious that the majority (87.6 %) measured between 18.0 and 22.9 centimetres. Consequently, the accuracy of the length-weight ratio in Fig. 1 can be regarded as good in this range. Below 18.0 centimetres the accuracy seems also to be fairly good, because the difference in weight at a given length was very small during the investigated time. Above 23.0 centimetres, however, great differences occurred between the captured fish, and as they were few in number the course of the curve is uncertain.

3. The stomach fullness

In Fig. 2 the stomach content is given as pro mille of the fish weight according to the length-weight ratio. The mean quantity of food found in the stomachs during a year is remarkably low; in the first year the amount

Table 3. Food items found in the stomachs of fourhorn sculpin, divided into C=carnivorous species, O=omnivorous species, D=detritusfeeding species, during the eight quarters of the two years of investigation, Tyresö-Brevik. (See text,)

(The missing percentages consist of unidentified food)

	Apr.—June			Juli—Sept.			Okt.—Dec.			Jan.—Mar.		
	C	O	D	C	O	D	C	O	D	C	O	D
1966/67	72	15	6	37	16	42	55	15	26	72	14	11
1967/68	74	7	15	15	21	62	30	32	35	72	14	11

was 8.5 pro mille of the weight and in the second year of investigation considerably lower, 5.6 pro mille. A comparison of the two years gives the same trend: the highest value in April—June and the lowest in October—December.

4. The frequency of empty stomachs

The frequency of empty stomachs varied during the time of investigation, as may be seen from Fig. 3. In the first year of investigation the frequency was very low from March—April; it rose in May—June, but was low again in July—September. The highest value was to be found in October—January, followed by a decrease in February—March. The second year began with few empty stomachs, but the amount then increased to reach high values in April—May. The lowest figures were obtained in the summer from June to mid-October. From November to the end of the investigation period the frequency of empty stomachs was fairly high.

5. The food components in the stomachs of fourhorn sculpin

In what follows the various species found in the stomachs are presented.

(a) Priapulids

Halicryptus spinulosus v. SIEB.

This species was found as a food item twice a year during the two years of investigation (Fig. 4). The occurrence was reduced practically to nil in April—June and in October—December, but in the periods July—September and January—March *Halicryptus* occurred as a food item of some importance.

(b) Mysids

In this part of the Baltic five species of the family *Mysidae* occur. All five have been found in the stomach of the fourhorn sculpin. *Praunus inermis*

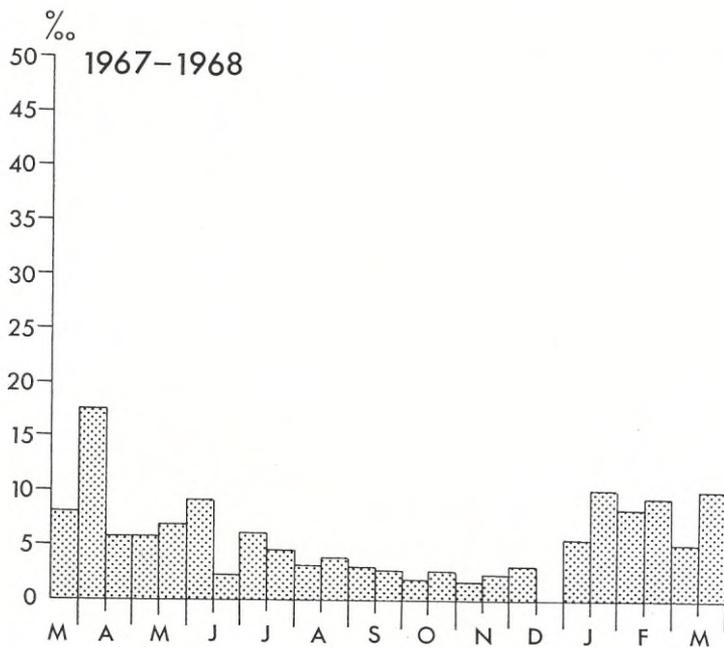
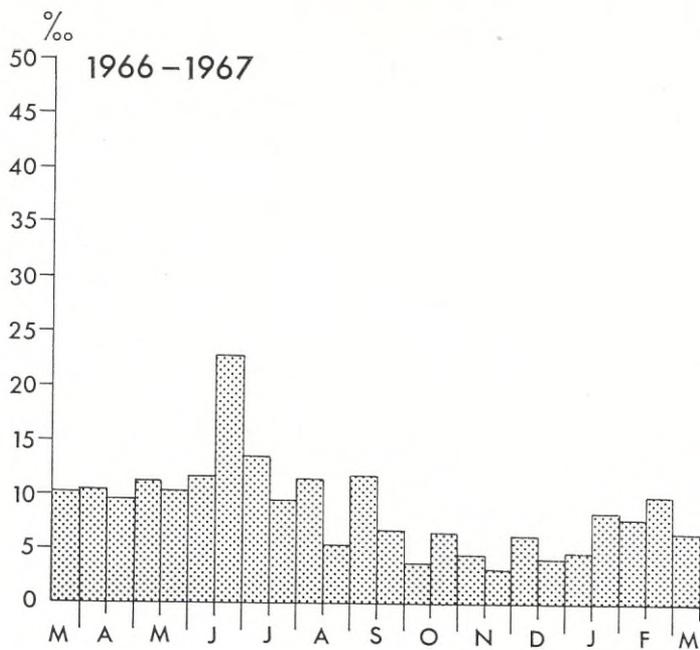


Fig. 2. The stomach fullness during the two years of investigation expressed as promille of body weight, Tyresö-Brevik.

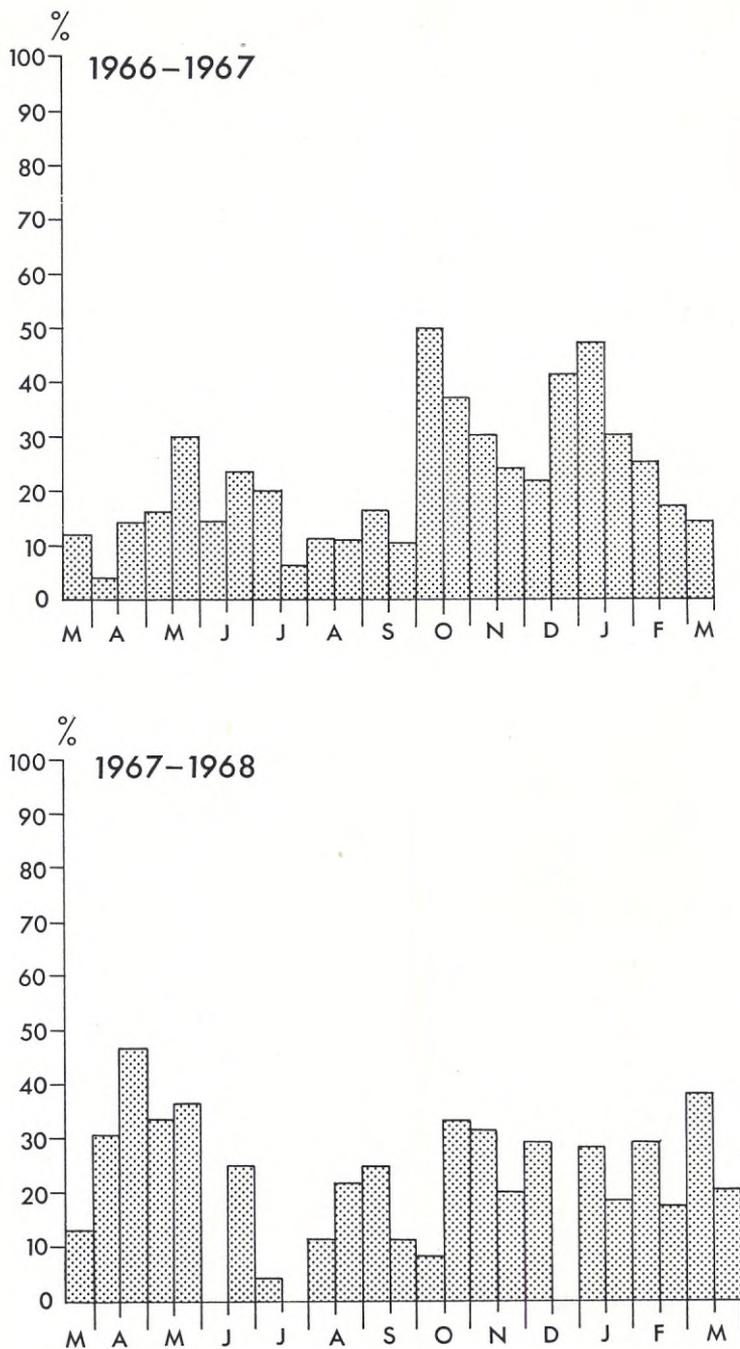


Fig. 3. The frequency of fourhorn sculpin with empty stomachs as a percentage of all fourhorn sculpin investigated during two years, Tyresö—Brevik.

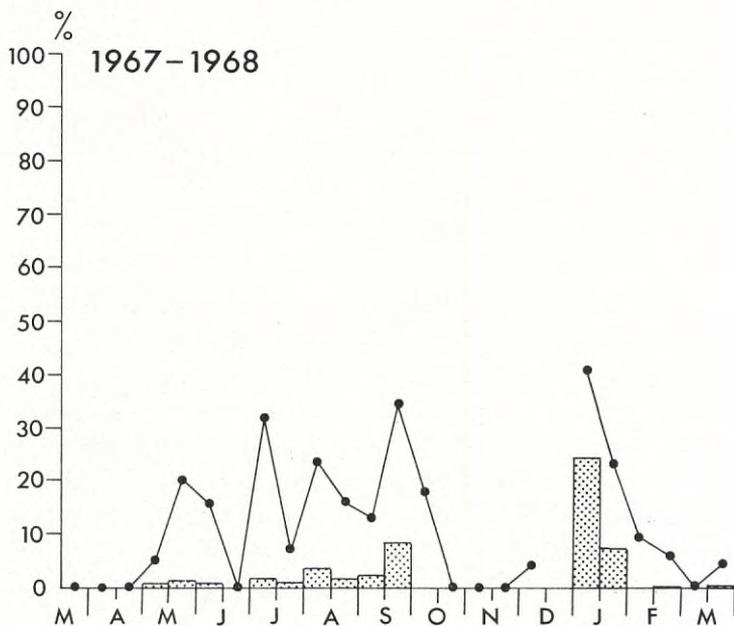
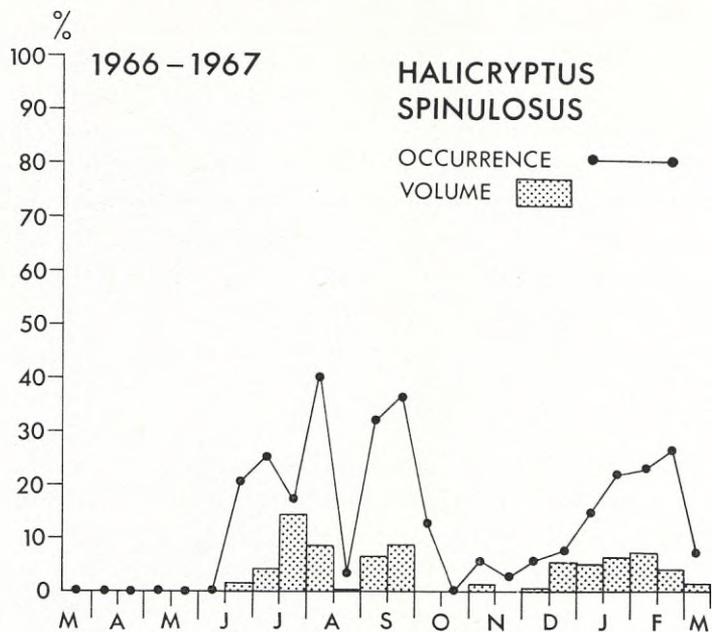


Fig. 4. *Halicryptus spinulosus* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

(RATHKE) and *Praunus flexuosus* (O. F. MÜLLER) have no importance as food, but they occur in low frequencies in January—March. The same is true of *Neomysis integer* LEACH, which is to be found rarely all the year round. The two remaining species, *Mysis relicta* LOVÉN and *Mysis mixta* LILLJEBORG, play a considerable role as prey, particularly in July—December (Figs. 5 and 6). In January—June they are of subordinate importance.

In Fig. 7 the species of the family *Mysidae* and those Mysids, which, owing to digestion, it was impossible to determine are put together. The importance as a food item for the sculpin is especially apparent in June—December.

(c) Isopods

Idotea baltica PALL.

This species occurred to some extent during the first year of investigation. In the second year, however, no *Idotea baltica* at all was found until the last months (Fig. 8).

Mesidotea entomon L.

This large isopod constitutes one of the basic food components to the fourhorn sculpin, and has its main occurrence in March—May, when about 40 per cent of the volume is *Mesidotea*. The proportion can occasionally be as high as 70 per cent.

In June—October this isopod normally occurs in low numbers or is absent altogether. There is thus agreement between the two investigation years as to the season of preying upon *Mesidotea entomon* (Fig. 9).

(d) Amphipods

Pontoporeia affinis LINDSTRÖM

At the investigation site only *Pontoporeia affinis*, one of the two *Pontoporeia* species occurring in the Baltic, was detected in the sculpin's stomachs. The *Pontoporeia* is restricted to the months July—December but mainly is at its peak only in July—September (Fig. 10). During this limited period, the species can be regarded as a food component of major importance. A comparison of the two years shows agreement as regards the time of feeding on this particular item; the amount, on the other hand, differs, being greater in the second year. In a period of two months about 60 per cent of the stomach volume consisted of *Pontoporeia*.

Gammarus spp.

Members of the genus *Gammarus* are most frequent from March to May and are practically absent from June to September. The two years agree both in amount and in the time of occurrence (Fig. 11).

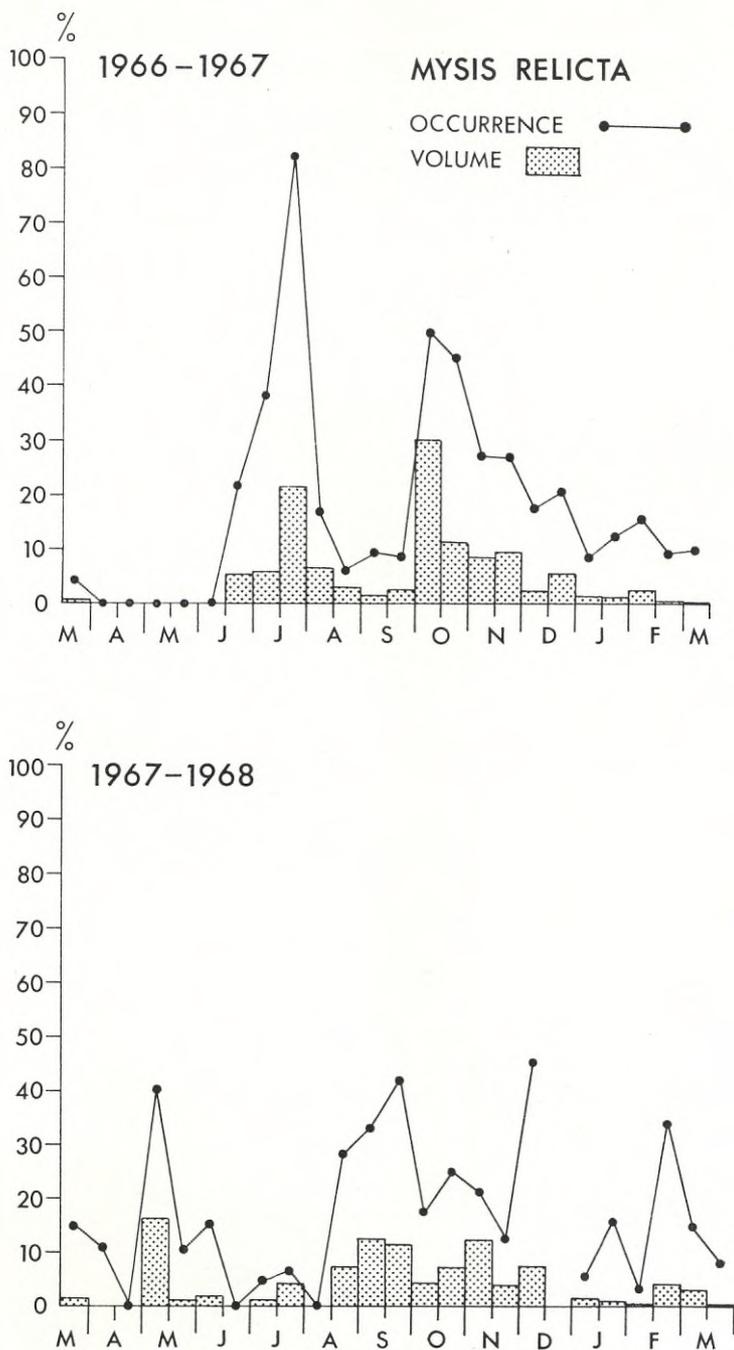


Fig. 5. *Mysis relicta* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

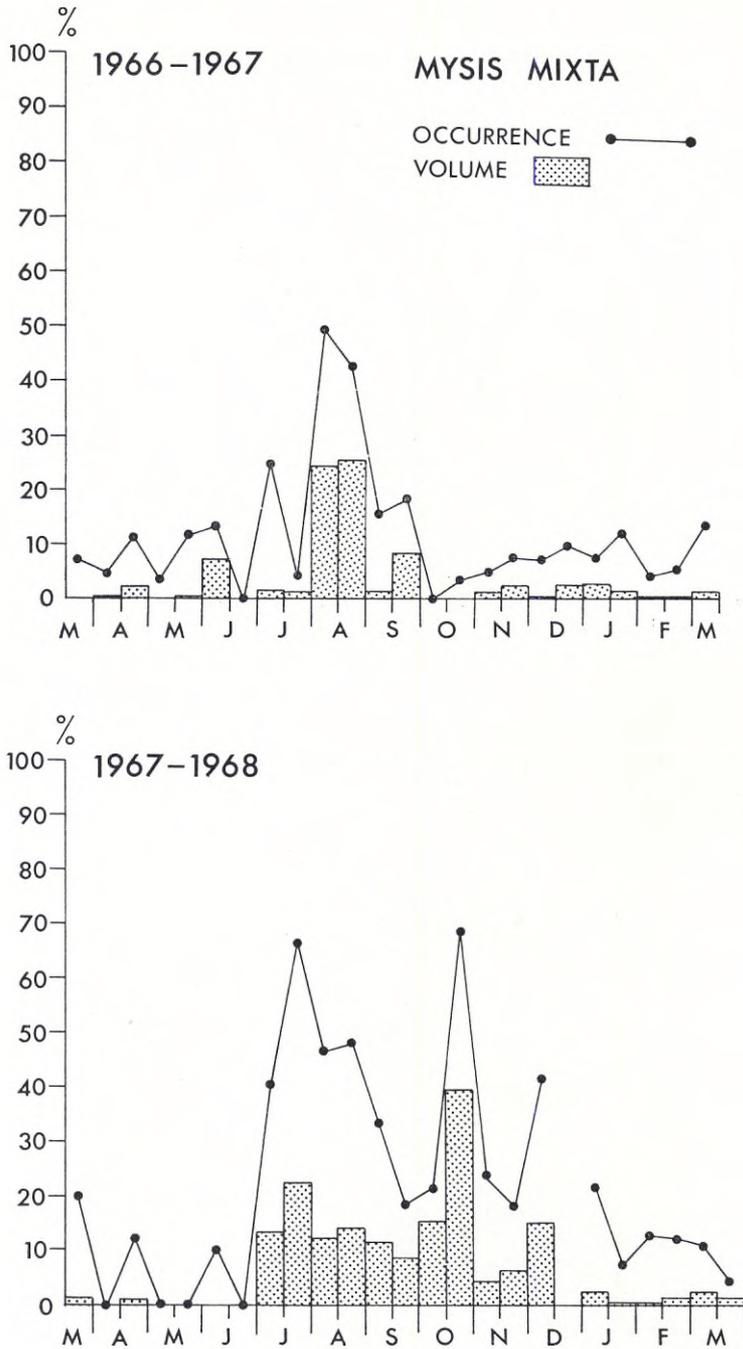


Fig. 6. *Mysis mixta* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

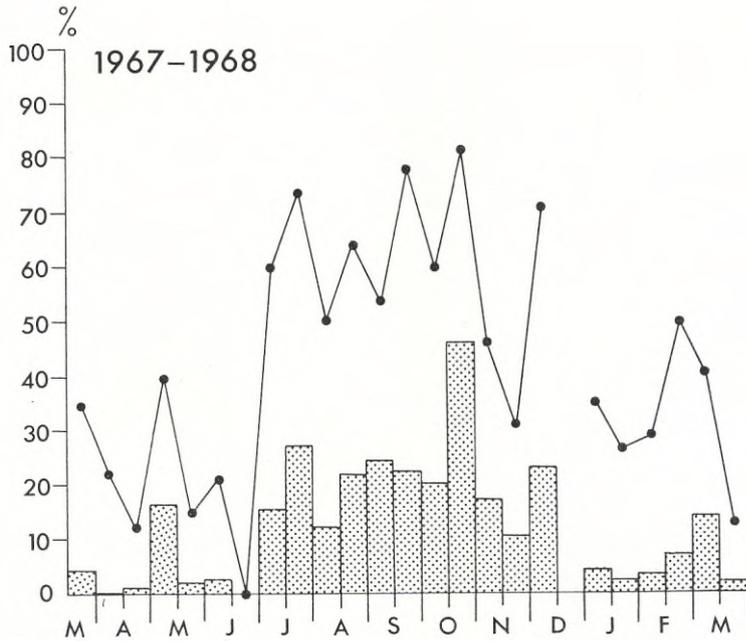
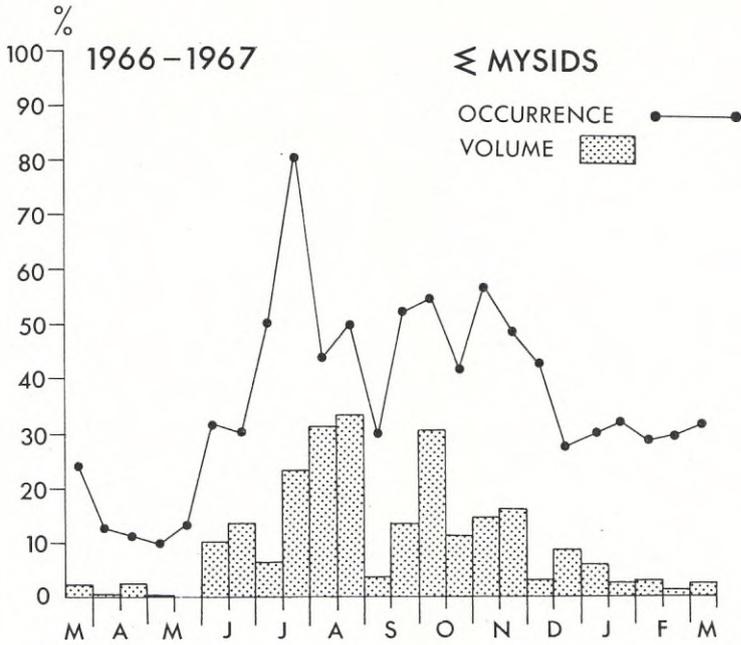


Fig. 7. Σ *Mysids* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

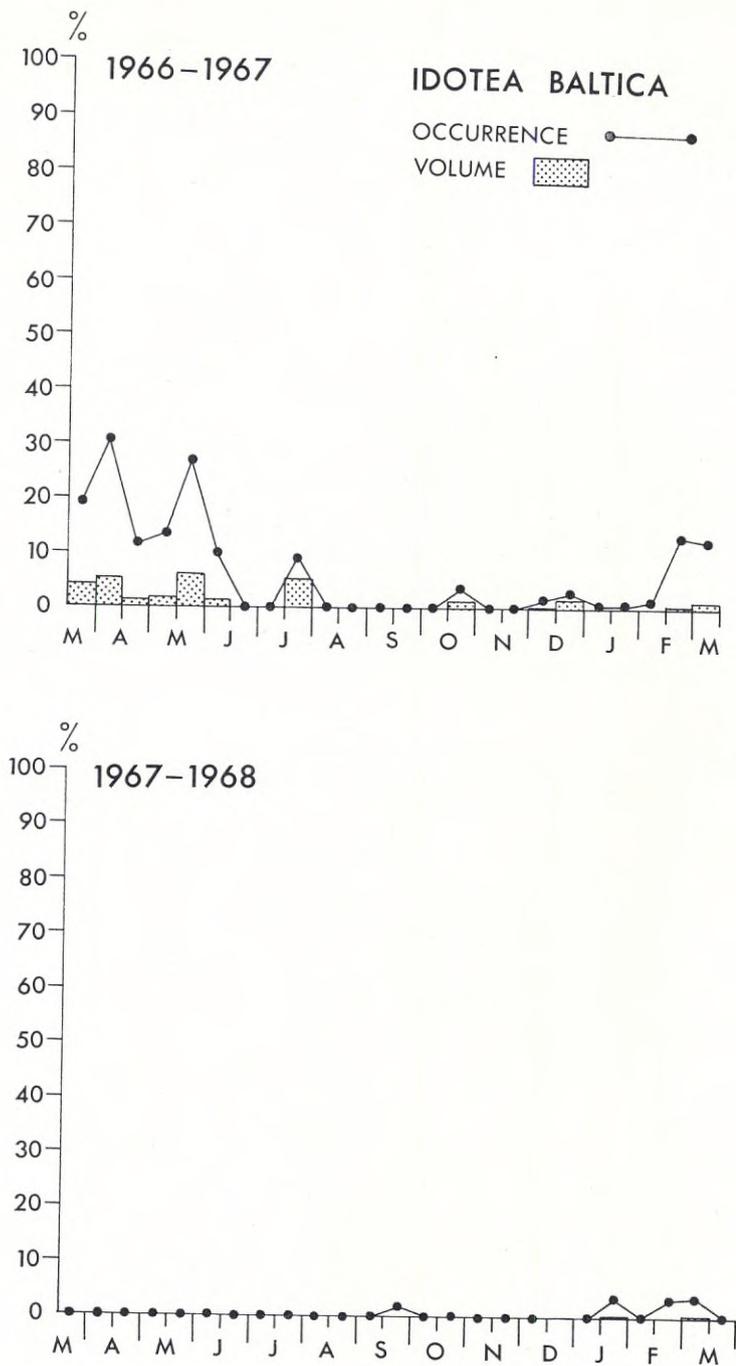


Fig. 8. *Idotea baltica* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

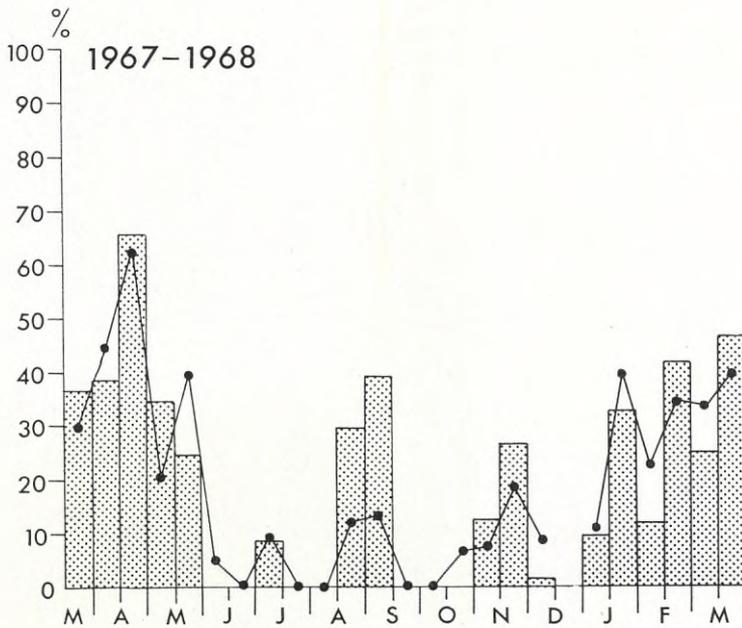
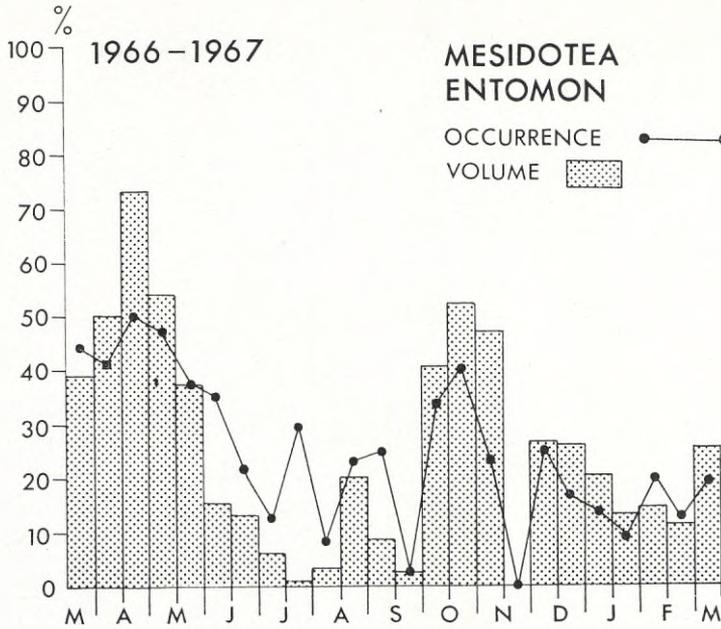


Fig. 9. *Mesidotea entomon* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

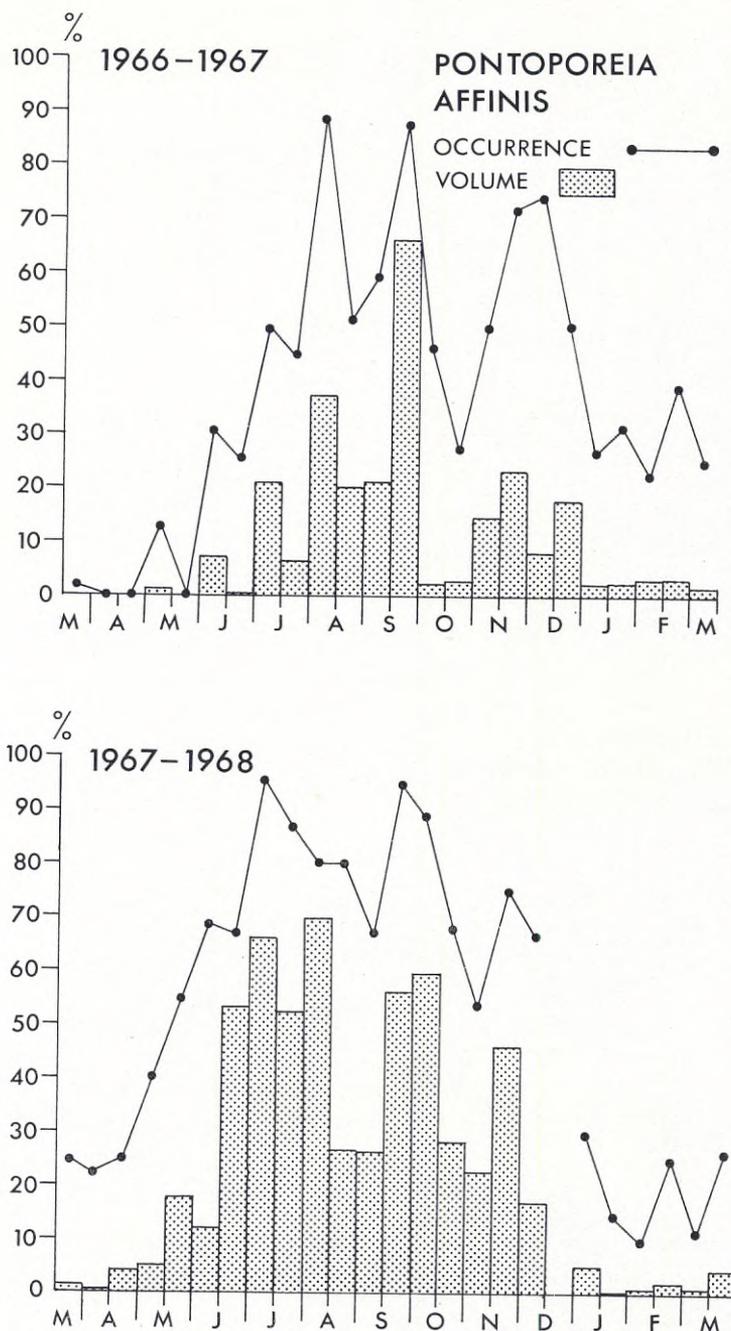


Fig. 10. *Pontoporeia affinis* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

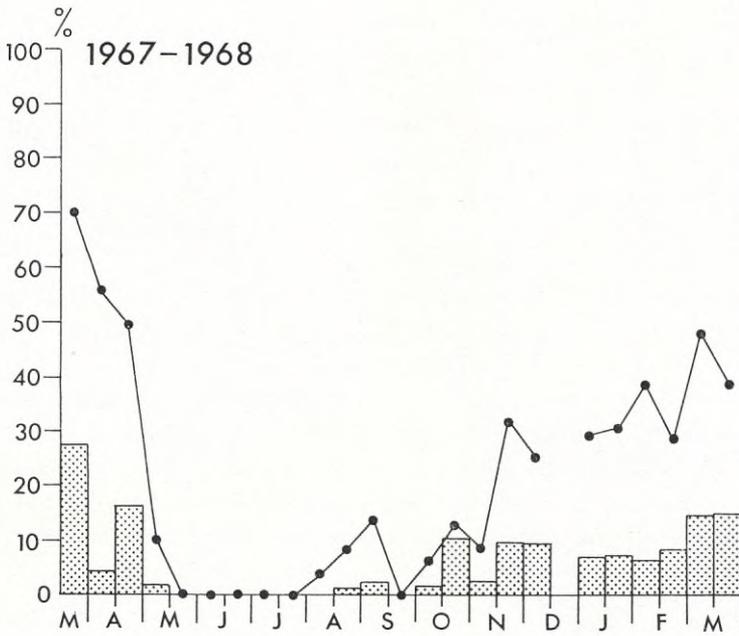
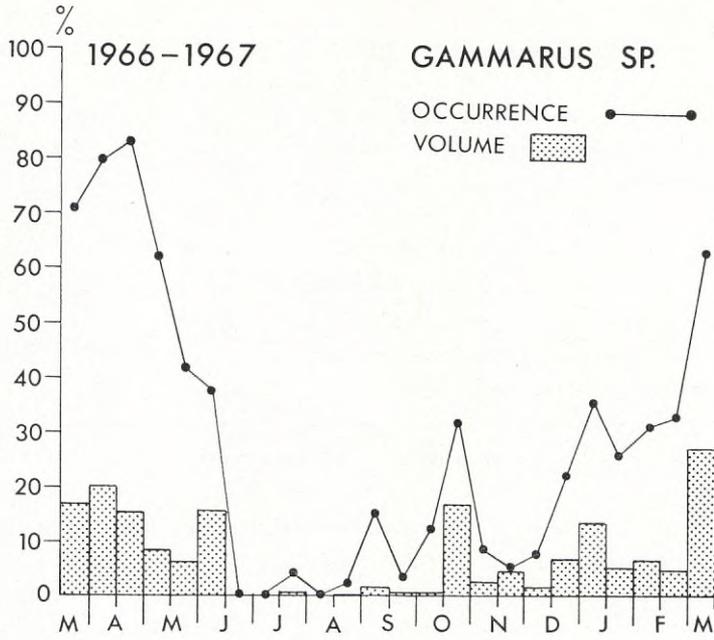


Fig. 11. *Gammarus* spp. in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

(e) Molluscs

The molluscs play a subordinate role as a prey for the fourhorn sculpin. The two bivalves *Mytilus edulis* L. and *Macoma baltica* L. are the only molluscs which appear regularly (Figs. 12 and 13). Regarding the *Mytilus*, which seems to be the more important of the two, no trend in the occurrence can be shown, and the same seems to be true of the *Macoma* too.

(f) Fish

From Fig. 14, where the entire contents of fish as food item from the stomachs are given, it is obvious that this kind of prey can also be regarded as a basic unit for the sculpins. This amount is made up of several fish species, such as smelt *Osmerus eperlanus* L., sprat *Clupea sprattus* L., herring *Clupea harengus* L., viviparous blenny, *Zoarces viviparus* L., three-spined stickleback *Gasterosteus aculeatus* L. and the common goby *Pomatoschistus (Gobius) minutus* PALLAS shown in Figs. 15 and 16. Returning to Fig. 14, where the entire fish consumption is presented, it is apparent that the feeding upon other fish species is most pronounced from November to March and falls in April—May, rises again in June—July and is at its lowest in August—October. The agreement between the two years was good. Among the fish species upon which the fourhorn sculpin preys, the common goby is the dominating species; it occurs in the course of the period November—March and is absent during the rest of the year (Fig. 16).

As regards the three-spined stickleback, the tendency is in accordance with that described above for the common goby (Fig. 15).

There is a close resemblance between the two years of investigation as regards both the time of feeding and the quantities of the last-mentioned two species consumed by the fourhorn sculpin.

(g) Fish roe

In this part of the Baltic the spawning of the fourhorn sculpin takes place around the turn of the year and the time of embryonic development is about a quarter of a year (WESTIN 1969). During this time the males protect the roe, but often with little or no success, as in the same period a considerable proportion of the volume of the stomach content consists of species-specific roe (Fig. 17). Only in the first year of investigation did roe appear in June too. In this case we have to deal not with species-specific roe but roe from herring. In the second year no roe was detected in June, presumably owing to that the gathering was twice a month instead of once a week.

(h) Miscellaneous

A summation of the volumetric percentages for the different food items presented would not give 100 per cent, because there always exists a varying degree of food which it has been impossible to determine. A small part of

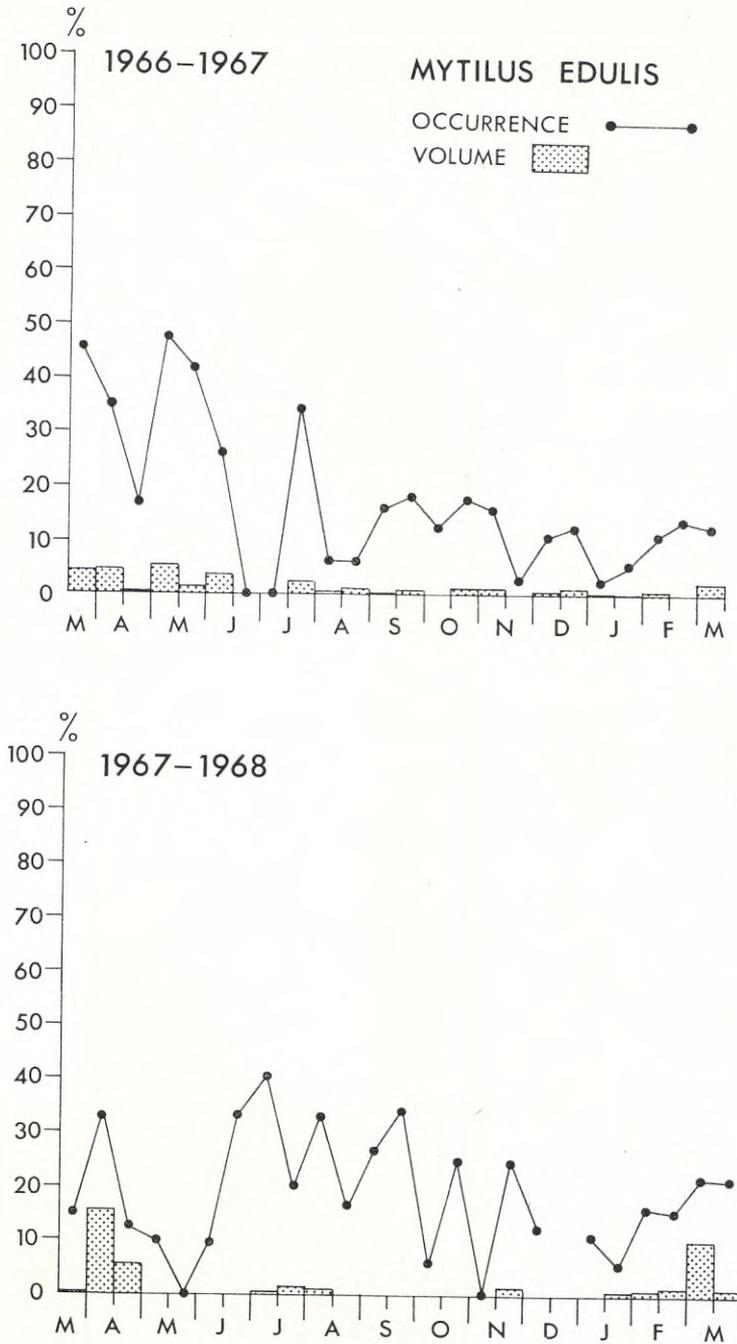


Fig. 12 *Mytilus edulis* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

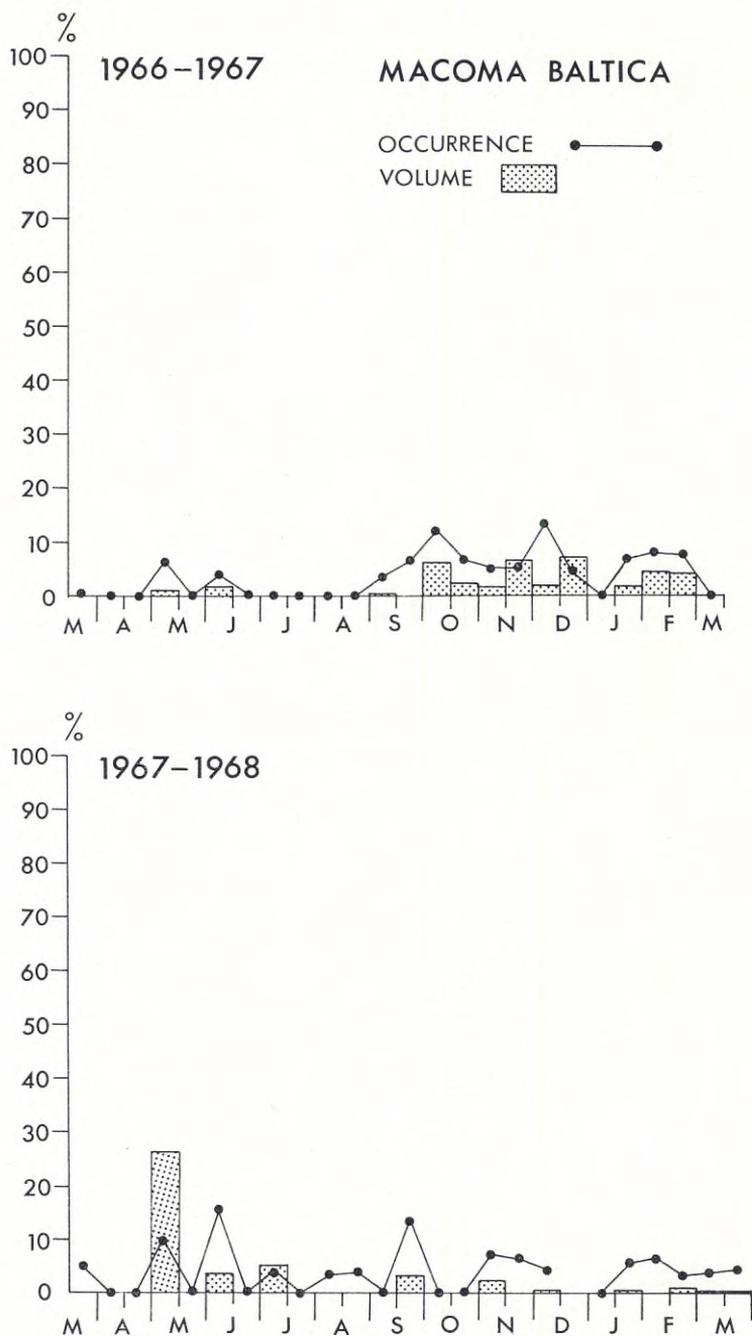


Fig. 13. *Macoma baltica* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

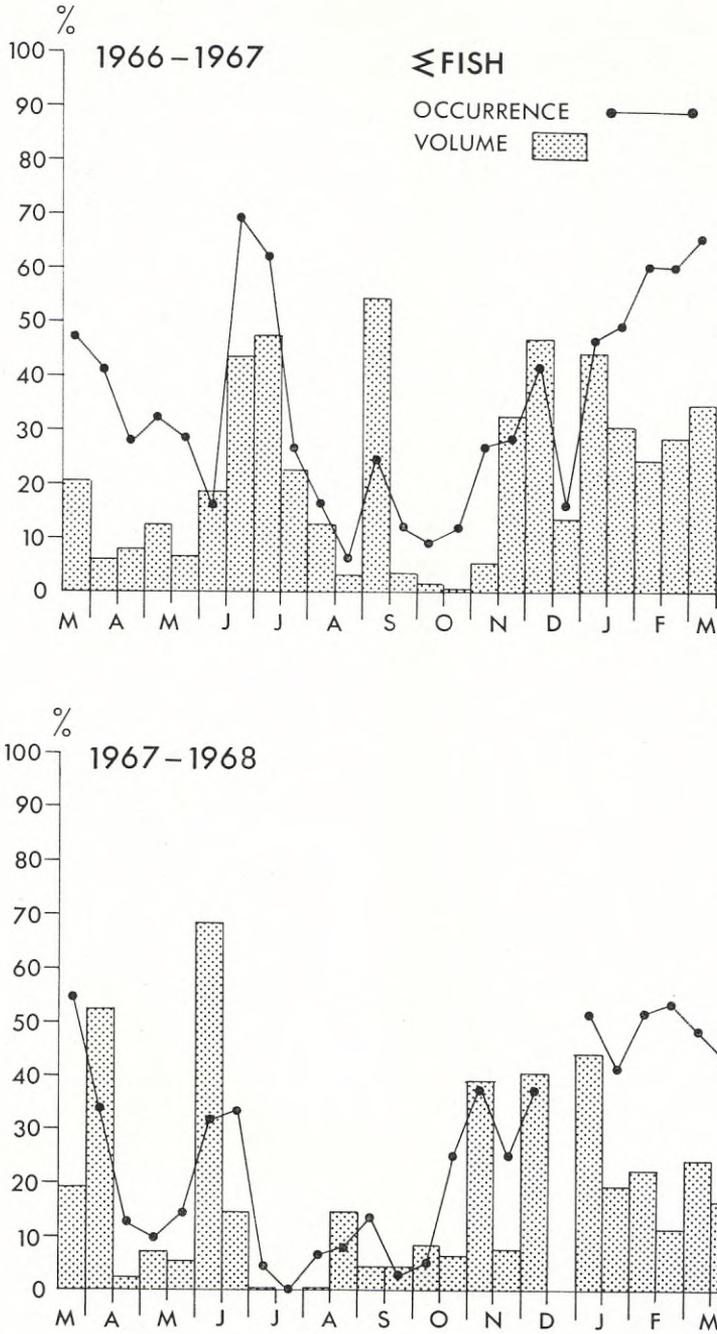


Fig. 14. Σ fish in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

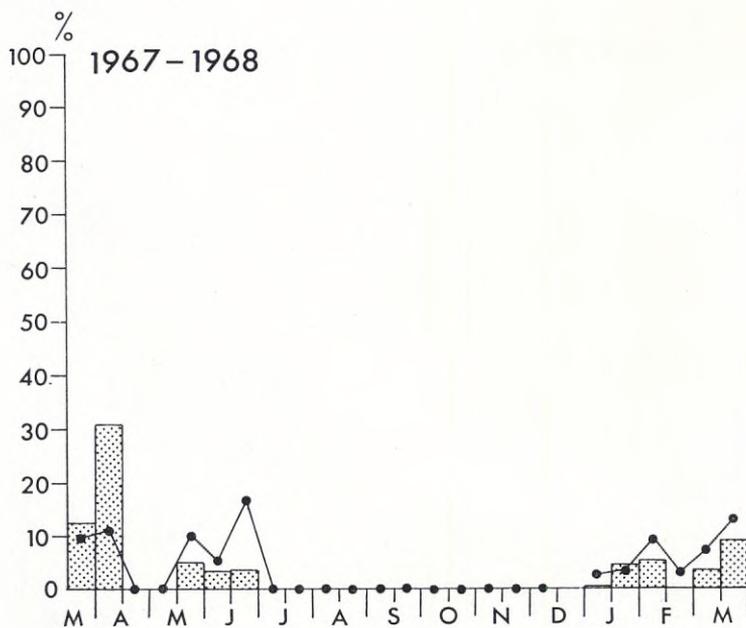
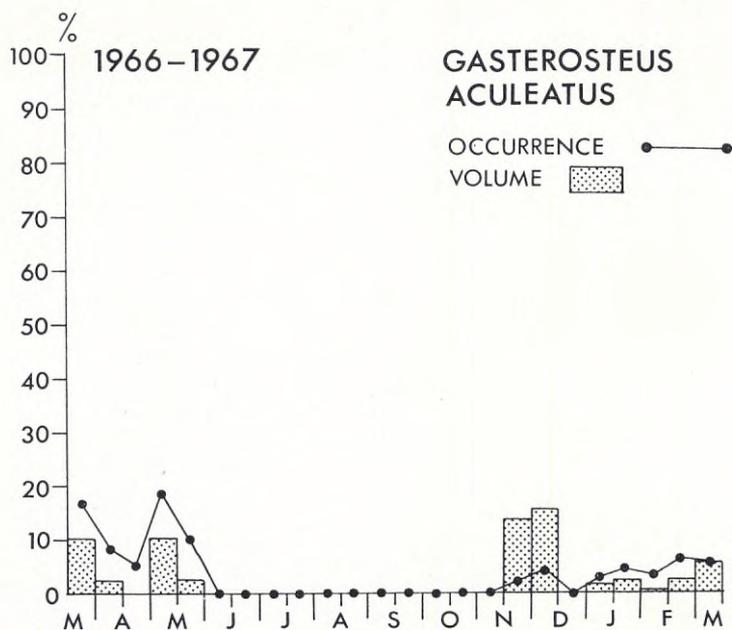


Fig. 15. *Gasterosteus aculeatus* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

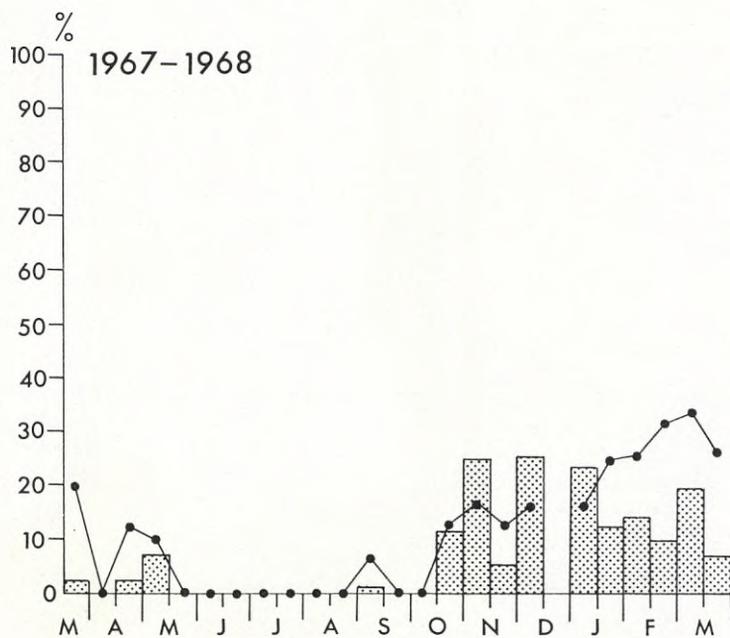
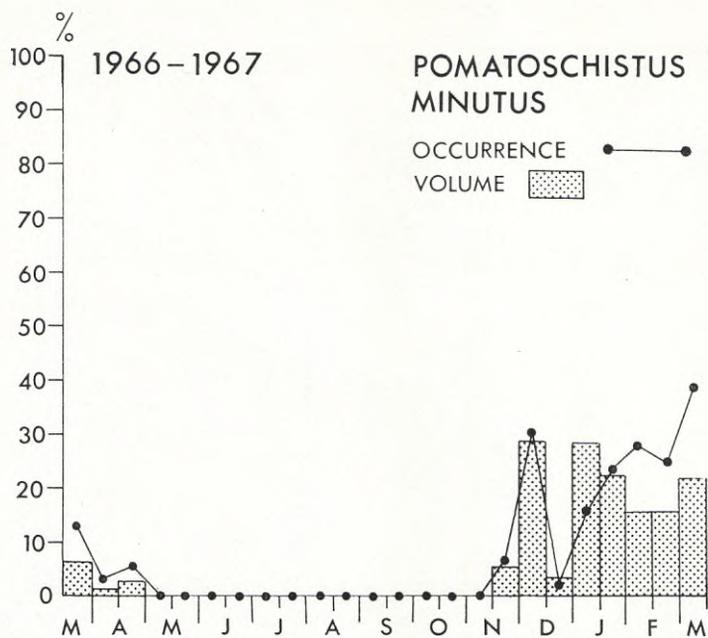


Fig. 16. *Pomatoschistus minutus* in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

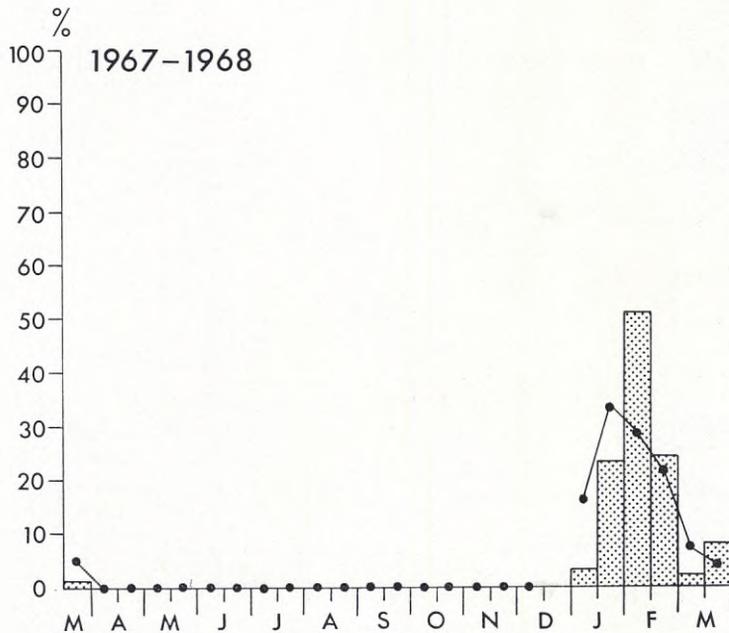
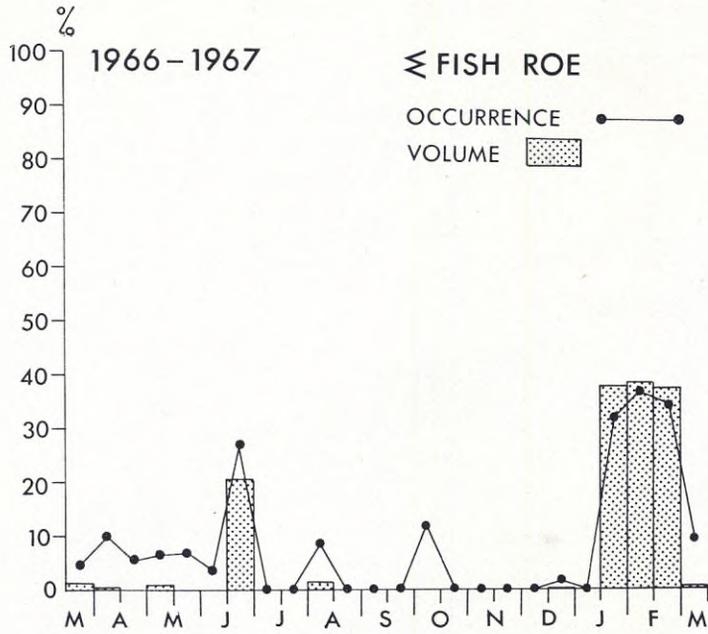


Fig. 17. Σ fish roe in stomachs of fourhorn sculpin during two years of investigation, Tyresö—Brevik.

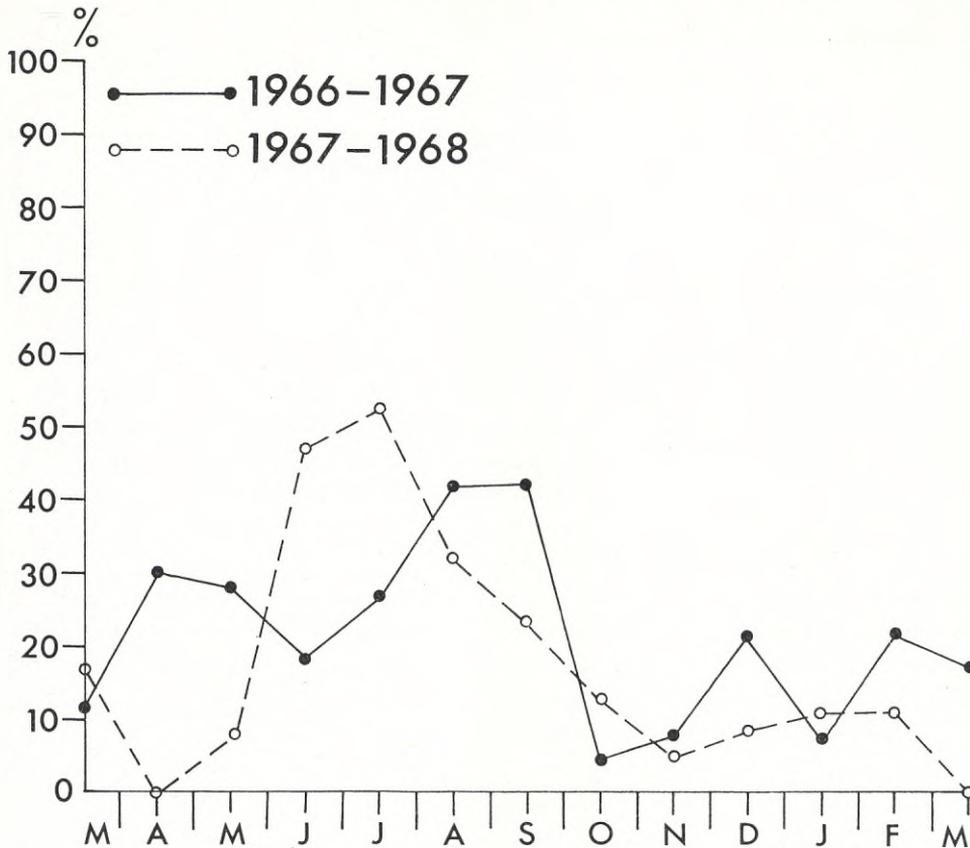


Fig. 18. The frequency of stomachs of fourhorn sculpin with parasitic Nematods expressed as a percentage of all stomachs examined during the two years of investigation, Tyresö—Brevik.

the missing percentage is made up of species of rare occurrence, such as *Crangon crangon*, *Corophium volutator*, *Harmothoe sarsi*, *Tricopthera sp.*, and certain molluscs such as *Cardium sp.* and *Lymnea peregra*. Sometimes algae and pebbles also occur in the stomachs, presumably as a result of having been swallowed inadvertently together with prey.

6. Other fish species trapped in gill nets at the investigation site

In connection with the gathering of fourhorn sculpin, there have been captured in the gill nets, several other fish inter alia *Clupea harengus*, *C. sprattus*, *Leuciscus rutilus* L., *Abramis blicca* BLOCH, *Coregonus lavaretus* L., *Osmerus eperlanus*, *Gadus morhua* L., *Perca fluviatilis* L. and *Zoarces viviparus* and *Myoxocephalus scorpius* (L).

Only one of the species enumerated, *Zoarces viviparus*, occurred through-

out the year. The frequency, however, was low. This species had predominantly fed upon molluscs, mainly *Macoma baltica*. Ranking second in amount is the cod, which had its major occurrence in the autumn. The size of the cod was 25—35 centimetres and the stomach contents were dominated by other fish species, including, among others *Clupea harengus*, *C. sprattus* and *Pomatoschistus minutus*. The remaining species were caught only on rare occasions.

7. Parasitic nematods

In the investigated stomachs of fourhorn sculpin, parasitic nematods occurred practically throughout the year. In Fig. 18 the numbers of nematods in every fish are not taken in consideration; only the percentage of stomachs with one or several nematods is shown during every month in the two years. The numbers of nematods, however, were relatively low, seldom amounting to more than 10 specimens. The nematods found have not been classified as to species.

The highest percentage of occurrence is found during the summer period, when 40—50 per cent of the captured fourhorn sculpin were affected. The lowest value was in October—November, the time of high percentage of empty stomachs and lowest stomach-content volume, when only about 10 per cent of the sculpins were affected by parasitic nematods.

In the remaining parts of the year the percentage of nematods fluctuated.

VI. Discussion

1. General remarks

(a) The method of collection

In calculating the length-weight ratio it is important to use samples of fish that are unbiased in respect of length and weight. Samples from a gill net of a particular size are usually unsuitable, because the net tends to select fat fish among the shorter ones and thin fish among the longer ones (KIP-LING 1962). This is not altogether valid for such a spiny species as the fourhorn sculpin because, regardless of mesh size, gill nets tend to be more efficient in capturing fish that have external roughnesses, spines, etc. The fact that no sculpins less than 11 centimetres have been caught is perhaps due to the comparatively large mesh size but comparative fishing was carried out at investigation site with gill nets of a knot-to-knot mesh size of 1 centimetre. In spite of this state of things the mean length of the sculpins captured was in agreement with those from the original gill net. I believe that the absence of the shortest fourhorn sculpin in gill-net catches at the

place of investigation is not due only to the large mesh sizes but also to the fact that young sculpins live in the depths. Fourhorn sculpins between 4.5 and 10 centimetres have been caught only below 35 metres. All of them had *Pontoporeia affinis* as their only food item.

Another source of error attached to a use of gill nets is that the net tends to capture those fishes in a population that are swimming, and it is possible that a fish with an empty stomach swims around more than does a fish with a well-filled stomach and thus has a greater chance of being captured. This is one possible explanation of the many empty stomachs and the low stomach-fullness value.

A study of diurnal and annual patterns of activity is invaluable in predicting the optimal time to make collections. The best time should be at the end of a feeding period, when the stomachs are filled and the digestion has not proceeded very far. In several fish species, the rate of digestion is rather short *inter alia* *Pomatoschistus (Gobius) minutus* (WAHLBERG, pers. comm.). This is not the case with fourhorn sculpin, where fish three days after capture and held in aquaria still had food items which it was possible to determine, owing to, for instance, the type of food and low temperature.

A comparison of the values of the two histograms, frequency of empty stomachs and fullness gives a rather good agreement. A high volume of food is linked with a low frequency of empty stomachs and a small amount of food is coupled with a high percentage of empty stomachs. It is remarkable that the period of lowest stomach content and consequently highest percentage of empty stomachs is to be found during a period of good food resources in the autumn, and during the period of scarcest food resources in the spring the highest food intake seems to occur. This indicates that factors involved in the preparation for the spawning at the turn of the year maybe are responsible.

A comparison of the two years of investigation gives the same trend both in stomach fullness and empty stomachs. The volume of the stomach content is noticeably lower during the second year of investigation. The reason for this is unknown but one explanation may lie in the differences in temperature between the two years in as much as owing to high temperatures in the late spring of the second year the fourhorn sculpin were pressed down to the depths earlier than in the first year with its exceptionally cold spring water temperature.

Thus the value for stomach fullness and that for empty stomachs are not to be regarded as quantitative measures but as providing a basis for comparisons.

One question of the utmost interest in connection with an investigation of this kind concerns the numbers of collections. Is it necessary to make collections every week, or is twice a month enough?

A comparison of the two years indicates that in the case of fourhorn scul-

pin it is sufficient to make collections twice a month. There is, however, a risk of missing some food types of short duration such as the roe of herring which occurred in the first year with sampling once a week but was absent in the second year when sampling was performed twice a month. No general advice can be given about the density of samplings as regards other fish species but in long-term investigations it seems to me that it is better to begin with dense samplings, which could become sparser as further experience is obtained.

(b) Remarks on the methods of studying
the food consumed

From the point of view of agreement between the two methods employed the different food species found in the stomachs (Figs. 3—16) can be roughly divided into the following three groups:

- A. The volumetric percentage of the stomach contents often exceeds the value for the occurrence percentage.
- B. The value for the occurrence percentage always greatly exceeds that for the volumetric percentage.
- C. The value for the occurrence percentage exceeds that for the volumetric percentage but not in such a high degree as in B.

The most prominent items in group A are the *M. entomon* and the species-specific roe. The various fish species found in the stomachs can also be incorporated in this group, but in a lesser degree.

Group C consists mainly of the various crustaceans. Here the correlation in general is good between the two methods employed. Sometimes, however, a fairly large difference occurs.

In group B the occurrence percentage may give a false picture of the importance of the species concerned. An example of species belonging to this prey group is *Harmothoe sarsi*, which mainly appeared in December—March. This species was determined solely by the jaws and bristles, these being the only remaining parts of the animal. A volumetric value was practically always impossible to obtain. As regards the *Halicryptus* (Fig. 4) the situation was often the same. The only remnant was the lengthwise rows of spines and pappilae from the proboscis. A third prey belonging to this group is the *Mytilus* (Fig. 12); often this was detected on the basis of pieces of the *periostracum*, which sometimes were the only remains.

The relatively high occurrence percentage and very low volume percentage may be due either to bristles, jaws and the horny *periostracum* remaining in the stomach a certain period after the soft parts have been digested. Thus, in such a case the occurrence method gives a false picture of the proportions. KLEMETSEN (1968), who investigated the feeding habits of brown trout, noted that sometimes the long caudal processes of the planctonic *Bythotre-*

phes were found in the folds of the stomach wall and that the frequency values for this type of food may therefore be too high owing to the accumulation of these processes in the stomach.

The conclusion from the comparison of the two methods used is that the volumetric studies alone tend to mask the importance of the smaller food items in favour of large items. The occurrence method demonstrates what type of food the fish have been fed upon, but gives no information about quantities and does not take into consideration the possible accumulation of food organisms resistant to digestion. Thus it is to be expected that the food items in group A are overestimated by the volumetric method and on the other hand are underestimated by the occurrence method because this comparatively large species tends to take longer to digest.

In group B the state of things is the opposite. The percentage occurrence is high and has no relevance to the values from the volumetric method, the reason perhaps being that some parts of the food organism are resistant to digestion.

In the last group (C) the greatest agreement between the two methods occurred.

2. Sex ratio

As has been stressed earlier (Table 1) the females exceeded the males in number during the two years of investigation at this particular locality. This circumstance has been treated statistically and the predominance of females seems not to be a chance occurrence.

Two possibilities exist. Either (1) the number of adult males was underestimated, something in their biology preventing them from being captured at this special locality, or (2) there is a real difference in the number of adults belonging to the two sexes.

From investigations of the spawning in fourhorn sculpin (WESTIN 1969) it is known that the male seems to spawn with one female only and violently attacks all sculpins who come within a certain distance of the egg mass. If the male could spawn with several females it would be easier to believe that there existed a real difference as regards the sex ratio.

One explanation of the lack of males captured in the gill nets is that the male, in connection with the spawning and after the spawning when he defends the egg mass, remains in a territory of his own and does not swim as much as a female. This fact can give a satisfactory explanation of the lack during a limited period only, namely from mid-December to mid-April. From recent investigations based on diving it seems that the sculpin male has a territory to defend already at the beginning of November, for the observed fourhorn sculpin females escaped, while the males attacked the divers (JANSSON, NYQVIST, pers. comm.).

This information, however, can only account for what happens in one half of the year; an explanation for the other half still has to be sought.

The second possibility is that a real difference in sex ratio of adults occurs. A reason for this might be that, owing to the more dangerous life (*e.g.* the fish attack enemies instead of escaping during the time of territorial behaviour and suffer stress during the guarding of the eggs) the males have a higher mortality. A combination of the two possibilities seems plausible.

In Lake Mälaren the sex ratio was roughly 1 : 1 from mid-May to mid-October (200 specimens). The period late October to February (152 specimens) yielded only 40.4 per cent males. In Lake Vättern in middle and late October only 7.3 per cent of the captured fish were males (41 specimens only).

3. Abiotic factors

(a) Salinity

The fourhorn sculpin population living in the Baltic, as well as these more and less dwarfed populations which are to be found in surrounding lakes, is no doubt derived from that circumpolar form known as *Myoxocephalus quadricornis labradoricus* (SEGERSTRÅLE 1957).

A survey of the present knowledge of the ecological nature of the ancestor of the relict *Myoxocephalus* of Northern Europe clearly indicates that it is not, as stated in the earlier literature on relicts, properly marine, but is in the main confined to brackish waters and does not, as a rule, occur at salinities above 24 pro mille; it even seems probable that for reproduction it requires a rather low salinity (SEGERSTRÅLE 1957).

In the Baltic the main range of the *Myoxocephalus quadricornis* seems to be confined to areas with a salinity below 6 pro mille. However, it must be remembered that this so-called relict form seems to have twice survived a freshwater stage of the Baltic basin as a result of which its salinity tolerance may be less pronounced than that of the ancestral form (PURASJOKI 1957, unpubl.).

My own experience of investigations now in progress regarding the salinity tolerance of the fourhorn sculpin lead me to believe that a salinity as high as 15 pro mille in long-term experiments does not affect, for instance, food search or survival. The assumption that the fourhorn sculpin requires a rather low salinity for reproduction is perhaps tenable in so far as the ecology of the fish is concerned but from my own as yet unfinished investigations it is clear that the fertilization of the eggs, the development of the eggs and also the hatching of the fry, can take place in a salinity of 20 pro mille. The fry, however, died after about 10 days. Presumably this was due to starvation, as the fry in the other aquaria with lower salinities also died.

(b) Temperature

My personal experience from the collecting of fourhorn sculpin at investigation site and from other localities in the Baltic area is that the fish seldom occurs in a body of water with a temperature exceeding 9—10°C. On one occasion a fourhorn sculpin was trapped at a depth of 8 metres, where the temperature was 13°C. The Baltic population of fourhorn sculpin has earlier been shown to have a very limited range of thermal tolerance (WESTIN 1968 b).

In Arctic North America and East Greenland, where the fourhorn sculpin is considered to be a shallow-water species and rarely extends deeper than 18 metres, the fish are to be found at surprisingly high temperatures, up to 12°C or even 14—15°C (MCALLISTER 1959).

From the facts stressed above it seems that the migration to deeper areas in late spring and the return to more shallow water in the autumn is due to the temperature, which is linked up with an increasing interspecific competition. The former is also revealed by observations in connection with diving, where the seemingly uniform bottom slanted downwards and the first fourhorn sculpin was to be seen just beneath the thermocline at a temperature of 7°C, although on the first day thermocline was situated in 13 metres and on the second day in 15 metres.

(c) Oxygen

It seems that the oxygen conditions do not normally act as a limiting factor in the Baltic for a coastal species like the fourhorn sculpin. So far as I know no value for the oxygen consumption in fourhorn sculpin from the Baltic population is available, but SCHOLANDER *et al.* (1953) investigated the Nearctic population and compared the value from several arctic fish with tropical fish at their natural habitat temperature. He found that the oxygen consumption for the tropical fish in general is about 4—5 times greater than that of arctic fish of the same weight.

(d) Light

When discussing the amount of light which penetrates the water column down to a depth of 80—100 metres, it would be of interest to know how important light is for a fourhorn sculpin when capturing a prey. It is thus merely a question of structure and organisation of the visual cells in the fish concerned.

From an investigation of the cone types and cone arrangements in teleost retinae (ENGSTRÖM, 1963) it has been pointed out that the cone mosaic is to a great extent dependent on the degree to which a fish relies upon vision. In eyes or regions of eyes which are adopted for acute vision the mosaic is very regular and the most regular mosaic are found in species feeding on fast-moving objects. Retinae or regions which are not adopted to the same

extent to sharp vision have a more loosely organized mosaic or no regular mosaic at all.

The cone mosaic of the fourhorn sculpin has been found to be regular (ENGSTRÖM, op. cit.) but the mosaic is not of the same regularity as in *Myoxocephalus scorpius* (L.). So far as I am aware this state of thing agrees very well with the food ecology of the two species.

The fourhorn sculpin is thus to a certain degree dependent on light when capturing fast-moving objects.

How deeply the light can penetrate the water column finally depends on the transparency of the water, which is a parameter with changing values according to locality, weather, and time of year.

However, for a human eye subjects are still visible half a metre away at a depth of 45 metres on a normal summer day at a locality in the vicinity of the Askö laboratory.

(e) Pressure

How the pressure acts upon the fourhorn sculpin, which lacks a swim bladder, is not known. A rapid change of pressure from that at a depth of 50 metres to that prevailing at the surface does not seem to have any serious effect.

4. General remarks on the prey fauna

The prey fauna of the fourhorn sculpin can be roughly divided into two groups. The first group constitutes mainly of the so-called relicts which are to be found in the stomachs during the period of deep occurrence in the summer.

The *Halicryptus spinulosus* occurred during the two years of investigation mainly in the summer and immediately after the spawning. The occurrence thus had two peaks, with a trough from October to December. That time is also the time of many empty stomachs and of little food in the remaining ones. Many explanations can be offered *inter alia* that the preference for this type of food is low and this kind of food resource is utilized during periods characterized by a scarcity of the more favoured items.

To the same group belong the two species of the family *Mysidae* which are of importance for the sculpin not only in summer but also in autumn. From Figs. 5 and 6 it can be seen that *Mysis relicta* and *M. mixta* often act as substitutes for each other.

The most important food item for the fish during the period of deep-water life is beyond comparison the amphipod *Pontoporeia affinis*, which sometimes occurs in 90 per cent of the stomachs. A comparison between the two years of investigation shows a great difference. During the period July—September in the first year the *Pontoporeia* made up only 35 per cent of

the volume, while during the same period of the second year the percentage was 55. The stock of *Pontoporeia affinis* is known to show marked annual fluctuations in abundance (SEGERSTRÅLE, 1960) but the unusually cold spring of the first year may also in part be responsible for the low amount of *Pontoporeia* eaten as the sculpin could remain in shallow water longer than usual. As can be seen from Fig. 10, it is obvious that *Pontoporeia* occurs in a relatively high degree not only during the summer season but also in October—December. The amount of *Pontoporeia* eaten at this time is dominated by mature males which occur in connection with the spawning, when the male develops elongated antennae and seems to have a more pelagic nocturnal life than the female.

Mature *Pontoporeia* males appeared in mid-November during the first year and late October during the second year, and were to be found until the last days of February in both years of investigation.

The *Mesidotea entomon*, which belongs to the so-called relicts, was for that reason expected to fall into the first group. Another reason for expecting that the *Mesidotea* would be found in the stomachs during the deep-water period is that the *Mesidotea* prey upon *Pontoporeia* (HESSLE, 1924) and judging from the stomach contents, *Pontoporeia* is very abundant below 20 metres. In spite of this, *Mesidotea* occurred only to a small extent in July—September, and thus belongs to the second group of prey, which was to be found during the time when the sculpin had migrated to shallow water. As mentioned earlier, the *Mesidotea* can be regarded as a basic food component making up 40—50 per cent of the stomach volume during the time of highest fullness values. Owing to the cold spring of 1966 the species was of importance as food for the sculpins in June also, which was not the case in the spring of 1967. The same state of affairs is apparent as regards the *Gammarus* species (*cf. Pontoporeia*). The second isopod, *Idotea baltica*, was absent in the second year, in contrast to the first year. A failure in reproduction owing to disturbance of the development of the *Cladophora* belt in the summer of 1966 (JANSSON 1969) may serve as an explanation.

The *Gammarus* species and the bivalve *Mytilus* are both to be regarded as shallow-water species and thus as belonging to the second group. *Mytilus* are normally not to be found below 20 metres at this locality owing to the bottom substrate, and the two species would be practically absent during the time of highest water temperature, when the sculpin is pressed down below 20 metres. This, however, is not the case as regards the *Mytilus*. A transport of living algae has been shown to occur and the fauna components attached to the algae are washed down into the depths, where the algaemasses form so-called submersed wrack strings (JANSSON, NYQVIST, WESTIN, 1969), which serve as a food reservoir with components of shallower origin.

The second group of basic food items is also made up of several fish species. The most abundant of these is the common goby, which together with

the three-spined stickleback, belongs to the second group and thus is absent as a food during the time of high water temperature. A glance at Fig. 14 will show that fish are to be found in the stomachs during the summer, but the occurrence is rather low, (higher in the first year than in the second) and we now have to deal with mainly pelagic species like smelt, herring, sprat and the bottom-dwelling viviparous blenny. These species, however, are more abundant in the period April—June than in July—September.

The roe consumed by the fourhorn sculpin from December to April have always been determined as species-specific in spite of the males' protection, discussed earlier (WESTIN, 1969). The roe which occurred in June 1967 was probably from herring, which had a spawning area at the place of investigation (Fig. 17).

5. The annual life cycle of the fourhorn sculpin

(1) July—September. The fourhorn sculpin has migrated to the deeper areas below the thermocline. This is the period with fewest empty stomachs and a rather high fullness percentages, which falls towards the end of the period. This is also the period of feeding upon a very limited number of species. The food consists mainly of so-called relicts, and the *Pontoporeia affinis* dominates over the other relicts.

(2) October—December. This period is characterized by the migration by the sculpin towards the shallower zone after the autumn turnover (when a state of homothermia prevails). At this time of the year the cylindrical holes are dug in the soft bottom by the fourhorn sculpins. At the end of the year spawning takes place and the females deposite the roe in the holes. The lowest value for stomach contents and a high percentage of empty stomachs distinguish this time.

(3) January—March. The sculpins mainly remain in the phytal where the males try to protect the roe during the whole period. This, however, seldom succeeds, as a heavy predation on the roe prevails. Thus this is the period of roe consumption. The percentage of empty stomachs decreases and the degree of fullness increases.

(4) April—June. A successive migration towards the depths takes place and the pelagic life of the newly hatched fry begins. The fry often swim in a peculiar upright position, which makes it easy to recognize them.

6. The food habits of inland-water and brackish-water populations of fourhorn sculpin of Palearctic and Nearctic origin

The fourhorn sculpin has a circumpolar distribution and also occurs in lakes both in the Nearctic and the Palearctic in lakes below the highest shoreline, depending on the glaciation. In the Nearctic the fourhorn sculpin is

divided into two species on morphological and ecological basis (MCALLISTER 1959). One species, the deep-water sculpin, *Myoxocephalus thompsonii* (GIRARD) inhabits the lakes, and the other, the fourhorn sculpin, is a coastal species. As regards the Palearctic fourhorn sculpin, it has recently been shown that there is only one species (NYMAN and WESTIN 1968, WESTIN 1968 a). The Palearctic populations in different lakes vary owing to different degrees of reduction in lateral tuberculation and in cephalic armature.

The lake-dwelling populations of Palearctic fourhorn sculpin are known to feed on relict crustaceans (JÄÄSKELÄINEN 1917). In my own investigations in Lake Mälaren from May to mid-October 1965, 90 per cent of the volume of the stomach contents was made up of *Pontoporeia affinis*. The percentage occurrence was as high as 95 per cent of the period of investigation. About 200 specimens were investigated.

From Lake Vättern a few specimens from October 1966 were available. In the stomach contents of these 41 specimens, *Pontoporeia* was practically absent and its place was taken by *Pallasea quadrispinosa* SARS, which occurred in 85 per cent of the fish examined. *Pontoporeia*, which is very abundant in Lake Vättern (GRIMÅS 1969), seems to be of subordinate importance as a prey for fourhorn sculpin in comparison with fourhorn sculpins trapped at the same depth and at the same season in Lake Mälaren. Unfortunately the material from the lakes concerned is very sparse and no conclusions can be drawn regarding a possible preference for the larger crustaceans such as *Pallasea* and *Mesidotea*: or are the larger crustaceans easier for the sculpin to capture than is the mud-dwelling *Pontoporeia*? A hint can be obtained from the occurrence of *Pontoporeia* in the stomachs of fourhorn sculpin from the Baltic. During the spawning of *Pontoporeia* in late autumn, the mature males are more pelagic and develop a very long antenna. During this time the *Pontoporeia* found in the stomachs are mainly males, while females are very rare. From the Baltic it is known that the smelt change in late autumn from preying upon Mysids to preying on males of *Pontoporeia* (SEGERSTRÅLE 1937).

The Palearctic population of fourhorn sculpin in the Baltic has recently been investigated with respect to its food habits (LAMPE, 1969). The results, which are based on the frequency of occurrence, give a good agreement with this investigation where the types of food item are concerned and also as regards the importance of the different food species, but a comparison is difficult to make because data on the time when the water is ice-covered are lacking. The importance of low temperature is, however, pointed out.

From the Nearctic the food of the deep-water sculpin has been little studied. In Lake Nipigon and in Port Credit DYMOND (1926) reported that the food consisted principally of *Pontoporeia affinis*, *Mysis relicta* and chironomid larvae. From coastal waters the food of fourhorn sculpin consists of *Mysis oculata*, *Gammarus locusta*, *Pseudalibratus littoralis* and *Mesidotea entomon*

(JOHANSEN 1912). It is interesting to note that the different populations of fourhorn sculpin both from the Nearctic and the Palearctic seems mainly to feed upon the same items.

7. Factors possible limiting the distribution of fourhorn sculpin in the Baltic

It is impossible to point to any single factor as being responsible for the present distribution of fourhorn sculpin in the Baltic. It is rather a question of an interaction of abiotic and biotic factors.

The main range of the Baltic *Myoxocephalus quadricornis* seems to be confined to areas with a salinity below c. 6 ‰ (PURASJOKI unpubl.). I, however, believe, from my own investigations, that in the Baltic the salinity alone does not act as a limiting factor as regards the distribution.

In some of the deeper basins in the Baltic a lack of oxygen occurs, but the fourhorn sculpin is considered to be a coastal species (SUNDEVALL 1855) and a limiting of the distribution owing to low oxygen values has not so far been reported.

The temperature obviously acts as a limiting factor for the fourhorn sculpin and forces it to migrate to deeper areas.

How the temperature affects the fourhorn sculpin is not known. (There is no doubt that the fish can survive, for instance, the temperature, prevailing at a depth of 10 metres during the period of highest water temperature.) From experiments with immature fourhorn sculpin, which have been hatched and held all their life in the same aquaria, where the temperatures have been the same as those prevailing at a depth of 10 metres, *i.e.* up to 20°C in the summer, a retardation in growth has been detected. The immature fourhorn sculpin (age II+) have from mid-May to mid-August, undergone an increase in length of only 3 per cent while the weight has decreased by 8 per cent. The food supply has throughout been sufficient.

It is obvious that the temperature can act as a limiting factor as regards the vertical distribution and cannot be responsible for the lack of fourhorn sculpin in the southernmost parts of the Baltic, where low temperatures also are to be found below a certain depth. A recapitulation of the seasonal variation in food habits of the fourhorn sculpin tells us, that in the period of shallow-water life a great many different food items are available. A disappearance of one species (*cf. Idotea baltica*) seems not to have any serious effect as several other items have always been available.

During the time of high water temperature and deep-water life the conditions are the opposite. Only a few food items are obtainable and among them one species is dominant. This species is the amphipod *Pontoporeia affinis*, which has been shown to undergo striking fluctuations in abundance in certain parts of the Baltic area (SEGERSTRÅLE 1937). It has not proved

possible to discover the reason for the striking decline in numbers, a decline which, I believe, must be very serious for the fourhorn sculpin during the summer period.

Information of the distribution of *Pontoporeia affinis* in the Baltic area can be obtained in HESSLE (1924) and EKMAN (1918) for the Gulf of Bothnia and the central Baltic, and for the South Baltic in THULIN (1922), DEMEL and MAŃKOWSKI (1951), DEMEL and MULICKI (1954) and in SEGERSTRÅLE (1962). The last mentioned author has made a combination of his own investigations and information from the literature.

The results obtained are that the area in which *P. affinis* is abundant also seems mainly to follow the 6 ‰ isohalin and that the distribution of *P. affinis* and that of *Myoxocephalus quadricornis* are in agreement so far as we know today. *Pontoporeia* are, however, known to occur further south, but not so abundantly, and the same also applies to the fourhorn sculpin. A question that arises in connection with the hypothesis above is, why cannot the fourhorn sculpin prey upon *Pontoporeia femorata*, a species which does not tolerate strong dilution of the water, the limit being about 6 ‰? (SEGERSTRÅLE, 1967). The answer may be, that *P. femorata* never reaches the high abundances typical of *P. affinis* (HESSLE 1924, SEGERSTRÅLE 1962). As I believe that the abundance of *P. affinis* is one reason for the distribution of the fourhorn sculpin, a new question arises: What factors limit the distribution of *P. affinis*?

HESSLE (1924) presumed that a combination of high salinity and low oxygen content were responsible for the distribution, and SEGERSTRÅLE (1962) adds that the scarcity of *Pontoporeia* in the open Baltic, even in areas with adequate oxygen supply, seems mainly to be due to the nature of the bottom substrate. Outside the deeps, which are more or less uninhabitable on account of their poor oxygen supply, the bottom generally consists mainly of coarse mineral components and is thus an unfavourable environment for the crustacean concerned. The adverse effect of this factor is accentuated by the fact that, in the southern Baltic, *P. affinis*, a species which is far more productive than *P. femorata*, is for reasons of salinity restricted to comparatively shallow water. By contrast, areas such as the Åland Sea, with its adjacent archipelagoes, and the Bothnian Sea include wide, well-oxygenated regions of low salinity with a high proportion of fine material in the bottom substrate and thus offer excellent conditions for *P. affinis*. The importance of a bottom substrate which is not composed of coarse mineral components is valid for the fourhorn sculpin in connexion with spawning, when the males dig a hole of cylindrical form (WESTIN 1969), which seems an impossible feat in the above-mentioned substratum. Available information about the spawning localities in the Gulf of Bothnia (JANSSON and NYQVIST, pers. comm.) and from my own experiences from diving operations in the vicinity of the Askö Laboratory (WESTIN 1970) show that a bottom substrate

consisting of coarse mineral products and gravel is avoided by the males. My opinion is thus that it is a combination of several factors which limits the distribution of fourhorn sculpin in the Baltic. The temperature during the time of highest water temperature is responsible for the migration to areas where the occurrence of *Pontoporeia affinis* is a condition of survival, and the abundance of the latter dependent on bottom substrate and salinity.

8. Trophic relationships

From the above-stated facts it is evident that the fourhorn sculpin changes habitat from shallower areas during the period of cold water temperature to deeper areas in time of higher water temperature. It is also evident that the prey fauna is changing at the same time.

The different food items found in the stomachs of fourhorn sculpin throughout the time of investigation can be roughly divided into three categories: carnivores, omnivores, and animals feeding upon detritus and the bacteria and fungi attached to the detritus. It must be said that an exact dividing line between the various food categories seldom exists in practice, and this applies particularly to the omnivores and the detritus feeders, also, the knowledge regarding the food ecology of the mentioned items below is often very scarce.

According to the food ecology, in so far as we know it, the different species have been placed in one of three groups as follows.

Carnivores: all fish and *Mesidotea entomon*.

Omnivores: mysids, *Idotea baltica*, Gammarids.

Detritus feeders: *Halicryptus spinulosus*, *Pontoporeia affinis*, *Mytilus edulis* and *Macoma baltica*.

In Table 3 the eight quarters of the two years are compared, and the values are given in per cent of the volumetric content of the stomachs.

A comparison of the corresponding quarters of the two years gives practically identical values for carnivores above 70 per cent, and about the same value of the two remaining groups during the period January—June: which also is the time of highest food intake. In the next quarter of the years the situation is the opposite. The detritus feeders now dominate as food items and carnivores are not of such high importance as in the first two quarters of the years.

The two years differ to some extent in this period and the same is true of the last quarter of each year, where the carnivores are the largest group, followed by the detritus feeders, which still have comparatively high values.

A comparison of the two years gives the same trend; carnivores are most important as food for the fourhorn sculpin in three out of the four quarters of the years while the detritus feeders dominate during the quarter with high

water temperature. The omnivorous species occurs all the year round to roughly the same extent.

Finally, it can be concluded that the fourhorn sculpin feeds on a high trophic level.

The adult fourhorn sculpin has few predators and, judging from net catches and diving, it occurs in a high density. Together with the fact that the fish reaches a comparatively high age, this leads me to believe that the fourhorn sculpin bind and use up a large amount of energy, but before this can be concluded with any certainty such basic information as the rate of digestion in the prevailing temperature and amount of food necessary to allow normal growth must be made the subject of further investigations.

VII. Acknowledgements

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VIII. Summary

The food habits of the fourhorn sculpin, *Myoxocephalus quadricornis* (L.) were investigated during a period of two years at the same locality, the archipelago off Stockholm. The sculpins were trapped with gill nets once a week in the first year and twice a month in the second year. About 2000 specimens were caught, the sex ratio being 39 per cent males to 61 per cent females, and were investigated as regards the food consumed. Two methods were employed, the volumetric and the occurrence method.

The food can be divided into certain basic units: *Mesidotea entomon*, fish (*Gasterosteus aculeatus*, *Pomatoschistus minutus*) species-specific roe; and because the fourhorn sculpin is a very cold stenothermal species, which has been shown to migrate to deeper areas during the season with the highest water temperature, the basic food items consist mainly of *Pontoporeia affinis* during this time and to a lesser extent *Mysis relicta* and *Mysis mixta*. The mature males of *Pontoporeia* are more pelagic than the females during their spawning time and exceed the females in number in that particular season.

The Molluscs play a subordinate role as a prey but a heavy predation on the species-specific roe was shown to occur.

The different food items are divided in three groups: carnivorous, omnivorous and detritus-feeding species. In three quarters of the year, the fourhorn sculpin feed mainly upon carnivorous species. In the remaining quarter, the period of deep-water life, the food of fourhorn sculpin is dominated by detritus-feeding species. There was, in the main, agreement between the two years of investigation as regards time of occurrence and abundance of the different food species, and the fourhorn sculpin was found to be feeding all the year round.

The methods of capturing and estimating the importance of the various food items, sex ratio, length-weight ratios and abiotic factors are discussed.

The annual life of the fourhorn sculpin can be roughly divided into four seasons which correspond to the quarters of a year, as regards the biology of the species concerned. The distribution of the fourhorn sculpin in the Baltic, which is confined to areas with a salinity below c. 6 ‰, is here tentatively explained, not by the higher salinity southwards, but by a combination of both biotic and abiotic factors, which act as follows. The high water temperature in summer forces the fourhorn sculpin to migrate to deeper areas to a temperature below 9–10°C, where the types of food items are scarce in contrast to the circumstances in shallower areas. The dominating prey during the deep-water time is *Pontoporeia affinis*, and the abundance of this species determines the distribution of the fourhorn sculpin in the Baltic. The distribution and abundance of the two species are roughly in agreement. The limiting factor for the distribution of *Pontoporeia* is the type of bottom substrate, which seems to be of some importance for the fourhorn sculpin too, in connection with spawning.

The food habits of inland-water and brackish-water populations of fourhorn sculpin of Palearctic and Nearctic origin are compared.

IX. References

- DEMEL, K. and W. MAŃKOWSKI. 1951. Quantitative investigations on the bottom fauna in the southern Baltic. *Prace morsk. Inst. ryback. Gdyni*. 6: 57–82. (In Polish, summary in English.)
- and Z. MULICKI. 1954. Quantitative investigations on the biological bottom productivity of the South Baltic. *Prace morsk. Inst. ryback. Gdyni*. 7: 75–126. (In Polish, summary in English.)
- DYMOND, J. R. 1926. The fishes of Lake Nipigon. *Publ. Ont. Fish. Res. Lab.* 27: 1–108.
- EKMAN, S. 1918. Studien über die marinen Relikte der nordeuropäischen Binnengewässer IV. Welche ist die marine Stammform der relikten *Pontoporeia affinis* LINDSTRÖM. *Int. Rev. Hydrobiol.* 8 (4): 321–337.
- EKSTRÖM, C. U. 1831. Fiskarne i Mörkö skärgård. *K. svenska VetenskAcad. handl.* 270–322. (In Swedish.)

- ENGSTRÖM, K. 1963. Cone Types and Cone Arrangements in Teleost Retinae. *Acta Zool. Stockh.* 44: 179—243.
- GRIMÅS, U. 1969. The bottom fauna of Lake Vättern, central Sweden, and some effects of eutrophication. *Rep. Inst. Freshw. Res. Drottningholm* 49: 49—62.
- HESSLE, C. 1924. Bottenboniteringar i inre Östersjön. *Medd. K. Lantbruksstyr.* 250: 1—52. (In Swedish.)
- HYNES, H. B. N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 19 (L); 36—58.
- JANSSON, A.-M. 1969. Introductory production studies in the *Cladophora* belt. *Thalassia Jugosl.* (In print.)
- JANSSON, B.-O., B. NYQVIST and L. WESTIN. 1969. Submersa tångbankar. *Zool. Rev. Stockh.* 31 (1—2): 25—28. (In Swedish.)
- JOHANSEN, F. 1912. The fishes of the Denmark Expedition collected and described. *Medd. Grönland.* 45: 631—675.
- JÄÄSKELÄINEN, V. 1917. Om Fiskarna och Fisket i Ladoga. *Finlands Fiskerier* 4: 1—92. (In Swedish.)
- KIPLING, CHARLOTTE. 1962. The use of scales of the brown trout (*Salmo trutta* L.) for the back-calculation of growth. *J. Cons.* 27: 304—315.
- KLEMETSEN, A. 1968. On the feeding habits of the population of brown trout (*Salmo trutta* L.) in Jölstervann, West Norway, with special reference to the utilization of planktonic crustaceans. *Nytt Mag. Zool.* 15: 50—67.
- LAMPE, S. 1969. Hornsimpans näringsvanor och uppträdande inom en biotop i Tvären. Information från Sötvattenslaboratoriet (5). 20 pp. (Mimeographed in Swedish.)
- LÖNNBERG, E. 1900. Några bidrag till kännedomen om hornsimpan. *Svensk Fisk. Tidskr.* 9 (1): 36—38. (In Swedish.)
- MCALLISTER, D. E. 1959. The Origin and Status of the Deepwater Sculpin, *Myoxocephalus thompsonii*, a Nearctic Glacial Relict. *Nat. Mus. Canada, Bull.* 172: 44—65.
- NYMAN, L. and L. WESTIN. 1968. On the Problem of Sibling Species and Possible Intra-specific Variation in Fourhorn Sculpin, *Myoxocephalus quadricornis* (L.). *Rep. Inst. Freshw. Res. Drottningholm* 48: 57—66.
- SCHOLANDER, P. F., W. FLAGG, V. WALTERS and L. IRVING. 1953. Climatic Adaption in Arctic and Tropical Poikilotherms. *Physiol. Zoöl.* 26: 67—92.
- SEGERSTRÅLE, S. G. 1937. Studien über die Bodentierwelt in südfinnländischen Küstengewässern. V. Das reife *Pontoporeia affinis*-Männchen als Saisonnahrung für den Stint (*Osmerus eperlanus* L.). *Comment. Biol. Helsinki.* 7 (3): 1—17.
- 1957. On the immigration of the glacial relicts of northern Europe, with remarks on their prehistory. *Comment. Biol. Helsinki.* 16 (16): 1—117.
- 1960. Fluctuations in the abundance of benthic animals in the Baltic area. *Comment. Biol. Helsinki.* 23 (9): 1—19.
- 1962. Investigations on Baltic populations of the bivalve *Macoma baltica* (L.). *Comment. Biol. Helsinki.* 24 (7): 1—26.
- 1967. Observations of summer-breeding in populations of the glacial relict *Pontoporeia affinis* LINDSTRÖM (*Crustacea Amphipoda*), living at greater depths in the Baltic Sea, with notes on the reproduction of *P. femorata* KRÖYER. *J. exp. mar. Biol. Ecol.* 1: 55—64.
- SUNDEVALL, C. J. 1855. Berättelse om Fiskeriet i Stockholms Läns Skärgård. *K. Hushållsällsk. Handl.* 141—214. (In Swedish.)
- THULIN, G. 1922. Bottenboniteringar i södra Östersjön i samband med fisktrålningar. *Sv. Hydrogr.-biol. Komm. Skr.* VII: 1—9.

- WESTIN, L. 1968 a. Environmentally determined variation in the roe colour in the fourhorn sculpin *Myoxocephalus quadricornis* (L.). *Oikos* 19: 403—407.
- 1968 b. Lethal Limits of Temperature for Fourhorn Sculpin, *Myoxocephalus quadricornis* (L.). *Rep. Inst. Freshw. Res. Drottningholm* 48: 71—76.
- 1969. The Mode of Fertilization, Parental Behaviour and Time of Egg Development in Fourhorn Sculpin, *Myoxocephalus quadricornis* (L.). *Rep. Inst. Freshw. Res. Drottningholm*. 49: 175—182.
- 1970. Observations on the nest digging of fourhorn sculpin, *Myoxocephalus quadricornis* (L.) *Rep. Inst. Freshw. Res. Drottningholm*. 50: 211—214.

Observations on the nest digging of fourhorn sculpin *Myoxocephalus quadricornis* (L.).

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The parental behaviour of several members of the family *Cottidae* is well developed and has been described.

From investigations of the reproductive behaviour of *Cottus gobio* L. and *Cottus poecilopus* HECKEL, we know that the male digs a hole underneath some solid object resting on the bottom and that the adhesive eggs are usually stuck to the inside wall of the cavity and protected by the male (MORRIS 1954, STARMACH 1962).

In *Myoxocephalus scorpius* (L.) the adhesive eggs are not hidden and no hole is dug. The eggs are stuck to a rock, to algae or put in a crevice where the male protects them.

In *Myoxocephalus quadricornis* GISLER described as early as 1748 the round hole dug by the fish and noted that the sculpin when irritated only swam in a circle and then placed its body above the egg mass again, giving its life if necessary. His observation has been confirmed recently (WESTIN, 1969).

After the turnover in the autumn, which normally occurs in October, the fourhorn sculpin has possibilities, owing to its cold stenothermicity (WESTIN, 1968), of migrating to shallower areas. From observations in connexion with scuba diving, it seems as if the fourhorn sculpin male has a territory of its own already in early November, because the females escape while the males stay in an aggressive manner when confronted by a diver (JANSSON and NYQVIST, pers. comm.).

In diving operations during the spawning period 1969—70 in the vicinity of the Askö Laboratory, some protecting males were found at a locality where the soft bottom was partly free from algae of littoral origin and was partly covered with the so-called submersed wrack string described earlier by JANSSON, NYQVIST and WESTIN (1969). The depth at this particular locality was 15—20 metres.

The male fourhorn sculpins with their nests could be found either in the algae masses or on the soft bottom free from algae. I never observed a male with a nest on a hard bottom or among stones and rocks. There is, however, a great difference between the nests among the algae and those on the clean soft bottom. The former is made by merely pushing aside the loose algae,

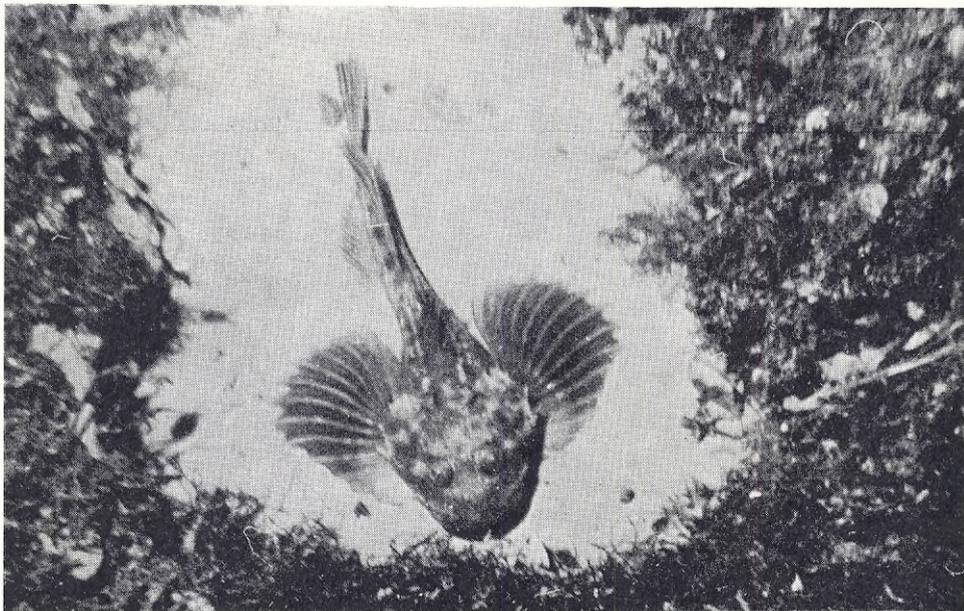


Fig. 1. A fourhorn sculpin male defending his hole in a submersed wrack string at a depth of 17 metres before spawning. December 27, 1969.

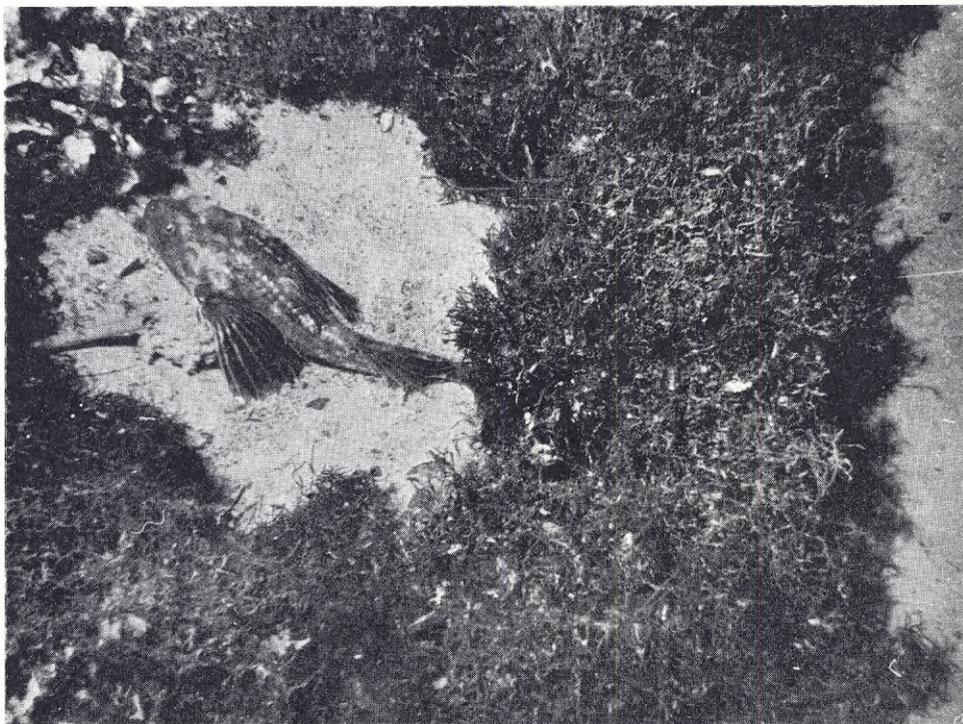


Fig. 2. A fourhorn sculpin male protecting the egg mass. The hole has been dug in a submersed wrack string at a depth of 18 metres. December 27, 1969.



Fig. 3. A hole situated on a soft bottom free from algae at a depth of 15 metres with the fourhorn sculpin male protecting the eggs. Note the wall around the hole. January 18, 1970.

and the mineral components remain intact (Fig. 2). The latter type (Fig. 3) is a remarkably large hole, which presumably takes a very long time to complete.

It seems as if the stimuli to dig disappear as soon as the wall which surrounds the male as a result of the digging has reached a certain height, irrespective of the time taken to finish the digging.

The fourhorn sculpin male in Fig. 2 was visited again three weeks later. He was still in his hole, but the roe which he had protected had been stolen.

The parental cycle of fourhorn sculpin, if undisturbed, is very long, lasting for approximately three months, owing to the low water temperature during the time of egg development (WESTIN, 1969).

References

- GISLER, N. 1748. Strömmingsfisket i April, Maj, Junius. *K. Svenska VetenskAcad. Handl.* 9: 115. (In Swedish.)
- JANSSON, B.-O., B. NYQVIST and L. WESTIN. 1969. Submersa tångbankar *Zool. Rev. Stockh.* 31(1—2): 25—28. (In Swedish.)

- MORRIS, D. 1954. The reproductive behaviour of the river bullhead (*Cottus gobio* L.), with special reference to the fanning activity. *Behaviour* 7: 1—30.
- STARMACH, J. 1962. Koppen in den Karpathenflüssen. I. Vermehrung, embryonale und larvale Entwicklung bei *Cottus poecilopus* Heckel. *Hydrobiologia* 4(3—4): 321—343.
- WESTIN, L. 1968. Lethal Limits of Temperature for Fourhorn Sculpin, *Myoxocephalus quadricornis* (L.) *Rep. Inst. Freshw. Res. Drottningholm* 48: 71—76.
- WESTIN, L. 1969. The Mode of Fertilization, Parental Behaviour and Time of Egg Development in Fourhorn Sculpin, *Myoxocephalus quadricornis* (L.). *Rep. Inst. Freshw. Res. Drottningholm* 49: 175—182.

Reports from the Institute of Freshwater Research, Drottningholm

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19. *Arne Lindroth*. Undersökningar över befruktnings- och utvecklingsförhållanden hos lax (*Salmo salar*). Deutsche Zusammenfassung. 1942. Pris kr. 0: 75.
- *20. *Lars Brundin*. Zur Limnologie jämtländischer Seen. 1942. Pris kr. 2: —.
- *21. *Gunnar Svärdson*. Studien über den Zusammenhang zwischen Geschlechtsreife und Wachstum bei Lebistes. 1943. Pris kr. 1: —.
- *22. *Gunnar Alm*. Befruktningsförsök med laxungar samt laxens biologi före utvandringen. (Fertilization-Experiments with Salmon-parr.) English summary. 1943. Pris kr. 1: 50.

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31. Annual Report for the Year 1949 and Short Papers. 1950. Pris kr. 3: 50.
32. Annual Report for the Year 1950 and Short Papers. 1951. Pris kr. 4: 50.
33. Annual Report for the Year 1951 and Short Papers. 1952. Pris kr. 8:—.
34. Annual Report for the Year 1952 and Short Papers. 1953. Pris kr. 8:—.
35. Annual Report for the Year 1953 and Short Papers. 1954. Pris kr. 8:—.
36. Annual Report for the Year 1954 and Short Papers. 1955. Pris kr. 8:—.
37. Report from the Institute of Freshwater Research, Drottningholm. 1956. Pris kr. 8:—.
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