FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 52

LUND 1972
CARL BLOMS BOKTRYCKERI A.-B.

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Contents

Age determination and year-class fluctuations of cisco, *Coregonus albula* L., in the Mjøsa hydroelectric reservoir, Norway

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I. Introduction

Age determination of vendace or the European cisco, *Coregonus albula* L., has been regarded as easy and has so far caused few problems. Nor have the North American *C. artedii* LESEUR, which may be conspecific (WALTERS 1955), offered any problems in this respect. The cisco is apparently caught very young and in most cases one distinct year class predominates in the catch. The main cisco fisheries take place in autumn, and it is generally supposed that fish on their first spawning migration constitute the bulk of the catches.

For the age determination, only scales have been used. Much work has been devoted to their interpretation, in Europe above all by JÄRVI (1920), WILLER (1922) and BAUCH (1949) and in North America by VAN OOSTEN (1929) and HILE (1936). The scales are apparently easy to read, checks and dense edges occur only in a limited number of fish. The results have rarely been questioned, although some authors admit that older slow-growing individuals present problems. Some investigators, *e.g.* HILE (*op. cit.*), discard the scales, which are supposed to be unsatisfactory for determination of age, and others, e.g. JÄRVI (1942 a), realize that errors may occur after a certain age. The uniform low age found throughout the distribution area of the cisco has been explained by its being a short-lived species. By following an introduction of cisco, SVÄRDSON (1949), however, concluded that individuals may be older than was generally supposed. Later the same author pointed to the fact that in some cases ciscoes may stop growing years before they die, with the inevitable result that the scales show a lower age than the actual one. The difficulties arise when the fish reaches an age of 5—6 years (SVÄRDSON 1964).

The deceptively easy use of scales may be the reason why otoliths and other organs have not been resorted to for age determinations. True, SELIGO (1908) reported that otoliths could show the age of ciscoes, but he was of opinion that their striped structure prevented a rapid and reliable determination. He also referred to the use of operculars, but he himself only used scales for routine investigations. Since then, only WAGLER (1941) has mentioned otoliths, but he merely states that the use of otoliths is of no advantage in Coregonids.

In order to investigate the effects of the impoundment of Lake Mjøsa on the recruitment to the cisco fisheries, a correct age determination was essential. The results of scale readings were, however, not confirmed by tagging experiments and length measurements, and subsequently otoliths were used for age determination. The preliminary results were briefly described by AASS (1971).

II. Materials and Methods

Lake Mjøsa is situated in the south-eastern part of Norway (Fig. 1). It is the biggest lake in the country, covering an area of 365 sq. km. The normal height above sea level is 122 metres, and the average and maximum depths are 153 and 449 metres respectively. Impoundments were implemented in 1858, 1912, 1940 and 1965 and the regulation height is now 3.61 metres. The reservoir is lowered during winter and filled in spring and summer. Numerous lakes in the catchment area have also been converted into reservoirs. The arctic mountains of Jotunheimen constitute a considerable part of the catchment area and during the thaw the main tributary, the River Gudbrandsdalslågen, carries large quantities of glacier silt. Consequently the northern part of the lake is clouded by the suspended solids in summer.

The spawning of the cisco takes place in the middle of October in the lower reaches of the River Gudbrandsdalslågen, where the river bed consists of stone and coarse gravel. A total of 544 spawners investigated in the autumns of 1967 and 1968 had a gillraker variation of 34—50, with a mean of 43.4. A few attain a length of 25—26 cm, though HUITFELDT-KAAS (1917) reports two specimens measuring 31 and 33 cm respectively. The estimated yearly catch in the period 1965—71 varied between 80 and 165 metric tons. The fishing starts in mid-summer, but the bulk is caught during the spawning run. Nowadays the biggest catches are made in the northern part of the lake, but the fishing continues in the river as the fish ascend. In running water the cisco is caught by three different kinds of landing nets, drifting nets and seines, in the lake almost entirely by the last-mentioned gear. The seines retain all fish bigger than 12—13 centimetres, *i.e.* all mature fish.

Fig. 1. The northern end of Lake Mjøsa and the lower reaches of the River Gudbrandsdalslågen. The damming effect on the river by the last three impoundments of the lake is indicated by the numbers 1, 2 and 3.

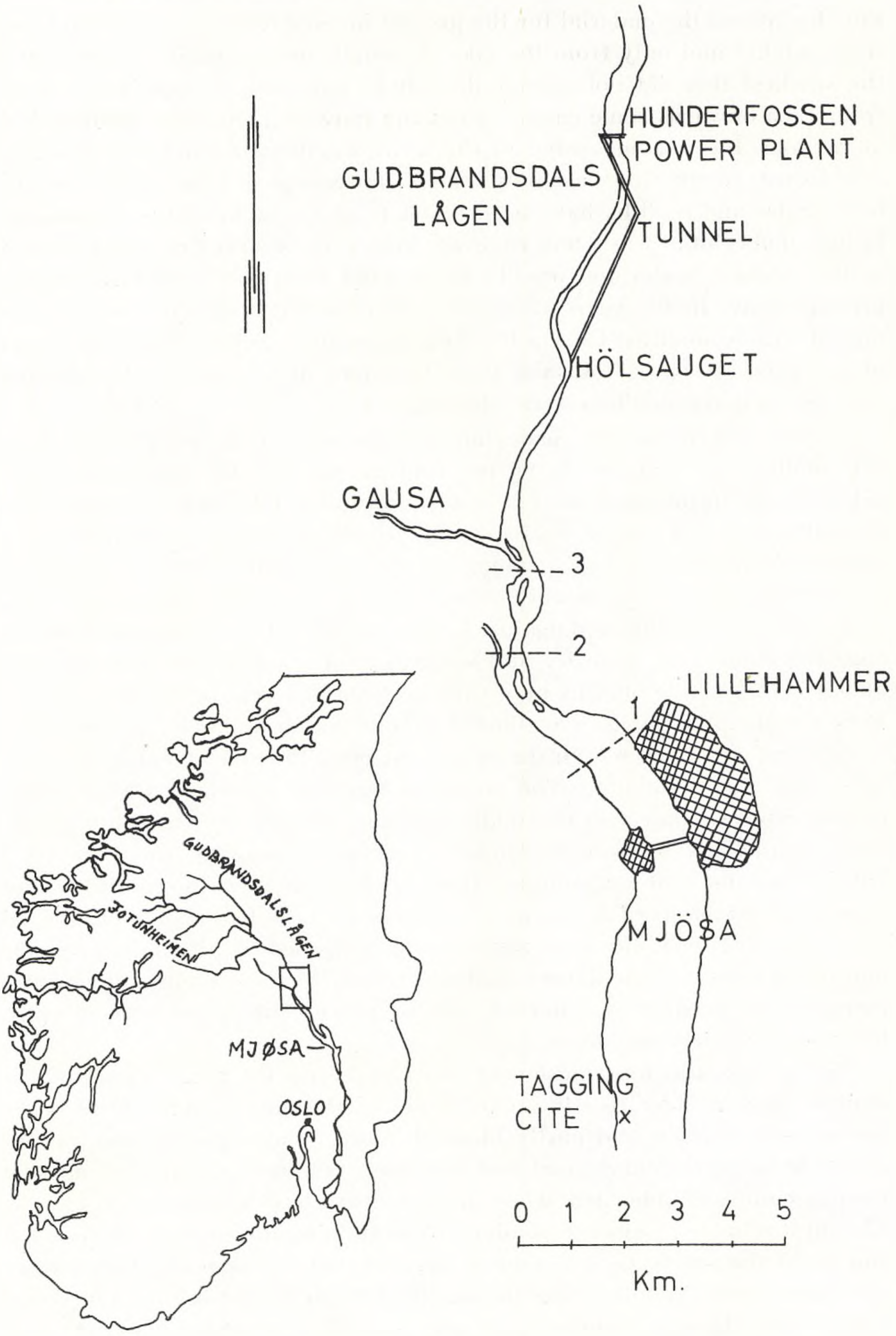
HUNDERFOSSEN
POWER PLANT
GUDBRANDSDALS
LÅGEN
TUNNEL
HÖLSAUGET
GAUSA
3
2
1
LILLEHAMMER
MJÖSA
TAGGING
CITE
x
0 1 2 3 4 5
Km.
GUDBRANDSDALSLÅGEN
JOTUNHEIMEN
MJØSA
OSLO

Fig. 1.

For this reason the material for the present investigation was collected from seine catches and only from the lake, as length measurements showed that the smallest fish did not ascend the whole spawning stretch. Every year from 1965 onwards some catches from the spawning run have been picked at random, the fish measured to the nearest centimetre and the sex ratio established. In the first year only scales were sampled, from 1966 onwards both scales and otoliths have been taken from the same fishes, if possible to the number of at least 30 of each sex from every centimetre group present in the catches. Scales and otoliths from 2,061 fish were examined for the present study. In the years 1966—69 a total of 2,122 mature ciscoes were tagged with a modified CARLIN tag without an intermediate link. The scales of the cisco are easily lost, and great care had to be taken to ensure that only fish in good condition were released.

For age determinations, scale impressions were made on plastic strips. The otoliths were cleared in 96 per cent alcohol for 18—24 hours before being moved to propandiol- (1.2), refraction index 1.43, and examined at a magnification of 40 or 64 ×. In young fish the otoliths are opaque with a number of hyaline zones depending on the age. Older fish, in the present material mostly four years old or more, acquire a narrow, thin edge which looks bluish when observed against a dark backgrund. The formation of this edge coincides with maturity and stagnation of growth. The transparency and structure of the otoliths may vary between different year classes. Some have otoliths of a rough crystalline structure, which makes them very hard to interpret. But even within the same year class the appearence of the otoliths may alter with time. The young or old fish may have otoliths with diffuse centres, while fish of middle age may have easily readable otoliths. The contrast between summer and winter zones may be small in thick whitish otoliths with a crystalline structure. In such cases the central winter zones are best observed as distinct grooves. Some otoliths may have a striped structure altogether, the year zones being composed of alternating opaque and hyaline zones, sometimes called split rings. In these otoliths the winter increment is finished by a narrow, black groove. The majority of otoliths, however, are fairly easy to read.

The nucleus and innermost year zones make up the greater part of the otoliths, and in older fish the outer zones of the dorsal and ventral edges are pressed together and partly blended. More reliable results may be obtained by using the curved end, but here there is alvays a chance of missing the outer zones of older fish, while the inner ones have a tendency to ramify. The most reliable results are obtained by examining the zones at the pointed end or in the notch, *i.e.* the excisur between the rostrum and antirostrum (SCHMIDT 1968). At both places the otoliths tend to project into a transparent brim where the outer winter zones are very close together. They are seen as hair-thin, black stripes in a bluish basic material if reflected light is used.

Table 1. Estimated age composition in per cent of the cisco spawning population in Lake Mjøsa based on scale readings.

Year	1+	2+	3+	4+	5+	6+	7+
1966	—	3.3	85.6	6.9	3.6	0.4	0.2
1967	1.8	5.4	77.8	8.6	6.4	—	—
1968	0.3	79.5	12.6	6.7	0.9	—	—
1969	1.4	2.0	75.0	20.5	0.7	0.4	—
1970	7.6	5.9	68.9	16.7	0.9	—	—
1971	0.1	23.8	44.1	29.5	2.5	—	—

In difficult cases, when no part of the intact otolith gives a clear impression of the number of zones, cross sections through the centre may be helpful. Grinding the cross-section surface is of little use, as is also polishing the lateral surface to make the centre more transparent.

III. Results and Discussion

Age determination

The scales of the ciscoes of Lake Mjøsa are apparently easy to read, being very clear and without any checks or visible dense edges. After reading, the age determinations were used to estimate the age composition of the spawning run, the length frequency and sex ratio being taken into consideration. The results are presented in Table 1. According to the scale readings, the catches in most years consist mainly of one age group, which constitutes between 69 and 85 per cent of the total catch. This main age group is either 2+ or 3+, and only once during the observation period did the same year class predominate in two consecutive years. The year 1971 forms an exception in that the predominant age group, 3+, constitutes only 44 per cent of the fish taken, which apparently are more evenly divided among several year classes than usual. The age groups 1+ to 7+ are represented in the total material, but not all of them every year. The oldest fish occur very rarely, and obviously it is difficult to observe more than five winter rings in the scales of the Lake Mjøsa cisco. To a certain extent this is consistent with the results of Huitfeldt-Kaas (1927), who determined the age composition on four occasions in the period 1908—22. Each time he found that the 2+ year old fish predominated in the catches, constituting 74—84 per cent of the spawning run; then followed the 3+ year old. If the scale readings are correct, the mortality in connection with the first spawning must be very high, and Huitfeldt-Kaas (1917) ascribes this to the effect of overfishing.

But if compared with length distributions and tagging results, the conclusions based on scale readings may be questioned. Of the 2,122 ciscoes

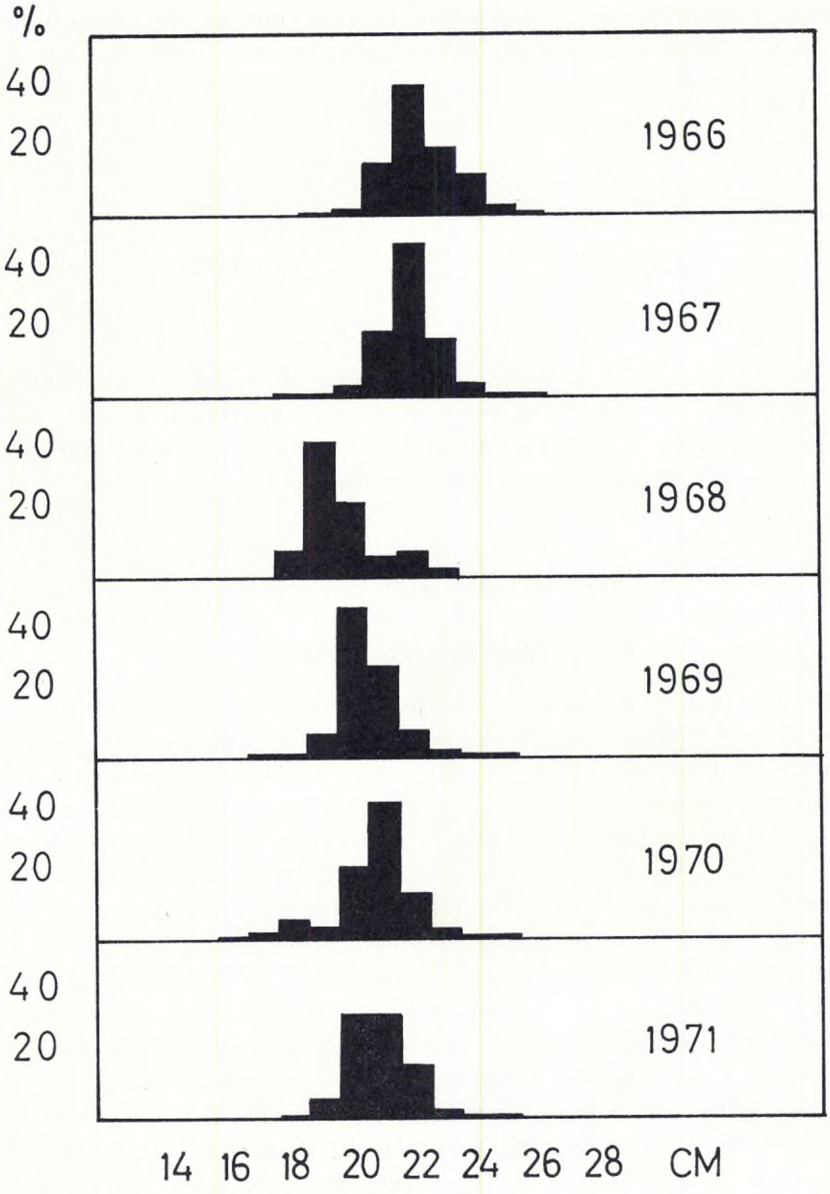

Fig. 2. Length distribution of cisco caught in Lake Mjøsa during the spawning seasons 1966—71.

tagged during the last phase of the spawning run in the period 1966—69, 300 were reported recaptured during the same run. Of the remaining 1,822, recaptures in the three years following tagging were reported to be 133, 25 and 5. If the difficulties in tagging ciscoes and in recovering tags are

Table 2. Estimated age composition in per cent of the cisco spawning population in Lake Mjøsa based on otolith readings.

Year	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+
1966	—	—	70.6	—	—	24.4	—	—	5.0	—	—	—
1967	—	1.5	—	66.6	—	—	29.6	—	—	2.3	—	—
1968	—	69.1	—	0.2	24.6	—	—	5.5	—	—	0.6	—
1969	—	—	66.1	—	—	33.5	—	—	0.2	—	—	0.2
1970	8.2	0.1	—	63.4	—	—	27.0	—	—	1.0	—	—
1971	—	19.1	0.9	0.9	56.9	—	—	21.8	—	—	0.4	—

considered, the rates of mortality of mature ciscoes are obviously not so great as supposed. The length increment between tagging and recapture is negligible; only a very few are reported to have grown between 1/2 and 2 centimetres. But this might be due to inaccurate measuring after recapture. The length distributions of randomly picked catches during the spawning run in the years 1966—71 are shown in Fig. 2. They confirm the impression given by tagging and recapture, namely that ciscoes grow little if at all after maturing. But they also show that in some years, *e.g.* 1968, small cisco occur in greater numbers than usual. In the following three years the peak of the histogram moves about one centimetre a year. Both observations lead to the conclusion that the life span of the Lake Mjøsa cisco is longer than has previously been assumed and that one year class may bear the weight of fishing for several years. If so, the scale readings cannot be reliable.

Age determination of the same material was then carried out by means of otoliths, and the age composition of the spawning runs estimated anew (Table 2). A comparison of the two sets of results is made in Fig. 3. The figure shows that the two methods of ageing give totally different age compositions. Disagreements between the readings occur at all age levels, but both sets record the entrance of a new predominant year class at an age of 2+. There is also a fairly good agreement for fish 3+ years old. Beyond otolith age 3+, there is little agreement and the agreement gets progressively poorer as otolith age increases. The scale ages are mostly lower than the otolith ages and the difference is in some cases as great as seven years. Only very rarely do the scale readings give a higher age than do the otoliths.

According to the otolith readings, the cisco matures at an age of 2+—3+ and a year class contributes considerabely to the fishery for five to six years. Some specimens may live to an age of 12+. The recruitment to the fishery seems to be very uneven; in the observation period predominant year classes come into existence only every third year, *viz.* 1957, 1960, 1963, 1966 and 1969. The contributions to the mature stock of the two intervening year classes are quite insignificant, and together they never amount to two per cent of the catch. The disappearance of whole age groups has also been demonstrated by Järvi (1942 a), who found that eight out of 32 year classes were missing in the catches from Lake Pyhäjärvi.

It seems clear that, owing to growth stagnation, scales are not usable for age determinations of the older ciscoes of Mjøsa. But as otoliths of ciscoes of known age are not available, the reliability of otolith readings can be proved only indirectly. The age composition of six consecutive spawning runs must be the strongest proof of the correctness of the age determination. The predominant year classes show a continued abundance during many years, and for every spawning run they become a year older (Fig. 3). The scarcity of the intervening year classes makes this very evident. The length distributions also support the otolith readings, provided that the sampling covers the period between two predominant year classes. After the occurrence of the year classes 1963 and 1966 it is possible to follow the peaks in the length-frequency histogram moving along the length scale, and this suggests that the mean age of the stock is increasing. When a new predominant year class enters the catches, this is evident both in scale and otolith readings and two peaks become apparent in the length-frequency histogram. This is especially so if the males are treated separately, because a greater proportion of the males mature at ages 1+ and 2+ than do the females. But even if the length distribution registers the occurrence of a new year class and its ageing, it does not show how many year classes a spawning run includes. The histograms in Fig. 2 are all composed of 3—4 year classes, which may differ in age by as much as nine years.

If the rate of mortality after the age of 3+ had been as high as is indicated by scale readings, the yearly catch would have been almost entirely dependent on one year class. As the recruitment may be affected by a number of factors, such a dependence could easily lead to rather violent fluctuations in the quantities caught. But except for 1967 the fluctuations are in fact rather small for a pelagic fish. The total catches of ciscoes for the years 1965—71 are conservatively estimated at 125—165—80—155—165—115—150 metric tons. The relatively small variations must to a large extent be due to the fact that several year classes take part in a spawning run.

Apparently, the Lake Mjøsa cisco ages can be determined more accurately from otoliths than from scales. This leads both to a higher mean age at capture and maximum age than has hitherto been supposed. Up to now it has been assumed that the age groups 2+ and 3+ make up the great majority of the catch, and the oldest cisco reported from Mjøsa was of the age 9+ (Huitfeldt-Kaas 1927 and 1932). Roughly, these figures agree with the results obtained from scale readings on the present material. Probably it is the ageing technique and not changes in age composition that causes the differene between the present and earlier investigations.

The results presented in the present study also differ from other investigations in Western Europe. German authors (Willer 1922 and 1929, Bauch

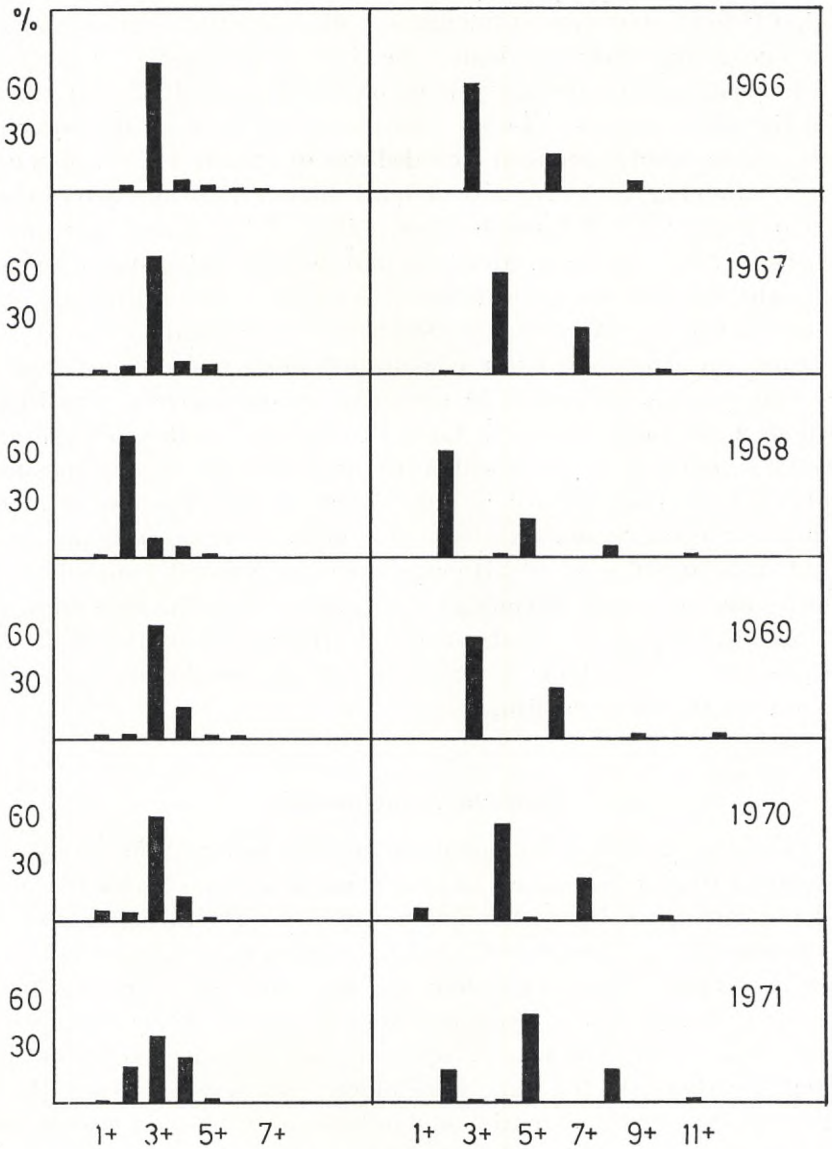

Fig. 3. Age composition of the spawning run of cisco from scale readings (left) and otolith readings (right), Lake Mjøsa 1966—71.

1949) state that the age groups 1+ to 3+ dominate the catches, and the oldest cisco reported from Germany was of the age 7+ (SELIGO 1908). In the former provinces of Prussia, age at capture used mostly to be 2+ and 3+, but exceptions occurred. In Jeziore Muchal the age groups 1+ and 2+ alternated in dominating the catch. Out of 3,257 age determinations the oldest fishes found were of the age 5+ (**Bauch** 1949). In Lake Nariensee the 1+ age group totally dominated the fishery and only 1—3 per cent of the fish taken were of the age 3+ or older (**Willer** 1922 and 1929). In Poland the age groups 1+ to 3+ constitutes the bulk of the commercial catches, and the oldest specimen recorded was of the age 8+ (**Leopold** *et al.* 1970). In summing up the results of more than 14,000 age determinations from a large number of Finnish lakes, **Järvi** (1950) stated that one- and two-year-old fish constituted about 33 and 50 per cent respectively of the cisco caught. Old fish are consequently scarce, the oldest identified specimen being of the age 7+. According to **Svärdson** (1966) three-year-old ciscoes predominate in Swedish catches, constituting more than 40 per cent. Next comes four-year-old fish with 26 per cent. In the material, consisting of more than 2,100 specimens from lakes throughout Sweden, all age groups between 0+ and 9+ are represented. By analysing the age composition of the catches from Lambarfjärden, Lake Mälaren, after the rise of a predominating year class, **Svärdson** (1956) was able to demonstrate an accumulation of scale ages 6+ to 8+. He suggested that a great proportion of old specimens were assigned to younger year classes than the true ones. Probably, this also applies to similar cases. Furthermore, in the light of the experience from Mjøsa, there is reason to believe that the inaccuracy could be reduced by the use of otoliths.

Year-class fluctuations

The changing yield and individual size usually met with in cisco fisheries have been ascribed to variations in year class strength. Though the fluctuations have been the subject of much research, no general agreement exists as to the reasons for their rise. According to **Huitfeldt-Kaas** (1917), variations in the Lake Mjøsa population are the effect of overfishing, which reduces the chances of an even recruitment. **Järvi** (1942 a and b) also discussed this factor, but was of opinion that climatic conditions during hatching and the early fry stage were more important. He especially drew attention to the supposed detrimental effects of wind and waves on the young fry. But a correlation between wind force and year-class strength may be difficult to establish, as pointed out for Lake Mälaren by **Svärdson** (1956). The positive relation between high spring and summer temperatures and strong year classes, repeatedly demonstrated in whitefish (*Coregonus sp.*) (**Svärdson** and **Molin** 1968), has never been proved for cisco. The importance of intraspecific predation was stressed by **Nordquist** (1944), who put forward the hypothesis that the individuals of rich year classes eat their own progeny, with the result that subsequent year classes become weak. This may apply to predatory species, *e.g.* perch (**Alm** 1952), but hardly to the planktivorous cisco. The research into the food of this species undertaken by many investigators, including HUITFELDT-KAAS (1917), AIRAKSINEN (1967) and VALLIN (1969), does not support the theory. The rise of strong year classes in cisco has not yet been convincingly explained.

The present investigation was prompted by the need to know whether the changed hydrological conditions in the Gudbrandsdalslågen River had any consequences for the recruitment. As mentioned, the cisco spawn in the lower reaches of the river, just above Mjøsa. Originally the stretch was about 9 kilometres long, but it has been divided in half by the impoundment of Lake Mjøsa, the last having been carried out in the summer of 1965. The reduction in area is still greater (Fig. 1). To regulate the discharge of the Gudbrandsdalslågen River, numerous lakes in the mountain catchment area were converted into reservoirs between 1921 and 1965. The effect has been a levelling of the water flow, reducing the spring flood and doubling or trebling the late autumn and winter discharge. In 1960 work started on the Hunderfossen dam and power plant situated on the Gudbrandsdalslågen River about four kilometres above the upper spawning places of the cisco. The tail water from the turbines empties through a tunnel at Hølsauget, just at the head of the spawning stretch. The plant was put into operation i July 1963, but the management causes no further regulation of the discharge below the tunnel. Minor fluctuations and short stops have, however, occured most winters except for 1967 and 1971, owing to the plant being idle. The most serious event occurred in the winter of 1964 when almost the whole river bed was laid dry for about 24 hours. To increase the height of fall on the turbines, the river bed just below the tunnel outlet was canalized in the winters of 1961/62 and 1962/63. This led to heavy and prolonged turbidity of the water.

In spite of a steady increase in the rate of regulation and more violent interference with natural conditions during the last ten years, three predominant year classes have been born in this period. Nor has the year-class cycle been disturbed. The 1963 year class was born after a part of the spawning area had been destroyed and the rest silted up for months. The 1966 year class was born after a severe reduction of the river area in the preceding autumn and this adverse factor also affected the 1969 year class. The strength of the 1966 year class can hardly be attributed to the 1965 impoundment of Lake Mjøsa which raised the level by 75 centimetres, and the 1969 year class certainly cannot. As the new, regulated water level did not exceed the former maximum flood level, the positive effect must have been insignificant; nor is it discernible in the growth rate.

The persistent regularity in the recruitment shows the cisco of Lake Mjøsa to be rather tolerant towards the man-made environmental changes. The reasons for this may be several. The regulation of the discharge has only shortened, not abolished, the spring flood peaks, and there is no shortage of water during spawning and hatching. The greater and more constant winter discharge may protect the ova in shallow water against draining and frost, thus reducing the effect of the loss of spawning area in the lower reaches. Furthermore, the tendency of the spawners to concentrate on the upper part of the accessible stretch may also contribute to the fact that reproduction is less influenced than the shortening of the river would indicate. The brief lowerings of the water level and partial draining of the river bed, which have occurred in several winters, obviously have little effect on the development of the ova, and this also applies to the silting. The unfavourable conditions have occured while the ova are in the hardy eyed stage. Crowding after hatching in spring is of little importance, as the fry do not feed while in running water. The river is only the hatching place and the fry leaves it after the yolk sac is exhausted. Impoundments and regulations may of course render recruitment impossible, but then the changes ought to be more radical than has hitherto been assumed.

But even if the periodicity in recruitment is unaltered, the year-class strength may be affected. A predominant year class is outstanding by contrast with weaker year classes, not necessarily by virtue of its own strength. Only the trend in yield during a long period can tell us wether the population density is influenced. No catch estimates from the years just prior to the last hydrological changes exist, but compared with the yield 60 years ago, the trend is not declining. HUITFELDT-KAAS (1917) estimated the average yearly catch at about 71 metric tons, or about half the present yield. This is not due to increased exploitation as a result of greater fishing efforts in recent years or more efficient gear. Apart from small changes, the same kinds of seines and nets have been in use for a long time. The impoundments have also drowned many of the better seining grounds, and traps adapted to the old conditions in the river have disappeared. Even if the changes have interferred with the spawning and later development of the ova, other factors must have counteracted their effect on the recruitment. The most probable explanation is the increased eutrophication and productivity of Lake Mjøsa (HOLTAN 1971). But the impoundments may also have changed the balance between whitefish and cisco to the advantage of the latter. The young whitefish of Lake Mjøsa exploits the planktonic crustaceans, competing with all age groups of cisco, but the adult changes to a large extent to bottom food (HUITFELDT-KAAS 1917). The littoral, now partly a barren and stony zone, can only support a reduced number. The yield of whitefish has decreased during a long period, and the total yearly catch is estimated to be only from a third to a half of the pre-impoundment quantity (HUITFELDT-KAAS *op. cit.*).

The year-class fluctuations are probably not due to man-made factors, and their striking regularity also ought to rule out physical environmental factors. But in the period 1957—69 the rise of strong year classes mostly

Table 3. Monthly mean air temperatures in degrees Centigrade at Lillehammer May—August 1957—69. After The Norwegian Meteorological Institute.

Year	May	June	July	August
1957	7.9	11.7	15.2	12.7
1958	6.8	13.1	14.6	13.3
1959	9.6	13.7	16.4	15.2
1960	10.3	14.9	13.6	13.3
1961	8.8	14.1	14.2	12.0
1962	6.5	11.6	13.3	11.2
1963	9.2	14.5	14.2	13.6
1964	9.6	11.7	12.7	12.5
1965	7.1	12.7	12.8	12.2
1966	7.1	15.3	15.1	12.6
1967	7.0	12.3	14.2	13.7
1968	6.9	14.6	14.5	14.4
1969	8.4	15.9	15.0	16.4

coincides with summer temperatures above normal. The summer mean air temperatures from Lillehammer, just where the River Gudbrandsdalslågen enters Lake Mjøsa, are listed in Table 3. They show that four of the five predominant year classes were born in summers with high temperature sums. The correlation with warm Junes is especially good. This fits in well with the observations of the local fishermen that the fry leave the river for the lake in late May or early June. The observation period, however, is short, and the correlation may be quite accidental, nor is it complete. No year classes emerged in 1959 or 1968, although the temperatures were above average. On the other hand, in the cold summer of 1957 a strong year class appeared.

The possibility also exists that the development of the rich year classes is dependent on a factor correlated with high temperatures. There is a tendency of the year classes to emerge in years with early spring floods. The May discharges were especially great in the years 1957, 1959, 1960, 1963, 1966 and, compared with the rest of the year, also in 1969. (Fig. 4). Apart from 1959 these years coincide with the rise of the predominant year classes. It is impossible to determine whether floods are of any importance for the development of year classes, or whether temperature must be regarded as the factor primarily responsible for the coincidence.

To establish whether climate really is the major factor in dimensioning recruitment, a long-term series of cisco is needed. Such series do not exist in Norway, but they do in Finland (JÄRVI 1942 a and b, 1947) and Sweden (SVÄRDSON 1956 and unpubl.). In these studies age determinations were based on scales, but the method is reliable in establishing the birth year of a strong year class. JÄRVI studied the population density in Pyhäjärvi and Keitele for 32 and 33 years respectively, but paid most attention to the

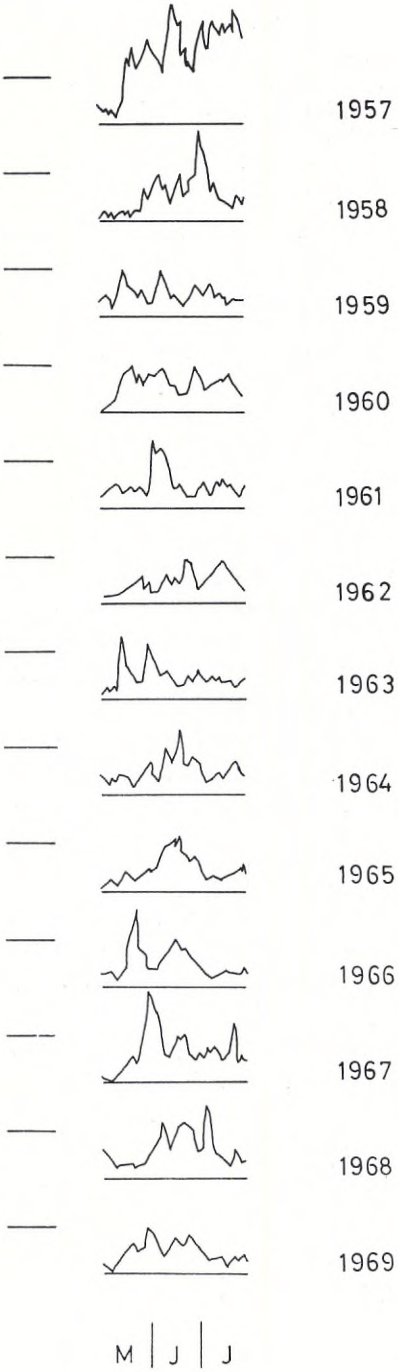

Fig. 4. River discharge at Losna, River Gudbrandsdalslågen, in May, June and July 1957—69. Horizontal lines indicate a flow of 1000 m^3/sec.

Table 4. Monthly mean air temperatures in degrees Centigrade at Stockholm May—August 1940—1969. After SMHI.

Year	May	June	July	August
1940	11.1	16.2	18.3	14.8
1941	8.7	14.6	20.5	15.8
1942	8.4	13.0	16.4	16.8
1943	11.4	15.8	17.1	15.3
1944	8.7	13.6	19.4	18.9
1945	9.5	14.1	19.1	17.7
1946	10.0	14.6	18.9	16.0
1947	12.9	17.1	19.1	18.0
1948	10.7	15.2	18.3	15.9
1949	12.5	13.4	18.0	15.4
1950	11.4	15.9	16.0	17.3
1951	8.3	14.4	16.5	17.4
1952	8.7	14.0	16.3	15.3
1953	10.3	17.4	17.3	16.1
1954	11.5	14.8	16.5	15.6
1955	7.6	13.3	19.6	19.6
1956	11.4	14.2	16.1	13.8
1957	9.0	13.4	17.7	15.5
1958	9.6	13.8	16.5	15.2
1959	10.6	15.3	19.3	18.6
1960	11.3	16.8	16.2	15.5
1961	9.7	16.6	15.7	14.7
1962	8.4	13.7	14.7	13.8
1963	12.4	15.3	17.2	16.6
1964	12.0	14.8	16.8	15.0
1965	8.6	15.2	14.9	14.6
1966	10.6	17.9	18.4	15.5
1967	9.2	14.9	18.2	16.4
1968	8.5	17.6	16.5	17.6
1969	9.3	17.2	18.8	18.7

influence of wind during hatching and early fry stage. Temperature data are not given. The Swedish samples have been collected regularly since 1945 in the basin of Lambarfjärden, Lake Mälaren, close to Stockholm. **Svärdson** analysed the effects both of wind and water temperature in the period 1945—52, without finding any correlation with year-class strength. Predominant year classes developed in Lambarfjärden in the years 1942, 1946, 1951, 1954, 1957, 1960, 1963 and probably in 1966. There is a tendency of a three-year cycle, and the birth years occur at the same time in Lambarfjärden and Lake Mjøsa. If a common factor regulated the recruitment in the two lakes, about 450 kilometres apart, it might be temperature. But while a positive correlation between summer temperatures and recuitment cannot be ruled out in the case of Lake Mjøsa, no such relationship can be observed for Lambarfjärden. In Table 4 the mean air temperatures in Stockholm from May to August 1940—69 are given. Of the eight predominant year classes born in this period only one, 1966, came into existence in a really hot summer. Four more emerged in summers with temperature sums just above the average for the period, and three in cold summers. No correlation between year classes and temperatures in separate months can be found. The observations indicate that temperature is not the decisive factor in cisco recruitment in Lambarfjärden, and this may also be true for Mjøsa since recruitment fails in some hot summers. The periodicity may then be due to some local factor and temperature may only influence the prevailing tendency.

Since neither man-made nor climatic factors seem to be of decisive importance to year-class formation in Lake Mjøsa, the cause may be found within the cisco population itself. With a three-year cycle and with most females maturing at an age of 2+, it seems as if a strong year class gives rise to a new one, *i.e.* a positive correlation between the number of parents and recruits ought to exist. Wether this is really so may be questioned. For instance, the strong 1966 year class was the result of spawning in the autumn 1965. In this the year classes 1957, 1960 and 1963 participated. The following autumn the same age groups took part in the spawning run, but the 1967 year class has been totally missing in the catches. It is difficult to assume that an extraordinarily high mortality took place before the hatching i 1967. The cisco young must then have perished between hatching and the third summer. It is highly probable that the great mortality takes place early in the first summer. Some years in late summer or autumn, schools of dead medium-sized ciscoes are found drifting in the lake or along the shores. Analyses have always shown these fish to belong to a future predominant year class. The age groups 0+ and 1+ of a poor year class have not been represented in such material.

If complete year classes disappear soon after hatching, the most probable cause is intraspecific food competition. A rich year class may exploit the crop of plankton to such a degree that a new one cannot emerge until the existing population is severely reduced. Both maturing and commercial exploitation start when the cisco is 2+. Mortality due to these factors may reduce the stock sufficiently to allow a new year class to grow up in the following year. In Lake Pyhäjärvi, 14 out of 32 year classes formed the basis of the fishery in the observation period. It is impossible to demonstrate a regular population cycle in this lake, but there, too, two rich or medium-sized year classes did not follow in subsequent years. In Lambarfjärden the rich year classes emerge at intervals of 3—5 years, with more or less reduced age classes in between. This indicates that the food competition is more severe in Lake Mjøsa than in Lake Mälaren, since the recruitment is never completely interrupted in the latter lake.

If intraspecific competition is the limiting factor of recruitment in Lake Mjøsa, there is no reason to restrict the fishing. Fishery regulations or planting of fry, often urged, would only result in increasing the pressure on the production of zooplankton. The participation of several age groups in the spawning run also makes the recruitment less vulnerable to overfishing or temporary adverse circumstances.

IV. Summary

1. The reliability of cisco ageing techniques was tested by examining scales and otoliths from 2,068 fish caught on the spawning run during the years 1966—71.
2. Disagreements between scale and otolith ages occur at all age levels, but increase markedly beyond otolith age 3+. In nearly all cases of disagreement otolith age is higher than scale age and the difference may be as great as seven years.
3. Age compositions and length-frequency distributions together with tagging results demonstrate that cisco ages can be determined more accurately from otoliths than from scales.
4. Otoliths show that most ciscoes mature at an age of 2+. Fish up to ages 7+—8+ are important for the commercial fishery. The oldest specimens identified were of the age 12+.
5. The requitment is very uneven. Only every third year does a rich year class arise. The intervening year classes are quite insignificant and may fail altogether to appear in the catches.
6. The fluctuations are probably not caused by river regulations or lake impoundments, nor by climatic factors.
7. It is suggested that intraspecific food competition is responsible for the population fluctuations.
8. At the present time there is no need for fishery regulations or artificially stocking of cisco in Mjøsa.

V. Acknowledgments

The author wishes to express his gratitude for the assistance and cooperation of Leidulf Fløystad and Fredrik Heitkötter and the valuable advice of his colleagues Kjell W. Jensen and Thorolf Lindström. Financial support has been given by the Agricultural Research Council of Norway (NLVF), K/L Opplandskraft and Glommens og Laagens Brukseierforening, and is gratefully acknowledged.

VI. References

AASS, P. 1971. Årsmelding om fiskeriundersøkelser i regulerte vassdrag. Direktoratet for Jakt, viltstell og ferskvannsfiske. 13 pp. (Mimeographed in Norwegian.)

AIRAKSINEN, K. J. 1967. The vendace (*Coregonus albula* L.) of Varmavirta in the northern part of Lake Saimaa (SE-Finland). *Suom. Kalatal. (Finlands Fiskerier)* 30. 32 pp. (In Finnish with Swedish and English Summary.)

ALM, G. 1952. Year Class Fluctuations and Span of Life of Perch. *Rep. Inst. Freshw. Res. Drottningholm.* 33: 17—38.

BAUCH, G. 1949. Untersuchungen über das Wachstum der kleinen Maräne (*Coregonus albula* L.) in den Gewässern Mitteleuropas. *Abh. Fisch. Hilfswiss.* 2: 239—326.

HILE, R. 1936. Age and growth of the cisco, *Leucichthys artedi* (LESEUR), in the lakes of the northeastern highlands, *Wisconsin. Bull. U. S. Bur. Fish.* 48(19): 211—317.

HOLTAN, H. 1971. Mjøsa og dens forurensningssituasjon. *Vann* 6: 135—139 (In Norwegian.)

HUITFELDT-KAAS, H. 1917. Mjøsens fisker og fiskerier. *K. norske Vidensk. Selsk. Skr.* 1916 (2) 257 pp. (In Norwegian.)

— 1927. Studier over aldersforholde og veksttyper hos norske ferskvannsfisker. Oslo. 358 pp. (In Norwegian.)

— 1932. Lagesilden og lagesildfisket i Mjøsen. *Naturen* 56: 135—150. (In Norwegian.)

JÄRVI, T. H. 1920. Siklöjan i Finska Sjöar 1. Keitele *Finlands Fiskerier* 1919. 5. 285 pp. (In Swedish.)

— 1942 a. Die Bestände der kleinen Maränen (*Coregonus albula* L.) und ihre Schwankungen. 1. Pyhäjärvi (Südkarelien). *Acta Zool. Fenn.* 32: 1—89.

— 1942 b. Die Bestände der kleinen Maränen (*Coregonus albula* L.) und ihre Schwankungen. 2. Ober- und Mittel-Keitele. *Acta Zool. Fenn.* 33: 1—145.

— 1947. Über den Kleinmaränenbestand (*Coregonus albula* L.) in dem See Vesijärvi (Südfinnland). *Acta Zool. Fenn.* 48: 1—43.

— 1950. Die Kleinmaränenbestände in ihren Beziehungen zu der Umwelt (*Coregonus albula* L.). *Acta Zool. Fenn.* 61: 1—116.

LEOPOLD, M., Z. MARCIAK & T. BACKIEL 1970. Coregonid fishery in Poland. In: C. C. LINDSEY and C. S. WOODS (Eds.) Biology of Coregonid fishes. Univ. Man. Press, Winnepeg: 553—560.

NORDQVIST, H. 1944 Några synpunkter på fiskevården i sydsvenska sjöar. *Skr. S. Sveriges Fisk. Fören.* 21 pp. (In Swedish.)

SCHMIDT, W. 1968. Vergleichend morphologische Studie über die Otolithen mariner Knochenfische. *Arch. Fisch. Wiss.* XIX (1) 1—96.

SELIGO, A. 1908. Hydrobiologische Untersuchungen. IV. Das Wachstum der kleinen Marene. *Mitt. Westpreuss. Fisch.-Vereins.* 20(2): 20—52.

SVÄRDSON, G. 1949. Gamla siklöjor. *Svensk Fisk. Tidskr. 58*(2 *: 29—30.* (In Swedish.

— 1956. Lambarfjärdens siklöja. *Svensk Fisk. Tidskr.* 65(5): 73—80. (In Swedish.)

— 1964. Siksläktet. Coregonus. *Inform. Inst. Freshw. Res. Drottningholm.* (9). 10 pp. (Mimeographed in Swedish.)

— 1966. Siklöjans tillväxt och utbredningsgränser. *Inform. Inst. Freshw. Res. Drottningholm.* (4). 24 pp. (Mimeographed in Swedish.)

— and G. MOLIN 1968. Growth, Weight and Year-Class Fluctuations in the Pike-Perch (*Lucioperca lucioperca* L.) of Lakes Hjälmaren and Mälaren. *Rep. Inst. Freshw. Res. Drottningholm.* 48: 17—35.

VALLIN, S. 1969. Siklöjans näringsbiologi i Lambarfjärden, Mälaren. *Inform. Inst. Freshw. Res. Drottningholm* (7). 57 pp. (Mimeographed in Swedish.)

VAN OOSTEN, J. 1929. Life history of the lake herring (*Leucichthys artedi* LE SUEUR) of Lake Huron as revealed by its scales, with a critique of the scale method. *Bull. U. S. Bur. Fish.* 44: 265—428.

WAGLER, E. 1941. Die Coregonen. *Handb. Binnenfisch. Mitteleurop.* 3: 371—501.

WALTERS, V. 1955. Fishes of western Arctic America and Eastern Arctic Siberia. *Bull. Amer Mus. Nat. Hist.* 106(5): 261—368.

WILLER, A. 1922. Beiträge zur Kenntnis der Kleinen Maräne (*Coregonus albula* L.) in Ostpreussen. *Mitteilungen der Fischerei-Vereins für die Provinzen Brandenburg, Ostpreussen und Pommern* XIV (5): 1—4.

— 1929. Neue biologische Beobachtungen über die Kleine Maräne (*Coregonus albula* L.). *Z. Fisch.* XXVII (2): 251—269.

Fecundity and growth of some populations of *Astacus astacus* Linné in Sweden

With special regard to introductions in northern Sweden

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I. Introduction

The crayfish *Astacus astacus* LINNÉ spontaneously occurs in Sweden up to about 61°N (VALLIN 1942). There are, however, some isolated self-perpetuating crayfish populations further to the north originating from deliberate introductions since the turn of the century. There is also evidence of introductions of *A. astacus* into southern Sweden from Germany in the 16th Century (BERNSTRÖM 1964, ABRAHAMSSON 1969), but the wide distribution of crayfish in southern Sweden — prior to the ravages of the crayfish fungus *Aphanomyces astaci* SCHIKORA (*cf.* UNESTAM 1969) and the destruction of crayfish habitats by human activities — indicates that *A. astacus* is native in Sweden. The natural dispersal of crayfish is slow (ABRAHAMSSON 1971 a). In order to locate suitable sites in northern Sweden for introduction of *A. astacus* an investigation was made to determine the effect of temperature on fecundity and growth. The changes in growth rate when *A. astacus* was introduced into new environments containing no crayfish was also investigated.

II. Study areas

The study was conducted in the following locations with native crayfish populations:

River Råne älv	(65°51′N, 22°19′E)
River Aleån	(65°40′N, 21°41′E)
River Ljungan	(62°30′N, 15°33′E)
River Iskan	(60°47′N, 15°51′E)
Lake Racken	(59°43′N, 12°39′E)
Lake Alkvettern	(59°23′N, 14°21′E)
Lake Jogen	(57°53′N, 13°38′E)
Lake Sämsjön	(57°49′N, 13°10′E)

A. astacus was experimentally introduced in the course of this investigation into the following waters:

Lake Bakvattnet	(63°50′N, 14°3′E)
River Indalsälven	(63°19′N, 13°33′E)
Lake Ansjön	(62°58′N, 16°5′E)
Lake Oxsjön	(62°42′N, 16°6′E)
Lake Hundbergssjön	(62°31′N, 16°21′E)
Lake Mellansjö	(62°20′N, 15°40′E)
River Galtström	(62°10′N, 17°30′E)
Lake Översjön	(58°50′N, 16°12′E)
Lake Allgunnen	(57°13′N, 14°36′E)
Rögle Ponds	(55°42′N, 13°19′E)

Some water quality data for the localities are given in Table 1 (see also ABRAHAMSSON 1971 b).

III. Methods

Crayfish were collected by hand and by means of cylindrical traps as described by ABRAHAMSSON (1971 a).

By inspection of the cement glands located under the abdomen (LEREBOULLET 1860, ABRAHAMSSON 1971 a) the reproductivity (mature eggs in the ovaries) of *A. astacus* could be ascertained approximately one month before the mating season on material collected with traps.

The clutch size of *A. astacus* females was investigated after wintering (May—June), by removing and counting pleopod eggs.

Differences in hatching time and growth rate of young crayfish at different localities were studied by keeping egg-bearing females in fine-meshed corves (60×60×40 cm), provided with a coarse-meshed dividing screen, 10 cm above the base of the corf. Egg-bearing females originating from the Rögle Ponds were placed on the screen in May. After hatching the juveniles dropped through the screen to the lower compartment where they were protected from being eaten by the adult females. The crayfish were supplied with a surplus of food.

The growth of adult crayfish was studied on individually marked specimens (method described by ABRAHAMSSON 1965). Body length of crayfish was measured as described by ABRAHAMSSON (1971 a). The length of chela (propodus length) was measured to the nearest mm from the tuberclelike projection, located centrally on the dorsal base of the propodus, to the tip of propodus. In the growth analysis, crayfish were generally grouped in 5-mm classes with reference to body length.

The stage in the moulting cycle could be ascertained on the basis of the

Table 1. Water quality data for study localities in Sweden.

Locality	Date	Total hardness DH°	pH	Colour mg Pt/l	Specific conductivity $H_{20} \cdot 10^6$	$KMnO_4$-reduction, mg/l
River Aleån	4.8.1966	1.2	6.9			
„ —	23.4.1971	1.3	6.4	65	47.0	47
Lake Bakvattnet ..	12.6.1964		6.5		20.7	
River Indalsälven .	5.8.1964	0.4	6.7		34.8	
Lake Ansjön	6.8.1964	0.7	6.9		54.3	
Lake Oxsjön	1.9.1965	0.8	6.9	35	32.0	32
„ —	10.3.1966	1.0	6.9	25	39.0	
„ —	22.6.1966	0.7	7.9	25	31.0	
„ —	4.8.1966	0.8	7.3	25	35.0	
„ —	1.9.1966	0.8	6.1	30	33.0	
Lake Hundbergssjön	1.9.1965	3.6	7.1	50	129.0	37
„ —	16.3.1966	6.7	7.5	25	210.0	
„ —	1.7.1966	0.8	7.2	35	69.0	
„ —	4.8.1966	2.6	7.1	40	102.0	
„ —	1.9.1966	2.3	6.5	40	85.0	
Lake Mellansjö ..	1.9.1965	0.6	6.4	50	26.0	20
„ —	14.3.1966	0.9	6.5	25	34.0	
„ —	1.7.1966	0.5	7.0	40	26.0	
„ —	4.8.1966	0.6	6.6	80	29.0	
„ —	1.9.1966	0.5	5.6	40	25.0	
River Galtström ..	1.9.1965	0.9	6.6	25	40.0	21
„ —	27.6.1966	0.6	6.9	20	36.0	
„ —	4.8.1966	0.7	6.9	20	44.0	
„ —	7.9.1966	0.8	6.5	25	41.0	
Lake Racken	1.8.1964	0.4	6.2		34.8	
Lake Sämsjön	23.4.1971	2.8	7.1	20	125.0	26
Lake Översjön ...	10.7.1963	0.6	7.1	80	103.0	

pliancy of the carapace, — as well as the colour and cleanliness of the exoskeleton.

Water temperatures were generally recorded 0.5 m below the surface by LAMBRECHT thermographs. The temperatures of the Rivers Ljungan (Parteboda Power Station) and Indalsälven (Mörsil Power Station) were obtained from daily readings at $07^{\circ\circ}$, $13^{\circ\circ}$, and $21^{\circ\circ}$, from which monthly averages were calculated.

IV. Fecundity

The reproductivity of *A. astacus* populations at different latitudes is shown in Fig. 1. With increasing latitude and altitude the average temperature of the year decreases in Sweden. In the colder waters of River Aleån and River Ljungan the spawning frequency of younger females was noticeably reduced. Only 62.7 and 52.6 per cent of the females between 80 and 100 mm body length in River Aleån and River Ljungan, respectively, were reproductive. The corresponding percentage of reproductive females in River

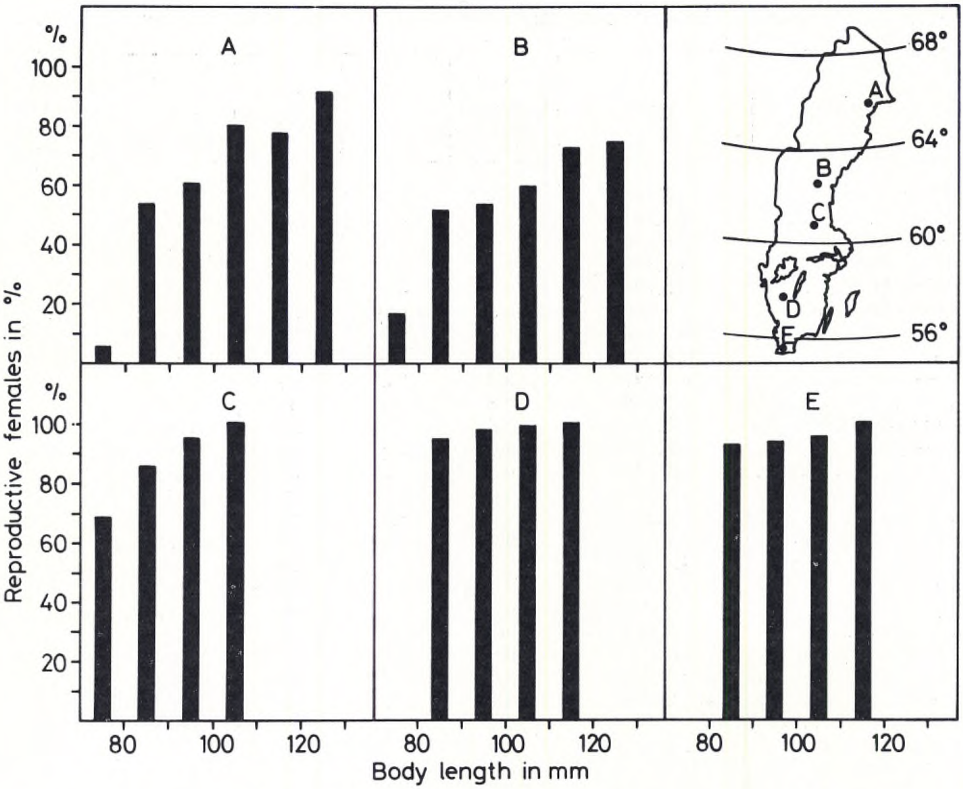

Fig. 1. The relationship between proportion of reproductive females and body length of *A. astacus* females collected prior to egg-laying during August—September. A: River Aleån, n=352. B: River Ljungan, n=2,634. C: River Iskan, n=147. D: Lake Sämsjön, n=627. E: Rögle Ponds, n=469.

Iskan, Lake Sämsjön and Rögle Ponds were 88.9, 97.3, and 93.2. Reproductivity of females larger than 100 mm was not much influenced by the temperature.

Besides temperature the food supply also seems to influence the reproductivity. In the oligotrophic Lake Jogen, which before the outbreak of crayfish plague in 1970 had a high density of *A. astacus,* only about 50 % of 182 examined females of 70—100 mm body length were reproductive in 1965. This agrees with observations from northern Germany by SCHIEMENZ (1905), who found that females of *A. astacus* propagate each year in food-rich lakes, but only every second year in lakes with little food.

Despite considerable individual variation in pleopod egg numbers, the number of eggs produced is clearly correlated with size of the female (ABRAHAMSSON 1971 a). The average pleopod egg numbers in relation to

Table 2. Pleopod egg numbers in relation to female body length in various populations of *A. astacus*.

Locality	Date	Number of individuals	Average body length in mm	Average number of pleopod eggs
River Aleån	June 1964 ..	33	110.7 ± 1.90	172.1 ± 12.75
River Ljungan	June 1963 ..	15	100.5 ± 2.17	148.1 ± 20.32
River Iskan	June 1963 ..	21	94.1 ± 1.82	91.2 ± 7.99
Lake Sämsjön	June 1963 ..	40	95.8 ± 1.29	113.7 ± 8.79
Rögle Ponds	May 1963 ..	86	90.3 ± 0.81	90.4 ± 3.98

average body length for various populations of *A. astacus* are shown in Table 2.

The reduced spawning frequency among younger crayfish females in the River Aleån and River Ljungan is compensated for by the age distribution. The *A. astacus* population in River Aleån was unexploited and therefore contained a high proportion of large individuals (Fig. 2). 60 per cent of trap-collected females were ≥ 100 mm body length. The prescribed minimum landing size for crayfish in River Ljungan is 100 mm (generally 90 mm in the rest of Sweden). Hence the population contains a high proportion of large individuals (51.4 % females ≥ 100 mm body length) capable of maintaining a productive crayfish population.

The density of the *A. astacus* population was high in the ponds of Rögle before the outbreak of the crayfish plague (ABRAHAMSSON 1971 a). In the dense population, males forced the females to resort to poorer areas (ABRAHAMSSON 1966). Hence the crayfish were stunted and on average produced relatively few eggs (Fig. 2, Table 2).

Although low water temperature apparently has an adverse effect on the spawning frequency, the egg production in corresponding size groups was similar in localities at different latitudes in Sweden (ABRAHAMSSON 1971 a).

V. Hatching and survival in relation to temperature

Differences in hatching time in relation to altitude and latitude are shown in Table 3. Hatching occurred in Lake Bakvattnet 41 days later than in the Rögle Ponds. In the experiment juveniles did not survive the winter in Lake Ansjön, River Indalsälven and Lake Bakvattnet. The low temperature of River Ljungan in 1962 as compared to normal years (Fig. 3) resulted in delayed hatching. In River Ljungan hatching normally occurs in the middle of July, but in 1962 the crayfish did not hatch until 15 August. The juveniles did not survive the winter of 1962—63. The crayfish introduced into Lake

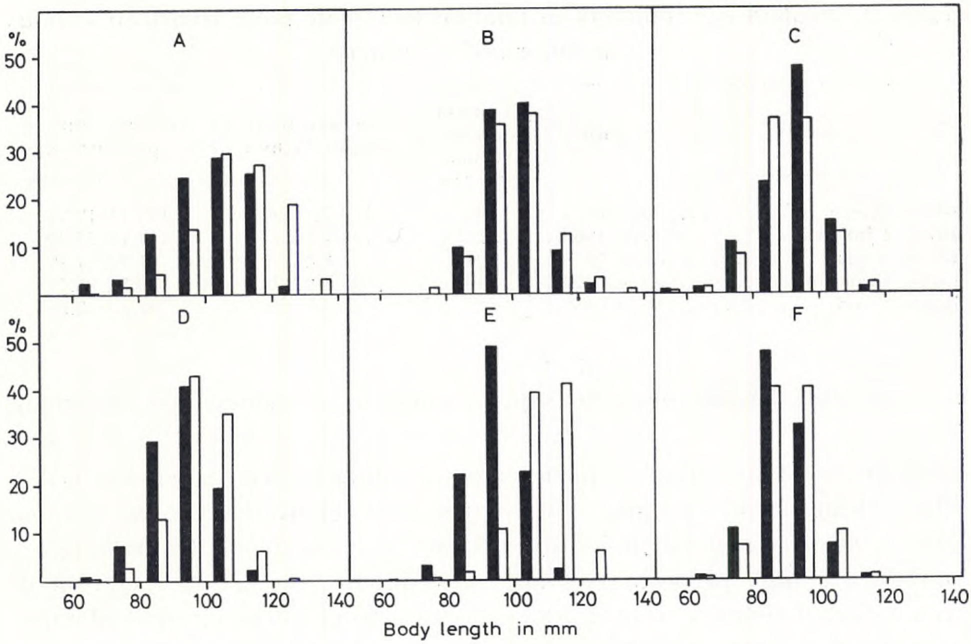

Fig. 2. Structure of *A. astacus* populations according to trapped samples. A: River Aleån, n=383 males and 118 females. B: River Ljungan, n=294 males and 286 females. C: River Iskan, n=721 males and 392 females. D: Lake Sämsjön, n=692 males and 481 females. E: Rögle Ponds, n=3,732 males and 589 females. F: Lake Jogen, n=3,996 males and 2,440 females. Black bars=females, white bars=males.

Hundbergssjön in 1965 did not breed. The females had pleopod eggs on 10 August 1966, when the water temperature was 13.1°C.

The most productive crayfish locality in the province of Norrbotten, River Råne älv, has a small water flow and a shallow river bed, resulting in a relatively high water temperature in the summer. However, at this locality crayfish juveniles are generally dependant on the female as late

Table 3. Hatching times of *A. astacus* transferred from the Rögle Ponds in May 1961 to various localities in the north.

Locality	Latitude	Altitude in m	Time of hatching 1961
Rögle Ponds	55°42′N	80	15 June
Lake Allgunnen	57°13′N	205	25 June
Lake Sämsjön	57°49′N	186	28 June
Lake Racken	59°43′N	94	4 July
River Iskan	60°47′N	137	8 July
Lake Ansjön	62°58′N	288	12 July
River Indalsälven (Mörsil) ...	63°19′N	317	19 July
Lake Bakvattnet	63°50′N	522	26 July

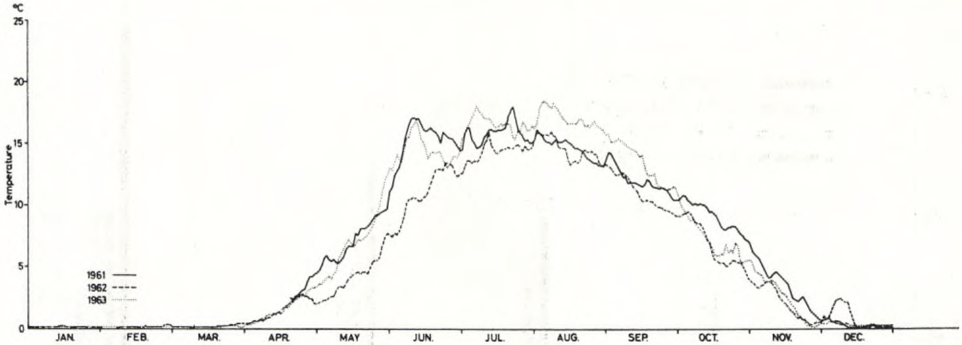

Fig. 3. Water temperatures in River Ljungan at Parteboda Power Station.

as at the start of the open season (August 7) indicating that the *A. astacus* population there exists close to the minimum temperature required for a self-perpetuating population.

VI. Growth of juvenile crayfish

Differences in growth rate of juvenile crayfish in various localities are shown in Fig. 4. Since crayfish were hatched and kept in isolated corves provided with surplus of food, the differences in growth rate may be attributed to the water temperature. In the cold year of 1962 the juveniles during the investigation period reached a body length of only 11.0 mm in the River Ljungan. In the warmer summer of 1963 (Table 4) hatching occurred in the end of July. Nine juveniles that were collected by hand averaged 16.1 ± 0.66 mm by the end of October. In the River Aleån, eight juveniles were 12.1 ± 0.58 mm on August 10 1963. Twelve "two-summer old" individuals

Table 4. Monthly mean water temperatures in May through September at various study localities.

Locality	Year	May	June	July	August	September
River Aleån (Selet)	1965	5.6	15.6	16.2	14.7	11.3
River Indalsälven (Mörsil) ..	1961	4.5	11.1	13.0	14.4	—
River Ljungan (Parteboda) ..	1961	7.1	15.2	15.8	14.5	11.8
,, —	1962	4.4	10.7	14.5	14.4	10.8
,, —	1963	7.3	14.4	16.5	17.4	12.9
,, —	1965	6.1	13.4	15.2	14.8	12.8
Lake Oxsjön	1965	5.1	14.3	14.8	13.7	10.4
Lake Hundbergssjön	1965	7.1	10.6	13.4	12.7	10.6
River Galtström	1965	8.0	15.1	15.9	14.1	10.6

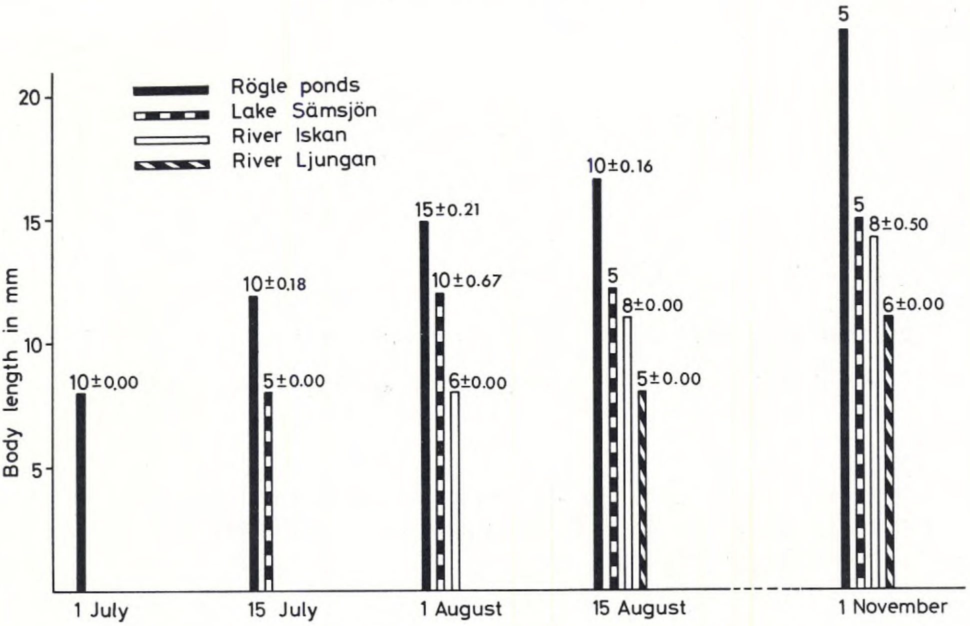

Fig. 4. Mean body length of juveniles of *A. astacus* at different localities in 1962. Figures above the bars indicate the number of measured individuals. Standard error of the mean given for groups ≥ 8 individuals or where all individuals were of the same size.

collected by hand in the same river in the middle of August 1964 averaged 26.9 ± 1.14 mm.

By analyzing length-frequency data of hand collected material from the ponds of Rögle "two-summer-old" crayfish 112 males were found to be 48.9 ± 0.47 mm and 131 females 46.6 ± 0.73 mm (ABRAHAMSSON 1966 and 1971 b). The results from these south Swedish ponds showing the effect of temperature on crayfish growth are in agreement with those obtained by JÄRVEKÜLG (1958) in Esthonian water systems.

VII. Growth of adult crayfish

The growth of adult females of *A. astacus* at different latitudes is shown in Fig. 5. A corresponding analysis of crayfish males was done by ABRAHAMSSON (1965). In 1963 the average increment per moult at 95—99 mm size was in Lake Sämsjön: males 9.95 ± 0.60 mm, females 6.10 ± 0.38 mm, River Iskan: males 6.73 ± 0.57 mm, females 4.20 (n=5), River Ljungan: males 8.13 ± 0.47 mm, females 5.53 ± 0.41 mm, River Aleån: males 6.06 ± 0.28 mm, females 5.00 mm (n=1), and at a body length of 100—104 mm in Lake Sämsjön: males 9.60 ± 0.30 mm, females 6.31 ± 0.38 mm, River Iskan: males

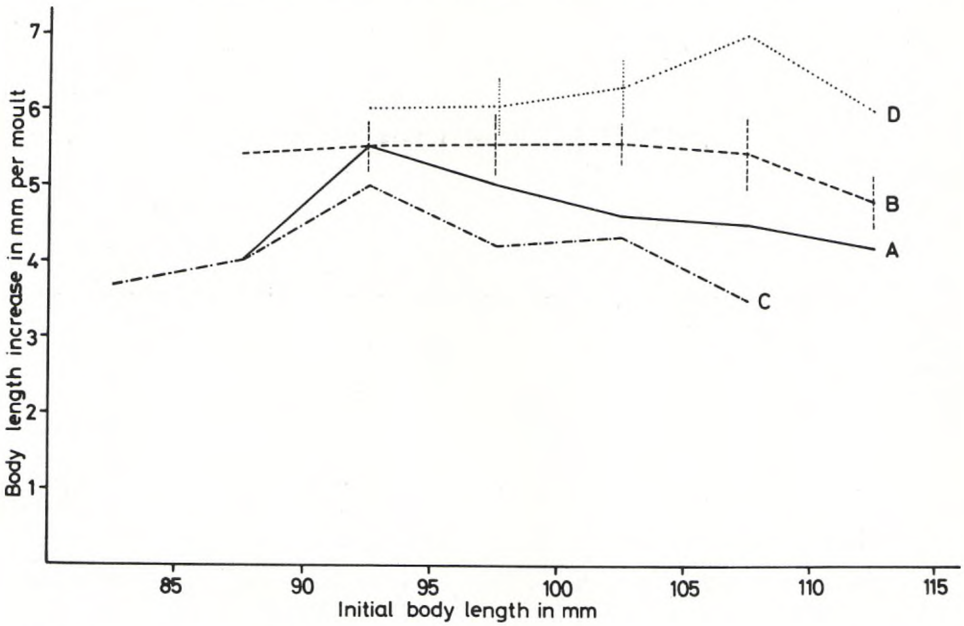

Fig. 5. Relation between increased body length per moult and body length of adult females of *A. astacus* at start of experiment. The crayfish were marked in June and recaptured in August 1963. A: River Aleån, n=17. B: River Ljungan, n=95, C: River Iskan, n=21. D: Lake Sämsjön, n=33. Standard error of the mean indicated by vertical lines for groups ≥ 8 individuals.

6.43 mm (n=7), females 4.33 mm (n=3), River Ljungan: males 7.79 ± 0.44 mm, females 5.56 ± 0.27 mm and River Aleån: males 6.65 ± 0.29 mm, females 4.60 mm (n=5).

The on the average lower growth rate of females might be partially due to reduced feeding activity during the incubation period. Male and female chelae growth at various localities in Sweden is illustrated in Fig. 6. As a result of differences in chelae growth rate there are differences in length-weigth relations. The strong development of the chelae of males gives them a dominating position in the competition for food (ABRAHAMSSON 1966).

Temperature, food supply, and population density are the most important environmental factors that influence the growth rate. The influence of temperature on growth of adult *A. astacus* was shown by ABRAHAMSSON (1966) when the weight increase per moult was compared between the cold year 1962 and the warmer 1963.

Not only was the body length increase per moult depressed by low water temperatures but the time for ecdysis was also delayed. This was evident in River Ljungan, where the decrease in food searching activity at moulting was reflected in the trappability (ABRAHAMSSON 1971 b). In the warm

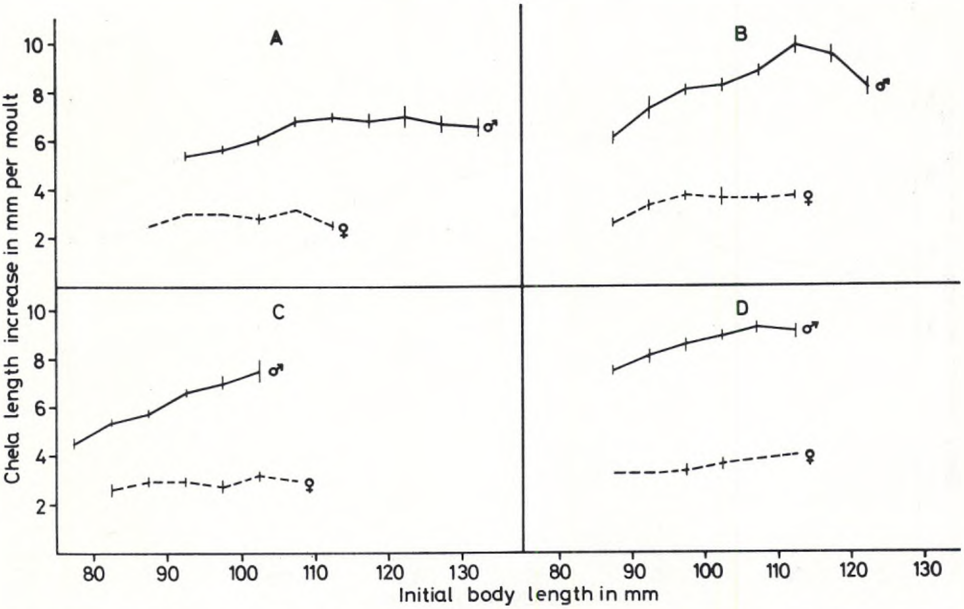

Fig. 6. Relation between increase in length of chela per moult and initial body length of adult males and females of *A. astacus*. Crayfish were marked in June and recaptured in August. A: River Aleån, n=220 males and 44 females. B: River Ljungan, n=192 males and 156 females. C: River Iskan, n=134 males and 80 females. D: Lake Sämsjön, n=186 males and 52 females. Standard error of the mean indicated by vertical lines for groups ≥ 8 individuals.

Table 5. Body length of *A. astacus* transferred from Lake Jogen (57°53′N) to various localities at about 62°N and to Rögle Ponds (55°42′N) in 1965—66. Standard error of the mean given for groups ≥ 8 individuals.

Locality	Sex	Body length increase in mm			
		Nos	Initial length 80—89 mm	Nos	Initial length 90—99 mm
Lake Oxsjön, 327 m a.s.l.	males	22	8.6 ± 0.25	7	8.3
	females	3	8.6		
Lake Mellansjö, 320 m a.s.l.	males	10	9.2 ± 0.79	19	6.7 ± 0.73
	females	10	8.7 ± 1.45	18	6.2 ± 0.57
Lake Hundbergssjön, 183 m a.s.l.	males	7	9.6	7	8.6
	females	5	7.8	9	6.0 ± 0.32
River Galtström, 5 m a.s.l.	males	29	10.9 ± 0.49	21	10.8 ± 0.26
	females	5	11.7	4	9.7
Lake Jogen 250 m a.s.l.	males	93	5.4 ± 0.17	62	5.4 ± 0.17
	females	36	5.0 ± 0.28	19	4.9 ± 0.38
Rögle Ponds, 80 m a.s.l.	males	45	20.6 ± 0.68	18	12.7 ± 1.48
	females	12	8.3 ± 1.23	12	8.7 ± 0.49

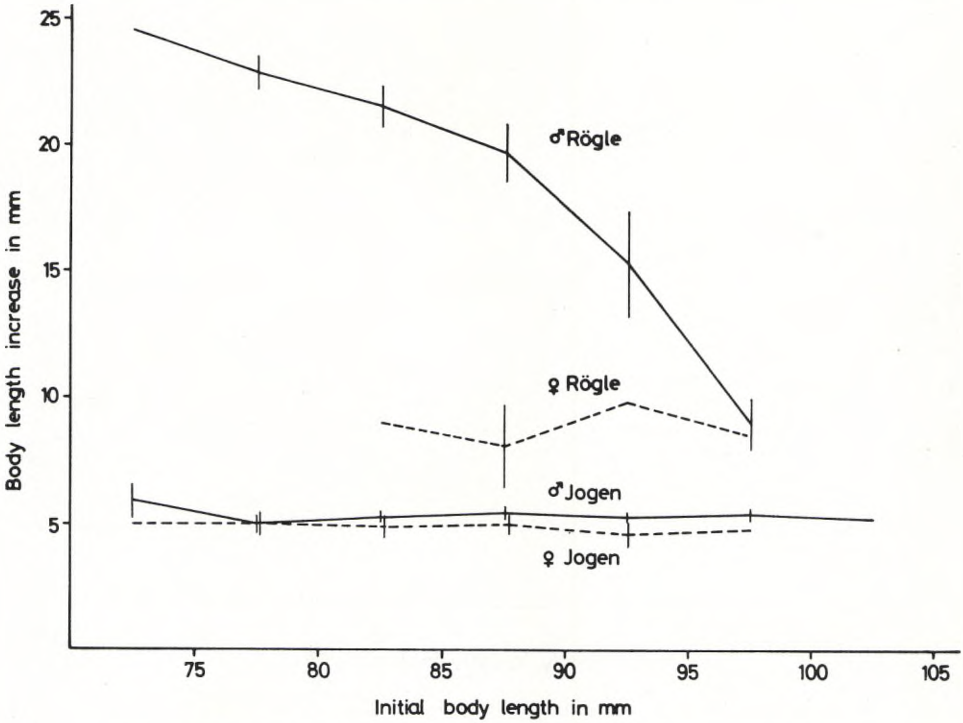

Fig. 7. Relation between initial body length and body length increase of adult *A. astacus* in Lake Jogen (n=193 males and 69 females) and in Rögle Ponds (n=80 males and 25 females). The crayfish were marked in September 1965 and recaptured in September 1966. Lake Jogen and Rögle Ponds average 230 and 280 days per year respectively, without frost. Standard error of the mean indicated by vertical lines for groups ≥ 8 individuals.

summer of 1961, 20 traps yielded 396 crayfish at the start of the open season (August 7), but owing to the inhibitory effect of low temperatures the corresponding number in 1962 was only 4 crayfish.

The moulting frequency is influenced by both temperature and food supply. Generally adult crayfish moult only once a year in Sweden, but when given high water temperature and ample food smaller crayfish (especially males) less than about 90 mm long moult more frequently.

Adult *A. astacus* transferred from Lake Jogen to water systems at about 62° N moulted once a year, but transfer to the warmer eutrophic Rögle Ponds enabled males up to about 90 mm size to moult twice or even three times a year (Fig. 7, Table 5). Neither the water courses at 62° N nor Rögle Ponds contained crayfish before this transfer. Hence the crayfish population as regards food resources had almost optimal conditions for growth. The multiple effects on crayfish growth of fighting caused by overcrowding,

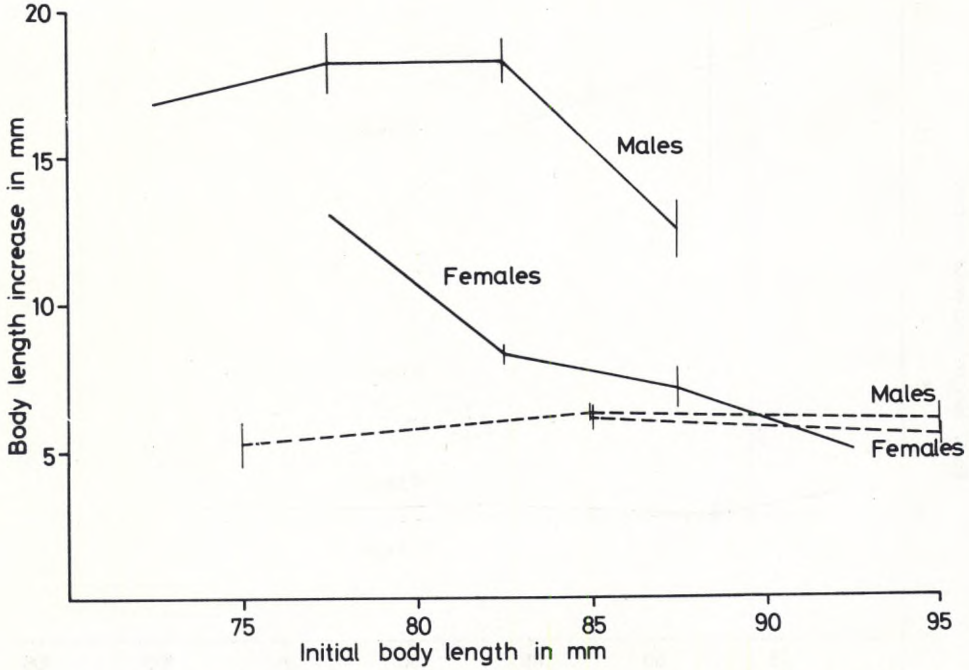

Fig. 8. Body length increase of adult *A. astacus* in Lake Alkvettern between June and August 1945, n=104 males and females (according to SVÄRDSON 1949) and crayfish introduced to Lake Översjön (August 1965—August 1966)(n=81 males and 55 females). Dashed line=Alkvettern, continuous line=Översjön. Standard error of the mean indicated by vertical lines for groups ≥ 8 individuals.

consequent loss of appendages (ABRAHAMSSON 1966), and poor food supply were seen in the dense crayfish population in Lake Jogen (Fig. 7). Before the outbreak of crayfish plague in Rögle Ponds in 1963—64 the *A. astacus* population was extremely numerous (ABRAHAMSSON 1966) and adult crayfish moulted only once a year. The average growth increase per moult was about 5 mm for males and 2 mm for females (ABRAHAMSSON 1971 a).

The reduced growth rate of crowded *A. astacus* as compared to the situation in previously empty environments is also apparent from the fact that crayfish transferred from Lake Alkvettern to Lake Översjön at about the same latitude moulted more frequently and increased more at each moult (Fig. 8).

VIII. Survival of introduced adult *A. astacus* in northern Sweden

Adult crayfish introduced at different localities at about 62°N were able to survive for some years (Table 6). However, the mortality was high and

Table 6. Yield and growth of *A. astacus* from Lake Jogen introduced into localities on different altitudes at about 62°N.

Locality	Number of introduced crayfish	Year	Yield		Average body length in mm	
			Total	Per trap	Males	Females
Lake Oxsjön 327 m a.s.l.	1000	1965			87	84
		1966	26	1.04	96	92
		1967	117	0.90	103	100
		1968	123	1.22	105	105
		1969	46	0.57	110	110
Lake Mellansjö 322 m a.s.l.	1400	1965			91	95
		1966	99	4.95	100	100
		1967	18	0.21	110	110
Lake Hundbergssjön 183 m a.s.l.	700	1965			88	90
		1966	72	1.60	102	100
		1967	98	2.45	105	105
		1968	60	0.80	115	115
River Galtström 5 m a.s.l.	1000	1965			88	85
		1966	64	3.20	98	103
		1967	241	1.61	100	105
		1968	256	3.20	115	115
		1969	136	0.76	99	99

the yield per trap low. Lake Mellansjö (1 hectare) and Lake Hunbergssjön (0.7 hectare) were drained in August 1967 and August 1968, respectively, and all crayfish were manually collected and counted. 56 surviving crayfish of 1.400 introduced two years before were found in Lake Mellansjö. The mortality during two years was thus about 96 per cent. The trap yields indicate that the mortality was extremely high in 1966—67. This may be ascribed to a lowering of the pH level in the lake (Table 1). pH dropped to 5.6 in September 1966, when the adding of lime to the inflowing water was discontinued. Water courses with a pH level below 6.0 were considered unsuitable for *A. astacus* (LARSEN 1947: Denmark, MUNTHE-KAAS 1969: Norway). When Lake Hundbergssjön was drained 195 crayfish were found of the 700 introduced. During three years the mortality in the cold water (Table 4) was thus about 72 per cent. No reproduction had occurred in the above-mentioned lakes. Several introductions of *A. astacus* from populations in north Finland to lakes and rivers at high latitudes in Sweden have been carried out during the last 25 years. Only a few of these localities have temperature conditions making self-perpetuating populations possible. However, in localities up to about 68°N in Sweden introduced adult crayfish have survived several years and grown to considerable sizes, but reproduction has not been observed in these localities.

IX. Concluding remarks

The northern distribution limit of *A. astacus* in Sweden is set by the lowest critical temperature in the most vulnerable stage of its life cycle. Although *A. astacus* can live in waters up to 68°N in Sweden, its breeding is confined to waters, the temperature of which during three summer months averages 15°C or more. The individual crayfish can, however, live and grow in colder water.

As a result of the temperature requirements of reproduction, the most northerly breeding *A. astacus* populations in Sweden are located in the warmer coastal region.

The continuous area for distribution of *A. astacus* extends as far as to 62°N in Finland compared to 61°N in Sweden (WESTMAN *et al.* 1968). Several connections between the water-courses facilitated the dispersal of crayfish in Finland. The more northerly continuous range of *A. astacus* may be due to the higher summer temperatures than at corresponding latitudes in Sweden. There are a few selfperpetuating, introduced populations in Finnish Lapland. As in Sweden these Finnish populations are mostly located close to the coast of the Gulf of Bothnia.

In southeast Norway *A. astacus* occurs in a continuous area up to about 61°N. By introductions in recent years some populations have been established as far north as 63°20′N in the county of Sør-Trøndelag and in the county of Hedmark at an altitude of 585 m a.s.l. (MUNTHE-KAAS 1969).

Owing to lower growth rate in cold waters the pre-reproductive age is longer at higher latitudes. The biotope must thus support the crayfish for a longer time before sexual maturity is attained. The long pre-reproductive period also incurs greater mortality. *A. astacus* populations in the north have better chances to survive and to approach maximal productivity provided that the reproductively most efficient females (≥ 100 mm) are not removed, particularly if the opening of the season is so early that it interferes with the hatching.

X. Acknowledgments

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X. References

ABRAHAMSSON, S. 1965. A method of marking crayfish *Astacus astacus* LINNÉ in population studies. *Oikos* 16(1/2: 228—231.

— 1966. Dynamics of an isolated population of the crayfish *Astacus astacus* LINNÉ *Oikos* 17(1): 96—107.

— 1969. Historik, allmän översikt och reformförslag beträffande fångst och handel med flodkräfta. *Fauna och flora* 64(3): 98—104. (In Swedish.)

— 1971 a. Density, growth, and reproduction in populations of *Astacus astacus* and *Pacifastacus leniusculus* in an isolated pond. Oikos 22(3): 373—380.

— 1971 b. Trappability, locomotion and diel pattern of activity of the crayfish *Astacus astacus* LINNÉ and *Pacifastacus leniusculus* DANA. In manus.

BERNSTRÖM, J. 1964. Kräftdjur. In Granlund, J. (Ed.) *Kulturhistoriskt lexikon för Nordisk medeltid.* Malmö 9: 487—494. (In Swedish.)

JÄRVEKÜLG, A. 1958. Joewähk Eestis. Eesti NSV Teaduste Akad. Zool. ja Bot. Inst. Tartu. 185 p. (In Estonian.)

LARSEN, K. 1947. Krebsebogen, krebsens naturhistorie, krebseavel og krebsefiskeri. Copenhagen. 65 pp. (In Danish.)

LEREBOULLET, A. 1860. Recherches sur la mode de fixation des oeufs aux fausses pattes abdominales dans les écrevisses. *Ann. Sci. nat.* 14: 359—376.

MUNTHE-KAAS LUND, H. 1969. Krepsen i Norge, dens miljøkrav og økonomiske verdi. *Fauna, Oslo* 22: 177—188. (In Norwegian.)

SCHIEMENZ, P. 1905. Zum Mindestmasse der Krebse. *Z. Fisch.* XII (1/2): 67—110.

SVÄRDSON, G. 1949. Stunted crayfish populations in Sweden. — *Rep. Inst. Freshw. Res. Drottningholm* 29: 135—145.

UNESTAM, T. 1969. Studies on *Aphanomyces astaci* Physiology and Parasitic Relationship to the Crayfish. *Acta Universitatis Upsaliensis* 134. 22 p.

VALLIN, S. 1964 Kräftan, *Potamobius astacus* (LINNÉ). *In* Andersson, K. A. (Ed.) Fiskar och fiske i Norden, 2: 505—512. (In Swedish.)

WESTMAN, K., O. SUMARI and H. DAHLSTRÖM. 1968 Kräftfrågan i Finland. *Fisk. Tidskr. Finl.* N. S. 12 (3): 58—64. (In Swedish.)

Netting for better angling in a small mountain lake

By Åke Fagerström

I. Introduction

Lake Långbjörsjön is a small mountain lake in north-western Jämtland close to the Norwegian border. Together with a number of other lakes it is situated in a region owned by a private organization. The area available for recreation and angling is thus very important in these small waters.

It is a common idea among anglers in Sweden as in other countries that gill nets, seines and other similar ways of fishing are entirely harmful to a water where the only important yield derives from recreation. But brown trout, which is the most common fish caught in these lakes, is rather small, with a length of about 25 cm and a weight of 0.15—0.20 kg. To the average sport fisher this is a small fish and it is thus important to make the fish a little more attractive, if possible, through suitable management.

Dahl (1943) showed in a classic paper that it was possible to improve the growth rate for trout in a small mountain lake in Hardangervidda in Norway if large parts of the population were removed by seine. Dahl and Sömme (1947) recommended that, in lakes with both trout and arctic char, the latter species should be kept in check as much as possible, caught during their spawning time, and so on, in order to decrease the pressure upon the trout with a view to making it more fast-growing and to improving the survival.

As part of a project to improve the trout fishing in the lakes in question, several experiments have been made (Fagerström 1970). Fertilization has been tried in some waters, predators in the shape of big trout from other lakes have been introduced, and different kinds of regulations for the fishing have also been tried. A further link has been an attempt to reduce the population of both trout and char in Lake Långbjörsjön by intensive fishing with gill nets and seines, and so on. Certain results have already been reported on. Different authors have dealt with tag shedding and growth rates (Fagerström *et al.* 1969), the local distribution of char and trout (Gustafson *et al.* 1969) and fishing pressure, growth and recruitment (Lindström *et al.* 1970).

The object of this paper is to summarize the evidence obtained and to give an evaluation of the methods tried in Lake Långbjörsjön as a means

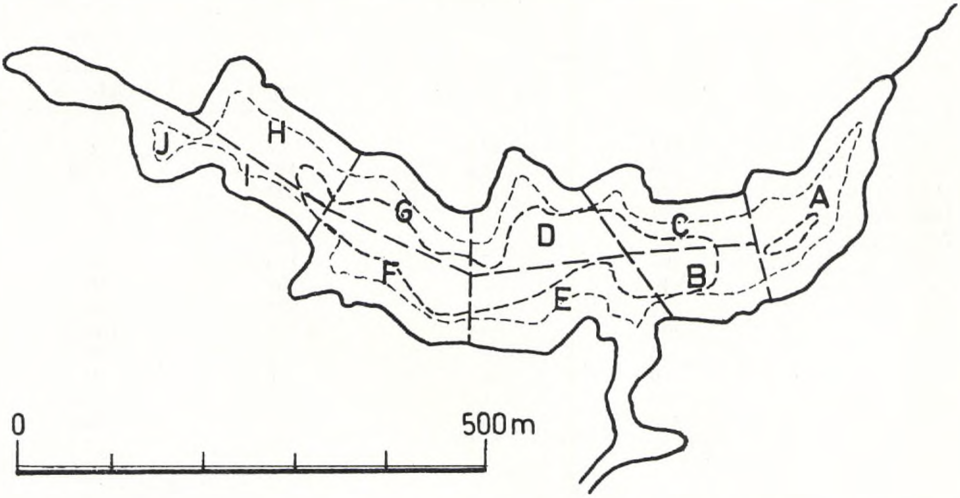

Fig. 1. Different sections in Lake Långbjörsjön. The first net area is bounded by the shore line and the thin contour of short dashes, 25 metres out in the lake. The 5 metres depth is indicated by two coarser contours of dashes.

of improving the yield of the sport fishing in terms of both fish caught and recreation.

II. Materials and Methods

Lake Långbjörsjön is situated 590 metres above sea level, has an area of 10 hectares, an approximate length of one kilometre and a maximum depth of 11 metres. The bedrock is slate and the vegetation consists mostly of *Carex* reeds in the bays.

To facilitate the test fishing, the lake was divided into sections as appears in Fig. 1.

The standard set of gill nets used for the fishing consists of 15 gill nets in the following mesh sizes.

Table 1.

Mesh size	12 v/a	16 v/a	18 v/a	20 v/a	24 v/a	28 v/a	36 v/a
knot-to-knot cm .	5.00	3.75	3.33	3.00	2.50	2.14	1.67
Numbers of nets in the set	1	1	2	2	3	3	3

The numbers of trout and char caught in Lake Långbjörsjön by other fishing than sport fishing are as follows:

Table 2.

Year	Trout		Char	
	Number	Weight (kg)	Number	Weight (kg)
1958	112	12.8	79	6.2
1959	270	26.0	410	34.0
1960	176	—	320	—
1961	414	—	456	—
1962	171	—	228	—
1963	65	7.0	115	—
1964	46	5.5	157	10.7
1965	127	15.7	224	16.7
1966	207	26.9	2,236	130.4
1967	0	0	0	0
1968	0	0	0	0
1969	89	11.1	273	21.4
1970	230	23.0	420	35.0
1971	13	1.3	32	3.3

The extensive removal of char in 1966 was effected during their spawning time with the aim of causing a substantial reduction of the population. Fourteen gill nets, mesh sizes 36 v/a, 28 v/a and 24 v/a, were used. The effort was identical each night from August 25 to August 30 inclusive, but the catch decreased continuously each night, implying that the reduction in the population was reflected in the catch. The catches amounted to:

Table 3. Gill net fishing for char August 1966.

Date	Trout		Char	
	Number	Weight (kg)	Number	Weight (kg)
Aug. 25	21	4.2	688	38.7
„ 26	14	3.2	467	26 8
„ 27	11	1.9	229	14.1
„ 28	15	2.1	204	11.4
„ 29	10	1.5	200	10.8
„ 30	7	1.6	181	9.5
Total	78	14.5	1,969	111.3

Using the formula from RICKER (1958), it was possible to estimate the number or arctic char in Lake Långbjörsjön at that time:

$$No = \frac{C}{1- b^{f}} \text{ where}$$

No = original population size
C = total catch
b = the complement of catchability
f = total fishing effort for the whole experiment

According to this formula the population of char amounted to 2,666.

Table 4. Mean catch in number of char and trout in different parts of Lake Långbjörsjön, *cf.* Fig. 1, a=trout, b=char

Sect.		Nets placed first in gang				Nets placed second in gang				Grand total	b/a
		36 v/a	28 v/a	24 v/a	Total	36 v/a	28 v/a	24 v/a	Total		
AB	a	15.2	6.8	6.8	28.8	2.7	3.0	6.1	11.8	40.6	1.3
	b	20.3	8.6	2.8	31.7	9.7	7.8	3.6	21.1	52.8	
C	a	12.0	5.5	6.2	23.7	1.0	1.3	4.0	6.3	30.0	1.8
	b	13.0	8.5	8.2	29.7	14.0	8.1	3.0	25.1	54.8	
D	a	6.0	3.0	—	9.0	—	1.5	2.5	4.0	13.0	4.0
	b	13.0	11.5	—	24.5	18.0	6.0	4.0	28.0	52.5	
E	a	8.0	3.0	6.0	17.0	0.5	3.5	4.0	8.0	25.0	2.0
	b	15.2	10.0	3.0	28.2	11.0	7.5	4.3	22.8	51.0	
F	a	10.5	13.0	5.7	29.2	2.0	1.8	1.0	4.8	34.0	1.6
	b	12.5	2.0	3.6	18.1	25.0	6.3	3.5	34.8	52.9	
G	a	4.5	4.5	7.5	16.5	0.5	1.0	1.3	2.8	19.3	3.4
	b	28.5	7.0	2.5	38.0	15.5	10.0	2.0	27.5	65.5	
H	a	5.0	7.3	6.3	18.6	1.0	—	2.0	3.0	21.6	3.0
	b	17.4	9.0	6.3	32.7	15.0	8.0	10.0	33.0	65.7	
I	a	6.5	5.0	5.5	17.0	1.0	1.0	—	2.0	19.0	4.5
	b	38.5	17.3	3.5	59.3	15.7	10.0	—	25.7	85.0	
J	a	7.7	2.5	1.0	11.2	3.0	—	12.8	5.8	17.0	3.4
	b	13.7	11.2	4.5	29.4	21.3	—	7.8	29.1	58.5	

It is thus evident that the gill-netting in August 1966 removed a very substantial proportion of the char, *viz.* roughly three quarters of the population of catchable char.

Ageing of trout was carried out from scales. These were taken from the side of the body just above the lateral line and below the dorsal fin.

Scales of char taken during the whole time appeared to be very difficult to interpret (as also were the opercles). Otoliths were therefore kept from 1966 from some char and these have been interpreted in the traditional way (NORDENG 1961).

III. Arctic char

Habitat within Lake Långbjörsjön

It is generally known that arctic char tends to be more abundant than brown trout when the two species live sympatrically. The more pelagic life of the char and its being less narrowly bound to limited spawning places could be the explanation of this. In the sport fishing in Lake Långbjörsjön, char are seldom caught, while the trout entirely dominates, owing to the fact that as a rule the fishing is performed with the fly, which is preferred by the trout. When fishing with gill nets it at once appeared that char were much more numerous, as was to be expected. Generally two or three char were caught for each trout. This ratio varied, however, from year to year and also in different parts of the lake, in spite of its smallness.

As appears from Fig. 1 the lake was divided into several zones. The data for mean catch per gill net during the years 1960—70 are shown in Table 4. The gill nets were placed in first or second place in a gang thrown perpendicularly from the shore.

It appears from the index char/trout that both species occur all over the lake, but that trout is most common in sections A, B, C, E and F. As will be seen from Fig. 1 these sections include the areas around in- and outlet as well as section F, where there is a broad littoral zone. These sections were united to form the "trout zone". The rest of the lake, including steeper shores and a more pelagic habitat, was dominated by the char — "char zone". The smallest trout were most littoral, as is proved by the fact that practically no trout were caught in the 36 v/a nets when placed as second net in the gang.

This distribution of the two species in the lake agrees with what is known of their feeding habits (*cf.* NILSSON 1955). A statistical examination of the significance of the different part catches has been made (see Appendix 1). The char is more equally distributed over the entire lake, as has already been pointed out in an earlier analysis (GUSTAFSON *et al.* 1969).

Determination of age

Most of the char caught were not aged. In the years 1966—71 a total of 193 specimens were aged according to their otoliths:

Age	1966	1967	1970	1971
2+	—	7	9	4
3+	9	6	16	4
4+	—	9	65	4
5+ and older	—	5	35	20

Since length was used as an indication of age (see below), the following sizes were noted for the age groups:

Age	1966	1967	1970	1971
2+	—	14.0—16.0	14.5—15.5	15.0—16.0
3+	17.0—19.0	16.0—19.5	17.0—19.0	17.0—18.5
4+	—	20.0—23.5	19.0—25.0	20.0—23.5
5+ and older	—	22.5—23.5	20.5—27.0	21.0—29.0

Since, selectively, only the fastest-growing 2+ char were caught in the nets and the age groups 4+ and 5+ merged into each other in their size distributions, it was concluded that only 3+ fish could reasonably be aged by their sizes, fish of 16.0—19.5 being judged to be predominantly in their fourth growth season.

Strength of year classes

Using this size measurement as an indication of age, it was possible to group the apparent strength of some year classes. Fish were caught in the same period of the summer in all years with the exception of 1961, when the fishing was performed one month later. An alternative index is given in brackets, for this year, when char of 20.0 and 20.5 cm were added to the catch but those of 16.0 and 16.5 were not included. Air temperature at the near-by station of Storlien was used for comparison.

Class born in	Caught in	Index	May—June temperature (Storlien) (over and under mean)
1958	1961	8.0 (6.2)	−0.75
1961	1964	25.7	+1.00
1962	1965	4.7	−1.85
1963	1966	9.3	+2.75
1966	1969	9.7	+1.65
1967	1970	3.0	−0.85

The three best year classes were all born in springs with higher than average air temperature during May and June. This is the same sort of relation that has been found repeatedly by Swedish fishery biologists in recent years for several species.

The year class 1961, however, seems to have been quite exceptional. In the years 1961 and 1966 the total elimination of competitors from Lake Långbjörsjön was highest and both year classes were the two best of the six studied. The reduction of the population density may thus have contributed to the survival of the young char in those years, albeit only during the later part of their first summer.

Change of growth rate

It was thought beforehand that the reduction of the char population in 1966 by almost 75 per cent would give the surviving char a better growth rate. The change, however, was rather small and also hard to prove. The aged fish are rather few in each age group and give too small samples, but 35 fish 5+ and older in 1970 had an average length of 23.1 cm, while 20 fish of the same age in 1971 were 24.9 long on average.

The gill net fishings in section J during the years 1966, 1969, 1970 and 1971 provide some material for a further support for a small improvement in the growth rate. The distribution between the different groups of length and gill nets was the following:

Length interval	1966				1969				1970				1971			
	36v	28v	24v	18v	36v	28v	24v	20v	36v	28v	24v	20v	36v	28v	24v	20v
15.0—15.5 ..	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
16.0—16.5 ..	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
17.0—17.5 ..	1	—	—	—	1	—	—	—	—	—	—	—	2	—	—	—
18.0—18.5 ..	—	—	—	—	2	—	—	—	1	—	—	—	2	—	—	—
19.0—19.5 ..	7	—	—	—	5	—	—	—	2	—	—	—	—	—	—	—
20.0—20.5 ..	4	1	1	—	7	1	—	—	1	1	—	—	1	—	—	—
21.0—21.5 ..	3	4	—	—	4	—	—	—	8	2	—	—	—	1	—	—
22.0—22.5 ..	4	5	1	—	4	3	—	—	5	3	1	—	2	1	1	—
23.0—23.5 ..	2	1	1	—	3	2	—	—	4	7	—	—	—	1	1	—
24.0—24.5 ..	—	2	—	—	2	2	4	—	1	4	4	—	2	3	1	—
25.0—25.5 ..	—	—	—	—	—	—	—	—	2	—	—	1	2	2	1	—
26.0—26.5 ..	—	—	1	—	—	—	—	1	2	—	1	—	1	—	—	—
27.0—27.5 ..	—	—	—	—	—	—	1	—	—	—	—	—	1	—	2	—
28.0—28.5 ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29.0—29.5 ..	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—
30.0—30.5 ..	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Average length	21.3				22.1				22.7				22.4			
Number char over 25.0 cm	1				4				6				10			

The absence in 1970 of char with a length of 15.0—17.5 in the gill nets with the smallest mesh size indicates, together with the higher average length of char caught this year in these gill nets, that year class 1967, which was than in its fourth summer, had grown somewhat better than usual. This year class was only slightly smaller than some of the others (see above) although the number of parents was much reduced.

Though a certain effect can thus be traced, it is very remarkable that the result of the drastic reduction of the population was so small. In other cases when a population of char has been reduced in a very high degree by rotenone the growth rate has markedly improved and the amount of food accessible in the form of Gammarus also increased rapidly (Fisk 1970).

Maturity

In July 1970 it was noted whether char which were caught were maturing or were immature. It was found that about half of the catch consisted of immature fish of both sexes.

	14	15	16	17	18	19	20	21	22	23	24	25	26	27	Total
males, immature	2	4	—	4	5	6	9	17	17	8	1	—	—	—	73
maturing	—	1	—	1	1	1	13	11	18	9	11	2	2	2	72
females, immature ..	1	1	—	4	3	5	12	23	25	6	7	4	—	—	91
maturing	—	—	—	—	—	1	7	20	26	24	12	7	2	—	99

Judged by the criterion of size this means that a few males are maturing in their fourth summer, half the males in their fifth but most of them in their sixth summer of life. The females, too, seem to mature at the same sizes and ages. There is no evidence of size difference between the sexes, the males being 21.1 cm and the females 21.8 cm. The sex ratio is likewise rather even, the males constituting 43 per cent of the sample.

IV. Brown trout

Changes of growth rate

These changes are shown in the following table (number of examined trout in brackets).

Catch year	Mean length (cm)		Average weight of fisherman's catch weight (kg)
	4+	5+	
1956	21.6 (5)	25.0 (8)	0.16
1957	20.0 (6)	26.0 (9)	0.17
1958	20.7 (36)	24.1 (55)	0.16
1959	19.6 (36)	24.2 (14)	0.13
1960	22.5 (27)	25.5 (24)	0.15
1961	25.1 (53)	27.6 (27)	0.14
1962	23.9 (27)	27.1 (9)	0.12
1963	24.1 (38)	27.8 (3)	0.14
1964	23.0 (9)	26.4 (23)	0.15
1965	22.8 (33)	27.0 (31)	0.10
1966	21.3 (31)	26.2 (35)	0.13
1967	20.7 (5)	26.7 (5)	0.15
1968	22.8 (7)	24.5 (6)	0.13
1969	22.7 (33)	25.1 (46)	0.16
1970	22.3 (36)	26.2 (25)	0.16
1971	23.5 (5)	27.3 (4)	0.21

(Age group 4+ was chosen as being the biggest group and 5+ as being the one most important for the fishermen.) The intensive fishing 1959—61 resulted in better growth rate during some few years. After that it decreased gradually to 1967 for 4+ and 1968 for 5+ trout. At present the growth rate is rising (as a result of the fishing for char in 1966?). The average weight in the fishermen's catch shows that the changes in growth rate are not always noticeable for the fishermen. The intensive fishing removes the old trout which are succeeded by young ones with a better growth. This better rate has not as a rule neutralized the rejuvenation. (The growth rate for trout is also treated by LINDSTRÖM *et al.* 1970).

A difference in the growth rate for trout in the "trout zone" and the "char zone" might be expected. Trout aged from 3+ to 6+ are bigger in the "trout zone" in 11 samples out of 13.

The strength of year classes

The strength of year classes has been dealt with by LINDSTRÖM *et al.* (1970). It was pointed out that "a permanent influence on the recruitment level of trout by the char population in the lake should also be expected". It is not possible to draw any conclusions from the reduction of char in

1966. In 1967 and 1968 the fishing was restricted. In 1969 and 1970 the usual gill-net fishing was performed (one standard set three nights running at the beginning of July). The age composition of trout in the four last years it was performed is given below.

Year	1965		1966		1969		1970	
	Number	%	Number	%	Number	%	Number	%
2+	8	8	16	13	7	7	6	5
3+	17	16	42	33	4	4	21	18
4+	33	31	31	23	33	33	36	32
5+	31	29	45	27	46	46	25	22
6+	17	16	5	4	10	10	24	21
7+	—	—	—	—	—	—	2	2

The comparatively high number of trout with an age of 5+ in 1969 and 6+ in 1970 may indicate a good year class 1964, but is more likely the result of the restricted fishing in 1967 and 1968.

V. Discussion

The aim of this experiment was to try to achieve better sport fishing by reducing the number of trout and char. How this aim has been attained appears from the survey of the sport fishing in Lake Långbjörsjön given below:

Year	Brown trout						Arctic char
	Fishing trips	Catch number	Weight (kg)	Av. weight (kg)	Per trip		Number
					Fish	Weight (kg)	
1948	34	272	51.9	0.19	8.0	1.53	3
1949	26	128	25.5	0.20	4.9	0.98	11
1950	28	224	36.9	0.16	8.0	1.32	18
1951	8[1]	25	4.6	0.18	3.1	0.58	3
1952	21	169	26.2	0.16	8.0	1.25	6
1953	23	95	15.4	0.16	4.1	0.67	1
1954	23	99	17.9	0.18	4.3	0.77	1
1955	16	64	12.9	0.20	4.0	0.81	0
1956	30	137	22.1	0.16	4.6	0.74	3
1957	33	97	16.6	0.17	3.0	0.50	3
1958	28	150	24.6	0.16	5.4	0.88	4
1959	14	54	7.2	0.13	3.9	0.51	7
1960	19	63	9.5	0.15	3.3	0.50	5
1961	29	142	19.5	0.14	4.9	0.67	23
1962	19	93	11.6	0.12	4.9	0.61	27
1963	38	190	26.1	0.14	5.0	0.69	36
1964	25	101	15.1	0.15	4.0	0.60	25
1965	28	123	12.7	0.10	4.4	0.45	27
1966	24	102	13.3	0.13	4.3	0.55	11
1967	19	130	19.3	0.15	6.8	1.02	29
1968	15	82	10.8	0.13	5.5	0.72	8
1969	26	111	18.0	0.16	4.3	0.70	27
1970	20	83	13.0	0.16	4.2	0.65	23
1971	34	133	27.4	0.21	4.0	0.84	109

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[1] not complete

Since 1961 the sport fishermen have been requested to kill and register all char caught.

There was a continuous deterioration in the fishing in Lake Långbjörsjön from 1948 onwards, with a culmination in 1959. This year the trout which were caught were very small, the average weight being 0.13 kg, and the number had dropped to half of the catch during the first years, when the registration of the fishing started. The interest of the fishermen had consequently also declined in a high degree and only 14 fishing trips to the lake were noted this year. Other lakes in the region appeared more attractive at this time.

Since this time the fishing has improved somewhat, probably as a result of the actions taken, though the changes are on the whole rather small. In 1963 Lake Långbjörsjön had 38 fishing trips, the highest figure on record, and also the highest catch of trout (with the exeption of the years 1948 and 1950) and the highest number of char since the recording started. It is true that the year was warm, which may have favoured the fishing, but it seems reasonable to interpret the fishing results as a consequence of the action taken.

After this year (1963) the fishing remained rather similar each year up to 1971, when the number of fishing trips amounted to 34, the next highest value, and the average weight of the trout which were caught, 0.21 kg, was even a little higher than when the fishing started. The number of char which were caught had risen to 109, which is an all-time record, the next highest being only one third of this figure (36, in 1963).

Considering the extensiveness of the actions taken the success may seem rather modest. Nevertheless, the downward trend from the beginning of the period, which perhaps was mainly due to the fact that only trout were caught and thus the balance trout/char deteriorated, was broken through the intensive fishing with gill nets and seine. Nor has the belief of anglers that gill-net fishing would entirely destroy their chances been confirmed.

As a final conclusion concerning the experiment it can be stated that a certain degree of success was achieved but that the input of labour was large. A more intensive fishing with a bigger reduction of the populations might have caused a more substantial improvement in the growth rate for both species but it would then probably be necessary to prohibit sport fishing for some few years in order to give the remaining fish the opportunity and time to grow. From the point of view of sport fishing such a development would probably have been a poor alternative.

VI. Summary

Angling in a small mountain lake close to the Norwegian border was registered during the period 1948—1971. A discouraging trend in the average

size of brown trout gave the impetus to a management experiment to reduce the fish density. The heaviest reduction was of arctic char, 75 per cent of the adult population of which was removed in 1966. Brown trout, too, was netted and seined.

Growth data and year-class analysis indicate that the overall effect on the fish population was slight. Some growth-rate improvement appeared in char and trout. The year classes were influenced by spring climate to the same extent as by exploitation by man of the number of spawners.

The fears of the average angler that the gill nets would ruin the angling possibilities were not fulfilled. The trend of a declining yield in angling was broken and in 1971 the average weight of brown trout was the highest on record. The same was true of the number of arctic char caught with the fly.

VII. References

DAHL, K. 1943. Ørret og ørretvann. (2nd edition.) Oslo. 182 p. (In Norwegian.)

— and S. Sømme. 1947. Om driften av fiskevann. (2nd edition.) *Landbruksdepartementets Småskrift* (75). 24 p. (In Norwegian.)

FAGERSTRÖM, Å. 1970. Sportfisket i några jämtländska fjällsjöar. *Inform. Inst. Freshw. Res., Drottningholm* (10). 35 p. (Mimeographed in Swedish with English summary.)

— K. J. GUSTAFSON and T. LINDSTRÖM. 1969. Tag shedding, growth and different mortality in a marking experiment with trout and char. *Rep. Inst. Freshw. Res. Drottningholm* 49: 27—43.

FISK, E. 1970. Fiskevård med rotenon i svältrödingbestånd. *Inform. Inst. Freshw. Res.* (14). 5 p. (Mimeographed in Swedish with English summary.)

GUSTAFSON, K. J., T. LINDSTRÖM and Å. FAGERSTRÖM. 1969. Distribution of trout and char within a small Swedish high mountain lake. *Rep. Inst. Freshw. Res. Drottningholm* 49: 63—75.

LINDSTRÖM, T., Å. FAGERSTRÖM and K. J. GUSTAFSON. 1970. Fishing pressure, growth and recruitment in a small high mountain lake. *Rep. Inst. Freshw. Res. Drottningholm* 50: 100—132.

NILSSON, N.-A. 1955. Studies of the feeding habits of trout and char in North Swedish lakes. *Rep. Inst. Freshw. Res. Drottningholm* 36: 163—225.

NORDENG, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North Norway. Age and spawning frequency determined from scales and otoliths. *Nytt Mag. Zool.* 10: 67—123.

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

Appendix

Trout caught in gill nets 36 v/a at first place in gang

Cause of variance	Degrees of freedom	Sums of squares	Mean square
Mean values between samples	1	277	277
within samples	30	1.20	34
Quotient between mean squares=8.1	Significance between 0.01 and 0.001		

Trout caught in gill nets 28 v/a at first place in gang

Cause of variance	Degrees of freedom	Sums of squares	Mean square
Mean values between samples	1	43	43
within samples	29	266	9.2

Quotient between mean squares=4.7 Significance between 0.05 and 0.01

In the same way the following values are arrived at.

Quotient between mean squares		Significance
Trout		
Mesh size 24 v/a first place	0.6	—
Mesh size 36 v/a second place	0.2	—
Mesh size 28 v/a second place	3.0	0.20—0.05
Mesh size 24 v/a second place	8.9	0.01—0.001
All nets at first place	8.9	0.01—0.001
All nets at second place	7.3	0.05—0.01
Char		
Mesh size 36 v/a first place	0.3	—
Mesh size 28 v/a first place	4.5	0.05—0.01
Mesh size 24 v/a first place	0	—
Mesh size 36 v/a second place	5.1	0.05—0.01
Mesh size 28 v/a second place	0.1	—
Mesh size 24 v/a second place	2.4	0.20—0.05
All nets at first place	5.0	0.05—0.01
All nets at secand place	6.9	0.05—0.01

Mean values for the samples

	Nets in first place			Nets in second place		
	36 v/a	28 v/a	24 v/a	36 v/a	28 v/a	24 v/a
	Number of trout			Number of trout		
"Trout zone"	11.7	6.8	6.1	1.6	2.2	4.6
"Char zone"	5.8	4.4	5.2	1.4	1.0	2.2
	Number of char			Number of char		
"Trout zone"	16.9	8.2	4.5	11.9	7.5	3.8
"Char zone"	19.0	11.6	4.4	17.2	8.0	6.3

The effect of temperature on incubation time, growth and lethality of embryos, larvae and juveniles of the ide, *Idus idus* (L.)

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Contents

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I. Introduction

The effect of the temperature on the incubation time in the ide, *Idus idus* (L.) has been observed by SUNDEVALL (1855), STANKOVITCH (1921), SEGERSTRÅLE (1926), POPESCU *et al.* (1958) and CALA (1970 a). LENKIEWICZ (1964) described its thermal preferenda, but the growth of the alevins and the temperature resistance of the species have not been observed under controlled condition.

The purpose of the present investigation was to determine temperature and time relationships with respect to incubation time, growth and survival.

II. Materials and Methods

Materials

The artificial fertilization was done in River Kävlingeån, 11 km NW Lund (55° 47′N, 13° 05′E), during the years 1965 to 1969, except in 1966 when spawning was very irregular due to long periods of low temperature. Every year sexually mature fish were electro-fished. 2 or 3 females (about 46 cm long and 1.60 kg heavy) and 3 or more males (about 45 cm long and 1.30 kg heavy) were selected when spawning.

The adhesive eggs were laid in river water at about 5° to 6°C in plastic vessels with dry pine-tree branches and transported to the laboratory and transferred to about 4° to 5°, approximately 2 hours after spawning. Conglomerating eggs were discarded in the tests in order to avoid the action of *Saprolegnia* sp. Besides, STOCKARD (1921) and KINNE and KINNE (1962) observed a reduced development rate of incubating eggs of cyprinodont species on account of the conglomeration. Twice a day temperature, numbers of dead embryos and hatched alevins were recorded and eggs with *Saprolegnia* were removed from the aquaria.

Incubation temperatures. Definitions

Constant temperature. After fertilization the eggs were placed in a constant temperature.

Rising temperature. After fertilization of the eggs the temperature was increased 1°C per day up to a fixed level.

Fluctuating temperature. After fertilization the eggs were exposed every 24 hours to alternating increase or decrease of temperature from about 4° to 9°, 11° or 12° during the incubation time (see Table 4). The tests took place in a room with a constant temperature of 4° ± 0.5°. The temperature was regulated with a glass-covered electric heater suspended in the aquarium.

Temporary exposure to low temperature. After fertilization the eggs were exposed to temperatures of 4° or 5° during 5, 10, 15 or 20 days (see Table 5). After this period the temperature was increased 1° per day up to 14°.

Growth

The newly hatched larvae were measured under a stereo-microscope by laying the specimen on a millimeter slide. The total length of the juveniles (tip of the nose to tip of the tail, lobes compressed) was measured in the same way on a millimeter paper.

The larvae were fed cultivated infusoria. Selected plankton obtained in a pond with a plankton net (mesh-size 90μ, 160μ, 200μ successively) was used to feed the juveniles.

Growth under constant temperature was investigated in three series of experiments at 16°, 17.5° and 22°C. At 17.5° the larvae hatched and remained in the same 35 litre aquarium. At 16° and 22° 600 larvae were transferred from the incubation aquaria to each of two 35 litre aquaria in order to control mortality and temperature during the first methamorphis stages.

Lethal Temperature

The method to determine the lethal temperature was essentially that used by BRETT (1952) who defines the lethal temperature as that at which 50 % of the population is dead after indefinite exposure. The duration of the tests was adjusted according to observations during the experiment, but prolonged as precaution until 12 hours. Fish were considered dead when no response to mechanical stimuli (small brush) was obtained. 24 hours before the tests the fish were not fed. The time at which each fish died was noted.

Two series of experiments were carried out:

Larvae

Newly hatched larvae 2 days old, 7.5 to 8.0 mm long and 0.003 gr mean weight, were transferred from incubation aquaria to lethal bath. Incubation temperature (16° and 22°) was acclimation temperature. There were 50 larvae in every test.

Juveniles

Juveniles 90 days old, 1.4—1.9 cm long (range of the means for different tests) and 0.02—0.06 gr weight (range of the means for different tests) were acclimated to certain temperature levels (6°, 12° and 18°) by increasing or decreasing temperature 1° per day until the desired temperature was

Table 1. Averages of physico-chemical properties of experimental water.

A=Water from River Kävlingeån.

B=Aquaria in constant temperatures of incubation.

C=Aquaria in rising temperatures of incubation.

D=Aquaria in fluctuating temperatures of incubation.

E=Acclimation aquaria of juveniles for lethal temperatures.

	Temp. °C.	No. of Analysis	pH	20.10^6	O_2		Ca+Mg mmo 1/1	DH°	Alcalinity mekv /1	CO_2 mg/1	HCO^-_3 mg/1	CO^{2-}_3 mg/1
					mg/1	%						
A	5.8	2	7.5	420	10.0	82	4.2	23.6	2.8	9.1	172.8	0.2
B	5.5	7	7.6	156	12.2	98	1.4	8.1	1.7	4.2	91.4	0.2
	7.0	1	8.0	488	10.6	91	4.9	27.6	3.2	3.4	193.6	0.8
	9.0	7	7.6	138	10.1	90	2.3	13.1	1.7	4.8	105.5	0.2
	13.5	4	7.7	139	9.3	92	1.3	8.3	1.6	5.4	101.3	0.2
	14.5	4	7.9	385	9.4	95	3.8	21.4	2.0	2.4	121.7	0.5
	15.5	4	8.1	380	9.4	97	3.8	21.0	2.2	2.0	132.8	0.7
	17.0	2	7.8	158	8.8	94	1.5	8.2	1.4	3.0	82.7	0.2
	17.5	4	8.8	389	8.6	93	3.9	21.6	2.2	2.0	131.1	0.7
	18.5	4	8.2	401	8.8	96	4.0	22.2	2.4	1.8	148.8	1.0
C	7.0	1	8.0	488	10.6	91	4.9	27.6	3.2	3.4	193.6	0.8
	8.0	1	8.0	500	8.5	74	2.1	11.8	3.1	3.4	180.8	0.8
	9.0	11	8.0	484	10.6	94	4.8	27.1	2.9	2.8	177.0	0.9
	10.0	1	7.8	427	10.3	94	3.8	21.5	2.6	4.9	155.5	0.4
	11.0	9	8.0	536	10.3	95	4.8	26.9	2.9	3.7	177.0	0.7
	12.0	1	7.8	488	9.8	86	4.4	24.9	2.6	4.6	162.7	0.4
	14.0	1	7.8	477	9.5	95	4.1	22.6	3.0	5.1	182.1	0.5
	18.0	5	8.1	461	10.2	94	4.8	26.9	2.8	2.7	170.2	0.8
D	3.8— 9.1—3.8	15	8.0	482	11.3	93	5.4	26.3	2.9	3.3	160.0	0.7
	3.2—11.0—3.2	14	8.0	504	11.8	93	5.0	27.8	3.1	3.2	199.1	0.8
	3.6—12.0—3.6	12	8.0	467	11.4	96	4.6	25.8	2.7	3.1	163.6	0.7
	4.1—12.1—4.4	12	8.0	471	10.8	93	4.5	24.5	2.7	3.2	163.2	0.7
E	18.4	2	8.1	467	9.2	99	4.4	24.7	2.2	1.7	135.2	0.7
	12.2	2	8.0	477	10.2	97	4.4	22.2	2.6	2.8	158.5	0.7
	6.1	2	8.1	472	12.0	99	4.1	22.8	3.2	3.5	193.6	0.8

reached. The fish were kept in acclimation temperature at least 14 days before each experiment started. There were 5 to 10 juveniles in every test.

General

Aluminium glass aquaria filled with constantly aereted water were used. The water was continuously filtered through charcoal. The temperature desired for incubation, acclimation, growth and lethal bath was thermostatically controlled (Jumo-type GKT 10—0, 200 V-GA, Jumo-Type TG-M1, 220V-15A and stainless-steel immersion heaters 500 W/Type 45, 220 V/TID) and maintained constant (±0.1°C). Experiments were carried out under artificial light conditions (LD 12: 12). Some chemical and physical parameters of the water were continuously determined according to the methods described by KARLGREN (1962). The results are expressed as averages in Table 1.

Table 2. Incubation and hatching at constant temperatures. The number of hatched eggs at 10° and 16°C was not controlled but the hatching time of the surviving embryos was noted.

Water Temp. °C.	5.5	7.0	9.0	10.0	12.0	13.5	14.5	15.5	16.0	17.0	17.5	18.5	22.0
Number of eggs	300	100	600	—	100	262	200	200	—	450	100	100	200
Hatched % ..	0	11	13	—	64	79	76	66	—	84	57	51	61
Time to beginning of hatching, in days	0	24	18	14	—	10	9	7	6	6	6	4	4
Time to 50 % hatching, in days	0	27	22	17	—	11	11	9	8	7	8	5	5

III. Results

Incubation

Water qualities

The water conditions remained relatively constant during the experiments (Table 1). Some diferences can be seen in the B experiments (5.5°, 9.0°, 13.5° and 17.0°).

Time of hatching

A batch of test eggs is defined as hatched when 50 % of the surviving embryos had freed themselves completely from the chorion. Hatching has started when 10 % of the eggs have hatched. The periods of embryonic development is expressed as the length of time between fertilization and hatching (Kinne and Kinne *op. cit.*). Low temperatures were found to retard, and high temperatures to accelerate development as observed for the species in earlier papers.

Effect of constant temperature

The hatching time ranges from about 5 days at high constant temperature to 27 days at low constant temperature (Table 2).

It was found that no hatching occurs in temperatures lower than 6° and that 50 % hatching is possible only in temperatures higher than 12°. The highest precentage of hatching was obtained between 13.5° and 17°C.

Effect of rising temperature

The effect of temperature on incubation in constant or fluctuating temperatures has been studied by several authors. There are no data, however,

Table 3. Incubation period and hatching at rising temperature. Each experiment was conducted with 100 eggs. At 8°, 12° and 19° (A, B) the test was triple.

Temp. °C.	8	9	10	11	12	14	18	19	
								A	B
Hatched %	41 42 24	61	48	63	45 47 50	45	82	67 58 66	65 68 66
Time to 10 % hatching, in days	25	25	21	17	17	15	14	14	14
Time to 50 % hatching, in days	32	28	25	21	19	18	15	15	15

on eggs incubated in controlled rising temperature. Nine experiments were started at 4° and the temperatures risen as shown in Table 3 (*cf.* p. 2).

For temperatures between 8° and 14° there is a decrease of the hatching time, but at 18° and 19°C the hatching time remains constant.

Effect of fluctuating temperature

The effects of changing temperature on the rate of egg development was studied by *e. g.* GRAINGER (1959, *Rana temporaria* L.) and FAHEEN (1965, *Acanthocyclops viridis* JURINE), but so far there are no data on fish.

Therefore, four experiments were carried out as shown in Table 4. The experiments demonstrate that the time to hatching is shorter when the temperature level is risen, as is generally the case when temperature increases gradually. The time of hatching varies from 51 to 32 days.

Effect of temporary exposure to low temperature

CALA (*op. cit.*) stated that the success of the spawning in River Kävlingeån is greatly influenced by fluctuating water temperature. He concludes that a high percentage of the eggs is lost when the temperature decreases after spawning. In order to study these circumstances under laboratory condition four experiments were carried out (Table 5).

It is evident that long early exposition to low temperature retards hatching. At the same time the percentage of hatching eggs decreases, so that after 15 days of adverse conditions just 5 % of the eggs hatch, while no eggs remain alive after 20 days.

Effect of temperature on the rate of embryonic development

The influence of temperature on biological processes has been expressed with the coefficient Q_{10} associated with van 't HOFF's law. KINNE and KINNE

Table 4. Incubation period and hatching at fluctuating temperatures. Each experiment was conducted with 100 eggs.

Average. temp. °C.	Hatched %	Time to 10% hatching, in days	Time to 50 % hatching, in days
3.8— 9.1—3.8	7	48	51
3.2—11.0—3.2	13	35	47
3.6—12.0—3.6	29	27	32
4.4—12.0—4.4	23	24	32

(*op. cit.*), however, questioned its application to biological relations citing several earlier papers.

It was found that, this coefficient when applied to the rate of development of the ide eggs, has a constant value of 3.4 in the temperature interval 7°—22° but changes with rising temperature. Thus $Q_{10}=4$ at temperatures ranging from 8 to 12° and 1.3 between 12° and 19°. *Cf.* Fig. 1 which is based on data from tables 2 and 3. The regression lines were obtained through the least square method, using a logarithmic scale for time of incubation.

Effects of Temperature on growth

Size of larvae

Newly hatched larvae were measured between stages 28 and 39 as described by BALINSKY (1948). Due to the diversity of the material no size differences were stated between the samples incubated at 13.4, 17.4 and 22.1°. But larvae hatching at 9° were clearly smaller (Table 6).

Table 5. Incubation period and hatching after temporary exposure to low temperature. Each experiment was conducted with 100 eggs. After a period of a constant low temperature the aquarium temperature was risen 1° per day to 14°.

Initial low temp. °C.	Days exposure to low temp. °C.	Hatched %	Time to 50 % hatching in days
5	5	34	21
5	10	45	25
4	15	5	28
4	20	0	0

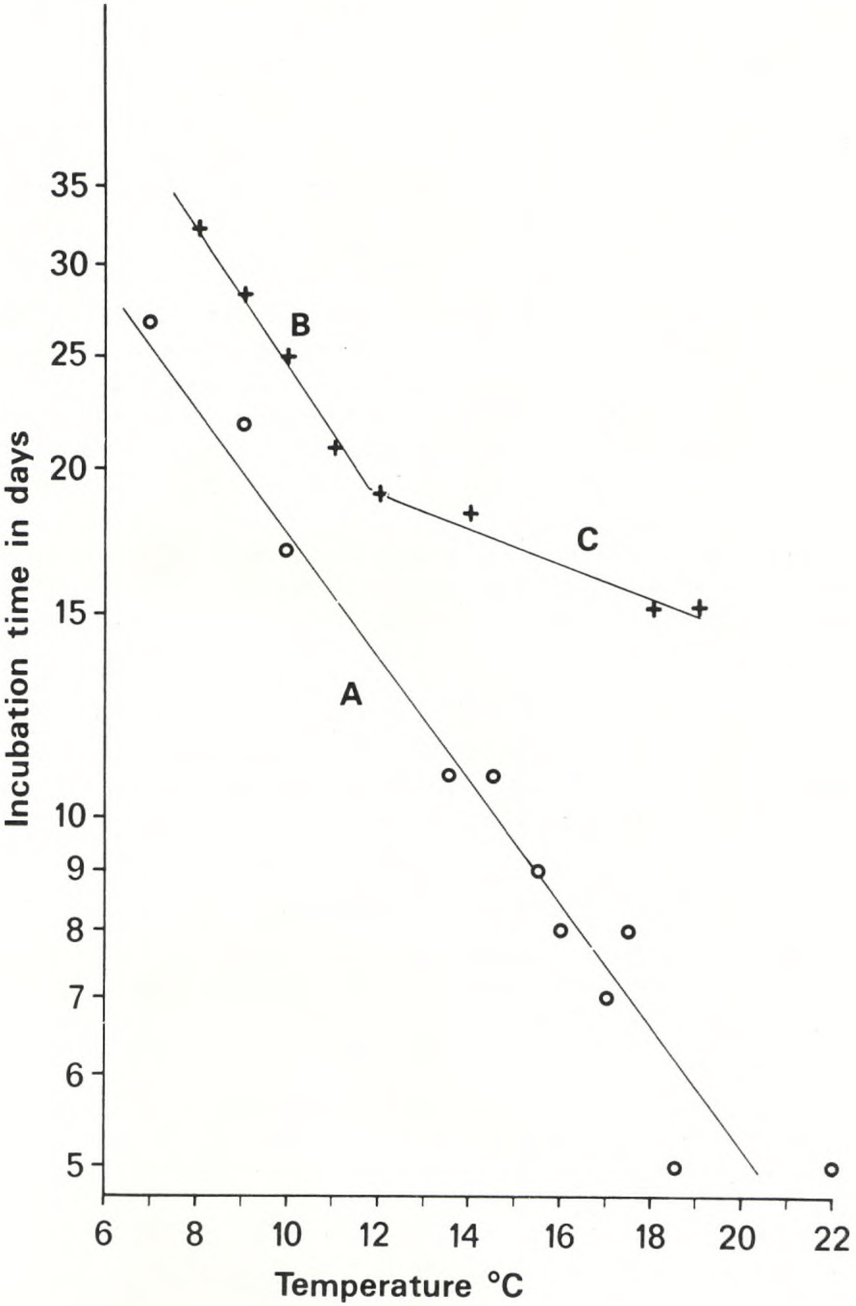

Fig. 1. Regression diagram showing the influence of constant (A) and rising (B, C) tempeatures on the time required for 50 % hatching of ide eggs.

Table 6. Length of the newly hatched larvae incubated at different temperatures.

Temp. of incubation °C.	9.0	13.4	17.4	22.1
Number of larvae	10	10	21	100
Average mm	6.6	7.3	7.1	7.4
Range mm	6.5—6.8	6.3—7.5	6.0—8.1	6.5—8.4

Growth

The growth of larvae and juveniles was studied under a constant temperature of 17.4° during 89 days. A few data were obtained under similar conditions at 16° and 22°. The result are shown in Table 7 and Fig. 2.

As observed by LASKER (1964) for *Sardinops caerules* (GIGARD) fast growth was registered during the first days of the fry stages. Similar observations were mentioned by CALA (*op. cit.*) concerning ide fry, reared at 18°C.

Further, at the temperatures examined the growth rate increased with increasing temperature. The size differences between 16° and 22° were 12 % after 10 days, and 30 % after 20 days.

Mortality of larvae

A great larval mortality is known to occur in the passage from nonfeeding to feeding stages. The mortality recorded at this time during the growth studies was 41 % at 16° and 47 % at 22°.

Upper lethal temperature

The relations between upper lethal temperature and acclimation temperature were studied in larvae, two days old, and juveniles, 90 days old. (Table 8, Fig. 3).

Table 7. Length increase of larvae and juveniles at different temperatures. The length is given as averages.

Designed temp. °C.	Days	1	3	6	9	10	11	20	23	43	59	78	89
16.0°	No. fish ..	100	—	—	—	100	—	78	—	—	—	—	—
	Length mm	7.4	—	—	—	8.8	—	10.8	—	—	—	—	—
17.4°	No. fish ..	20	10	20	20	—	20	—	20	20	20	20	32
	Length mm	7.1	8.8	9.7	10.0	—	10.0	—	11.2	14.6	16.7	19.3	20.5
22.0°	No. fish ..	100	—	—	—	100	—	59	—	—	—	—	—
	Length mm	7.4	—	—	—	10.0	—	13.7	—	—	—	—	—

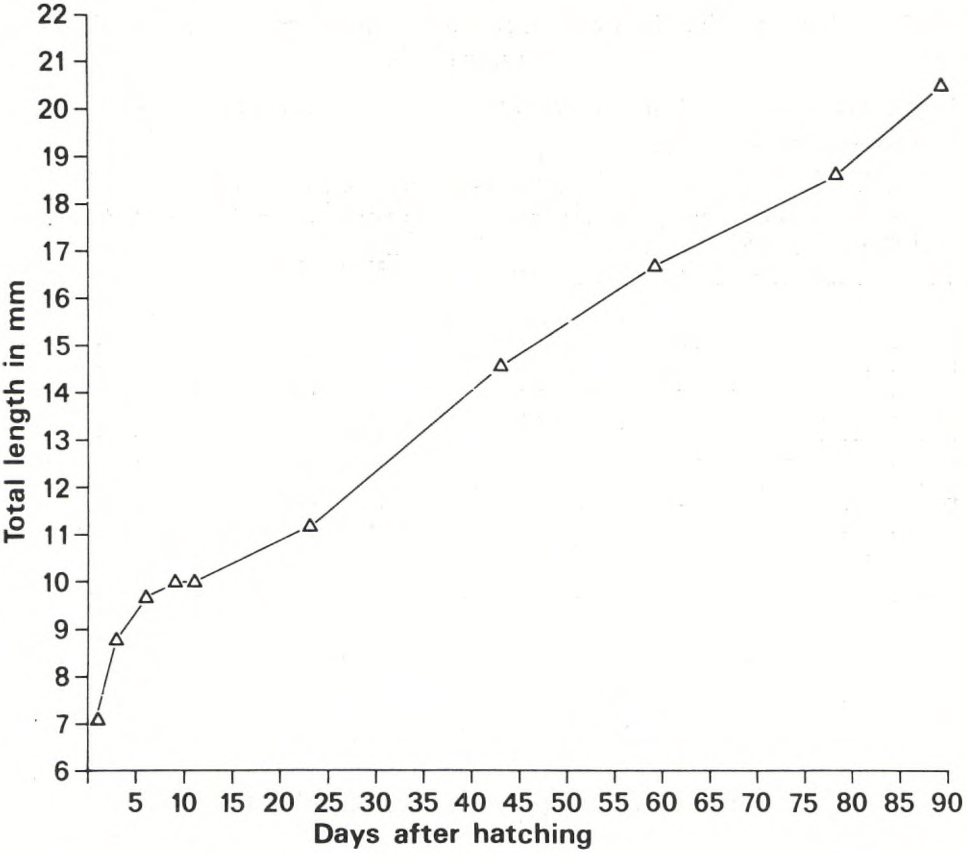

Fig. 2. Growth of the larvae and juveniles of Ide under constant temperature.

According to LENKIEWICZ (*op. cit.*) the temperature preferendum zone of the ide is very broad (9.7°—23.7°). The acclimation temperatures investigated fit comparatively well the preferendum amplitude. For juveniles the relation is linear (see Fig. 4) and increases 0.3° (with 95 % confidence limits 0.2—0.4) in the upper lethal temperature for each 1° of acclimation, while among the larvae this relation increases 0.8° (with 95 % confidence limits 0.4—1.2) as far as indicated by the few values obtained.

Resistance time

The relation between resistance time and temperature is described for several species. It is well known that it varies not only with specific characters but also with increasing acclimation temperature. In juveniles I found that the relation between acclimation and lethal temperature means an increase in the resistance time (Table 9).

Table 8. The relation between upper lethal temperature and acclimation temperature in ide.

No.=Left, number of tests and right, total number of fish examined.
%=Percentage mortality.

Upper test temp. °C	ACCLIMATION TEMPERATURE														
	90 days age 6°			90 days age 12°			90 days age 18°			2 days age 16°			2 days age 22°		
	No.		%	No.		%	No.		%	No.		%	No.		%
23.0	2	10	20	—	—	—	—	—	—	—	—	—	—	—	—
23.5	2	10	30	—	—	—	—	—	—	—	—	—	—	—	—
24.0	3	15	73	—	—	—	—	—	—	8	400	51	—	—	—
25.0	—	—	—	—	—	—	—	—	—	8	400	59	—	—	—
26.0	—	—	—	3	15	20	4	25	28	6	300	80	—	—	—
26.5	—	—	—	7	35	55	5	30	40	—	—	—	—	—	—
27.0	—	—	—	6	30	63	6	40	57	3	150	92	5	250	17
27.5	—	—	—	3	15	87	6	36	42	—	—	—	—	—	—
28.0	—	—	—	—	—	—	6	35	63	—	—	—	5	250	26
28.5	—	—	—	—	—	—	3	16	69	—	—	—	—	—	—
29.0	—	—	—	—	—	—	—	—	—	—	—	—	5	250	29
30.0	—	—	—	—	—	—	—	—	—	—	—	—	4	200	68
31.0	—	—	—	—	—	—	—	—	—	—	—	—	2	100	94
50 % dead .	23.7			26.6			27.2			24.1			29.1		

IV. Discussion

Influence of Temperature on incubation time

Constant temperature

Very well known is the effect of water temperature on the incubation time of fish eggs; 5.5 days at a mean temperature of 13.8°, 12.8 days at a mean of 10°, 17 days at a mean temperature of 10.1° and 23 days at a mean of 9.3° were established by CALA (*op. cit.*) for the beginning of hatching for ide incubated under laboratory conditions.

At constant temperature conditions (Table 2) the ide began to hatch after 4 days at temperatures ranging between 18° and 22°, after 6 days between 16° and 17.5° and at temperatures ranging from 7° to 16° the time to hatching varied from 6 to 24 days. Thus, approximately the same retardation as found by CALA (*op. cit.*) in a range of 4.5° of decreasing temperature, many occur at an interval of 9°.

Rising temperature

Studying the effect of a gradual change of the temperature on the incubation time is a new approach intending to give data from conditions more similar to the field environment than the usual procedure of constant

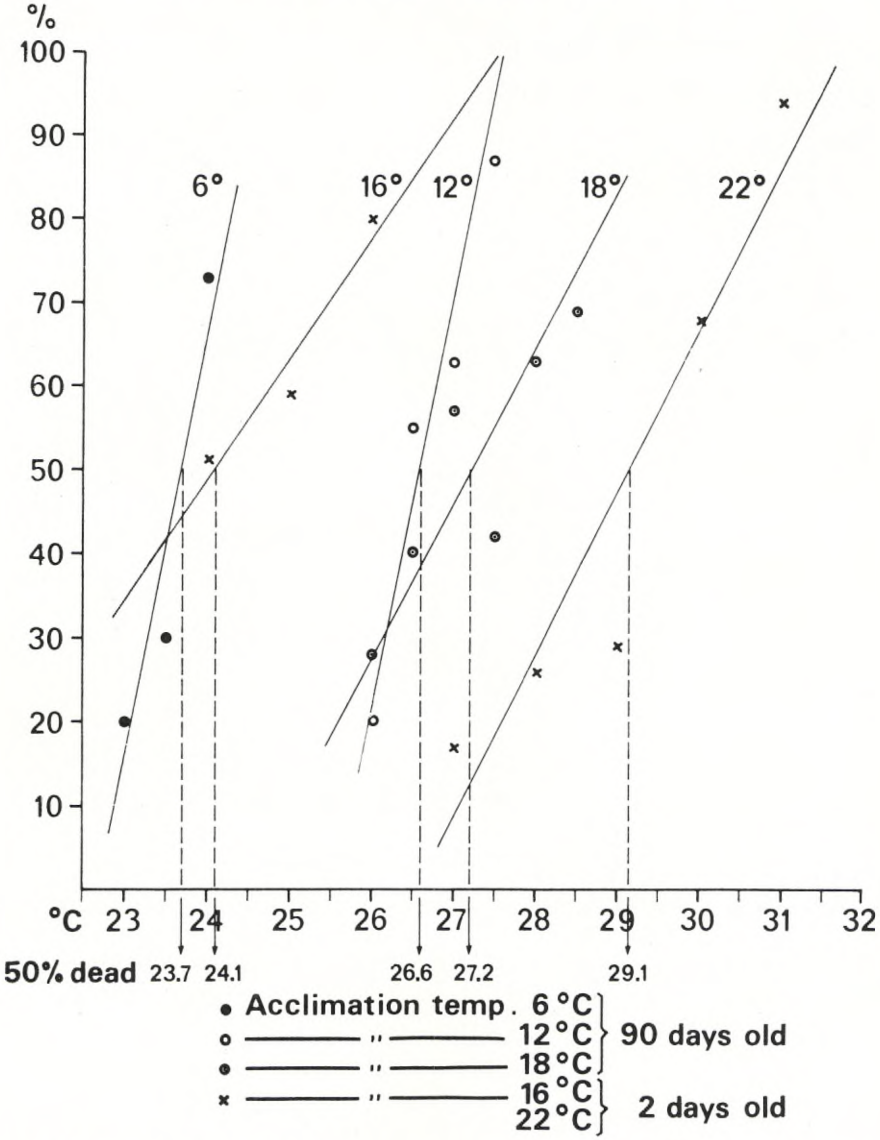

Fig. 3. The survival of larvae and juveniles acclimated at different constant temperatures.

temperature, without losing the possibility of a continuous control. The results are impressive compared with those at constant temperature (Fig. 1). It was found that at rising temperature the biologically doubtful coefficient Q_{10} (*cf.* p. 11) because of the accelerated rate of development, results in two different values. The rate of development reaches a maximum at 18°, beyond this temperature an impetuous hatching takes place. This maximum rate of development is the *rising temperature effect.*

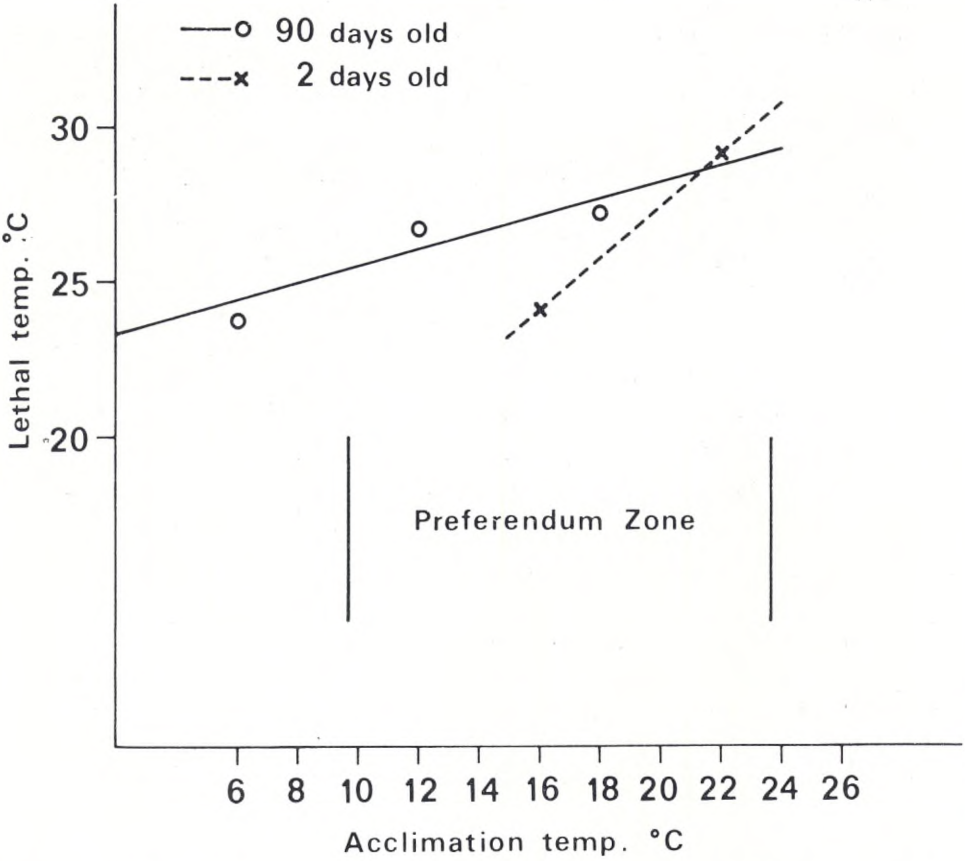

Fig. 4. The relation between temperature of acclimation and the upper lethal temperature at which 50 per cent of the larvae (dashed line) and juveniles (solid line) survive. The temperature preferendum zone is according to LENKIEWICZ (1964).

Fluctuating temperature

Preliminary observations established a relation similar to the experiments at constant and fluctuating temperatures. Low temperatures retard hatching.

Table 9. Resistance time in relation to the lethal temperature at different acclimation temperatures.

Acclimation temp. °C	6	12	18
Lethal temp. °C	23.7	26.6	27.2
Resistance time in hours	6	2—4	3—10

Temporary exposure to low temperature

The embryonic development is inhibited at temperatures lower than 6.0°. A constant temperature of 5.5° kills the eggs (Table 2). However, a shorter exposure to sublethal temperatures may not give total mortality. Table 5 gives a rough idea of the time during which different sublethal temperatures can be tolerated. The results agree with the field observations by CALA (*op. cit.*) in River Kävlingeån in 1966, where soon after the spawning a fall in temperature to <5° occurred; this situation lasted for two weeks.

Growth

Growth and rate of development were well studied by CALA (*op. cit.*), but laboratory investigations were carried out only for 6 days, so I reared larvae from hatching until 89 days old. A higher rate of development during the first 20 days is found in larvae reared in aquaria compared with those bred in nature, but a successive decrease of this rate is later observed. Forty days old larvae from nature were considerably larger than specimens of the same age in an aquarium. While larvae in the nature were 52 mm after 80 days, larvae in aquaria were 19 mm. The accelerating effect of laboratory rearing on young larvae was described by BLAXTER and HOLLIDAY (1958).

Upper lethal temperature

Since 1927 several authors have worked on lethal temperatures in fish to establish their zones of tolerance. FRY *et al.* (1946) in a study of the thermal tolerance of *Salvelinus fontinalis* partly based on data from BRETT (1941), demonstrate a discrepancy between different age stages which becomes evident at lower levels of acclimation. In the present investigation there were increasing differences in the upper lethal temperatures between larvae and juveniles and these differences are significant ($P < 0.05$) (Table 8, Fig. 4).

V. References

BALINSKY, B. I. 1948. On the development of specific characters in cyprinid fishes. *Proc. Zool. Soc. Lond.* 118 (II): 335—344.

BLAXTER,, J. H. S. and F. G. T. HOLLIDAY. 1958. Herring (*Clupea harengus* L.) in aquaria. II. Feeding. *Mar. Res.* (6): 1—19.

BRETT, J. R. 1941. Tempering versus acclimation in the planting of speckled trout. *Trans. Amer. Fish. Soc.* 70: 397—403.

— 1952. Temperature tolerance in young Pacific salmon, genus Oncorhynchus. *J. Fish. Res. Bd. Can.,* 9 (6): 265—323.

CALA, P. 1970 a. On the ecology of the ide *Idus idus* (L.) in the River Kävlingeån, South Sweden. Rep. Inst. Freshw. Res. Drottningholm 50: 45—49.

FRY, F. E. J., J. S. HART and K. F. WALKER. 1946. Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). *Univ. Toronto biol. Ser.* 54; *Publ. Ont. Fish. Res. Lab.* 66; 1—35.

FAHEEN, K. M. 1965. The effects of constant and varying temperatures on the development of *Acanthocyclops viridis* (Jurine). *Proc. R. Irish Acad.* 64 Sect. B.: 117—130.

GRAINGER, J. N. R., 1959. The effect of constant and varying temperatures on the developing eggs of *Rana temporaria* L. *Zool. Anz.* 163: 267—277.

KARLGREN, L. 1962. Vattenkemiska Analysmetoder. Uppsala. 118 p. (In Swedish)

KINNE, O. and E. M. KINNE, 1962. Rates of development in cyprinodont fish exposed to different temperature-salinity-oxygen combinations. *Canad. J. Zool.,* 40: 231—253.

LASKER, R. 1964. An experimental study of the effect of temperature on the incubation time, development, and growth of pacific sardine embryos and larvae. *Copeia* 2: 399—405.

LENKIEWICZ, Z. 1964. Temperature preferendum of some freshwater fishes. *Fol. Biol.* Warszawa 12 (1): 95—140.

POPESCU, E., V. ZIEMIANKOWSKI, and A. ROTARU. 1958. Citeva observatii asupra fecundatiei artificale si dezvoltarii embrionare si postembrionare la vaduvita (*Leuciscus idus* L.). *Bul. Inst. Cerc. pisc.* XVII (2): 57—64.

SEGERSTRÅLE, C. 1926. Från en fiskbiologs arbetsfält. I. Idfiske på Sarvlax. Allas Krönika, Illustrerad Veckoskrift, 23 (27): 685—686. (In Swedish.).

STANKOVITCH, S. 1921. Étude sur la morphologie et la nutrition des alevins de poissons cyprinides. *Trav. Lab. Piscic. Univ. Grenoble* XIII: 1—182.

STOCKARD, C. R. 1921. Development rate and structural expression: an experimental study of twins, "double monsters" and single deformities, and the interaction among embryonic organs during their origin and development. *Am. J. Anat.* 28, 115—277.

SUNDEVALL, C. J. 1855. Om fiskyngels utveckling. *K. Svenska Vetensk.Akad. Handl.* 1: 1—24. (In Swedish.)

Influence of oxygen concentration on growth and survival of larvae and juveniles of the ide, *Idus idus* (L.)

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Contents

I. Introduction

The influence of the oxygen regime on fish development, growth and survival has been examined by several authors, *e. g.* Graham (1949), Downin and Merkens (1957), Davison *et al.* (1959), Moss and Scott (1961), Stewart *et al.* (1967). It has been shown that a decrease in oxygen concentration retards development (Garside 1959), while an increase accelerates it (Kinne and Kinne 1962). In the same way growth of the fish may be retarded (Whitworth 1968). There is usually an interaction between temperature and oxygen.

It is well known that the ide tolerates a considerable variation of oxygen concentration, though this has not been investigated experimentally. On the other hand Cala (1970 a) describes incidences of fish mortality at periods of lack of oxygen in the South Swedish river Kävlingeån.

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Table 1. Averages of some physico-chemical properties of water used at tests.

A = Aquaria for acclimation of juveniles for studies of lethal levels of oxygen.
B = Aquaria for controlled diet.
C = Aquaria for repletion diet.

	Temp. °C.	No. of analyses	pH	ϰ 20.10⁶	O_2		Ca + Mg mmo 1/1	DH°	Alkalinity mekv /l	CO_2 mg/l	HCO_3^- mg/l	CO_3^{2-} mg/l
					mg/l	%						
A	18.4	2	8.1	467	9.2	99	4.4	24.7	2.2	1.7	135.2	0.7
	12.2	2	8.0	477	10.2	97	4.4	24.2	2.6	2.8	158.5	0.7
	6.1	2	8.1	472	12.0	99	4.1	22.8	3.2	3.5	193.6	0.8
B	*18.5	1	8.2	538	7.4	80	5.4	30.2	3.7	2.5	224.1	1.5
	18.3	3	8.1	514	9.5	101	4.5	25.2	2.1	1.8	125.7	0.6
	18.5	3	8.1	442	—	—	3.9	22.2	2.6	2.2	156.6	0.8
	18.6	3	8.1	442	—	—	3.9	22.2	2.8	2.4	167.1	0.9
C	*18.4	2	7.9	467	8.5	92	2.4	13.7	3.0	3.9	182.9	0.9
	18.1	3	8.0	382	9.4	101	1.9	10.5	2.1	1.8	126.3	0.7
	18.0	3	8.1	396	—	—	1.8	10.1	2.5	1.4	144.8	0.9
	18.0	3	8.1	393	—	—	1.8	10.3	2.5	1.4	150.5	0.8

* Corresponds to the acclimations for the respective tests.

The present paper deals with the effect of temperature on oxygen requirements of larvae and juveniles, and with the influence of oxygen concentration on growth of juveniles at constant temperature.

II. Materials and Methods

General

The material of *Idus idus* (L.) was obtained from the River Kävlingeån, South Sweden (see FLOREZ 1972).

The concentration of oxygen in the water used at the experiments was maintained at a constant level by using a fractionating column (FRY 1951). The water current in the column was effected with a water pump in a closed circuit. Dissolved oxygen concentration was determined by the WINKLER method.

Nitrogen flow was maintained constant by an ordinary two stage gas regulator and the flow meter Rota L. 10—976. Velocity of the water current in the test flasks was controlled with a manometer and a graduated test tube. The fishes were acclimated by increasing or decreasing the temperature 1° daily until the temperature wanted was reached. Temperature was thermostatically controlled and the test temperatures did not deviate from the stated average values more than 0.5°. The length of the fish was measured from the tip of the snout to the tip of the tail to the nearest millimetre.

In all the experiments the fish were subject to stimulation by changes of

Table 2. Characteristics of juveniles (A) and larvae (B) used in tests on lethal oxygen levels.

	Temp. of acclimation °C.	Σ fish	Age in days	Weight (g)		Length (cm)		Oxygen test flask	
				Average	Range	Average	Range	Water velocity in ml/min.	Temp. °C.
A	6	130	80	0.013	0.008—0.019	1.25	1.19—1.35	214	6.1—6.0
	12	130	80	0.046	0.035—0.065	1.72	1.64—1.80	150—250	12.0—12.3
	18	128	70	0.055	0.050—0.060	1.77	1.74—1.81	180—250	18.0—18.1
B	16	1.200	2—4	—	—	—	—	186—300	16.4—16.5
	22	800	2—4	0.003	—	0.74	0.65—0.84	187—260	22.0—22.1

light and dark by manipulations at sampling and by other environmental factors.

Tap water was used in all the aquaria and some chemical and physical properties recorded by the same procedures as in FLOREZ (1972) are given in Table 1.

Lethal levels of oxygen

The lethal levels of oxygen were found by a series of shock tests. The fish were transferred from the acclimation temperature in oxygen saturated water to a critical level of oxygen concentration at the same temperature for periods of 24 hours. The fish were placed in one litre glass flasks with plastic cork stoppers, penetrated by a tube for circulating water and thermometer. The flasks were submerged in a water bath of constant temperature. Twelve hours before starting the experiment the fish were fed and placed in the flask with oxygen saturated water (GRAHAM 1949). The water was replaced by tubing water from the gradient column. The water and nitrogen flow was started in the column 1 hour or 30—45 minutes before the test. An average of 20 minutes is given by SHEPARD (1955) as sufficient to obtain the wanted gradient of decreasing oxygen concentration.

The oxygen content of the water was checked twice before the start of the tests and two to five times during the tests. At the same time water velocity and temperature were recorded (Table 2).

The number of fish succumbing at low oxygen tension was recorded more or less continuously during the first eight hours, and then after 12 and 24 hours. A fish was considered dead when no opercular respiratory movements were observed. The water was changed before every test series. Tests were carried out in double sets. The results shown in Table 3 are the averages of both the tests. Larvae and juveniles were tested in order to compare the effect of low oxygen concentration on different ages.

Larvae

Newly hatched larvae were transferred from the incubation aquaria to the test bath. There were 50 larvae in every test. Incubation temperatures (16° and 22°) were acclimation temperatures. Weight and length (see Table 2) of newly hatched larvae were measured on material hatched at 22° which was considered valid also for material at 16°.

Juveniles

Juveniles hatched and reared under laboratory conditions were kept at the acclimation temperature for 14, 30 and 40 days at temperatures of 18°, 12° and 6° respectively.

After each test the fish were weighed (Table 2). There were 5 specimens in every test.

Oxygen and growth

The influence of a reduced oxygen concentration on the growth of the ide was studied at different diet conditions. The oxygen concentrations tested were obtained by taking water from two levels of the fractionating column and from an aquarium with oxygen saturated water. During the tests fish were placed in an 8 litre perspex-box hermetically closed and flushed through with water from the above mentioned column. A thermometer was inserted through the wall of the box for temperature control. The box was submerged in a constant temperature bath. Five determinations of oxygen content were carried out daily.

The oxygen concentration was kept at a constant level at each experiment, expect that it was increased to a fixed level 11^{00}—17^{00} every day to stimulate food intake (STEWART *et al.* 1967). The fish were fed at about 11^{00} and 15^{00}. The flow of water through the aquaria was interrupted briefly at the time of feeding. Excrements were removed daily.

Water velocity and temperature in the aquaria were recorded twice a day (Table 4). The water was filtered through charcoal before entering the column.

For the tests fish of approximately uniform size were selected from the available stock, discarding the largest and smallest individuals.

At the weight and length measurements the fish were slightly anesthetized with MS 222 (tricaine methanesulphonate) in water of their acclimation

Table 3. Mortality and survival of larvae and juveniles in a gradient of low concentration of dissolved oxygen at different temperatures. Dashed line is the lethal level.

T = Time to death in hours.
M = Percentage mortality during 24 hours.

Dissolved oxygen (mg/l)		Age: 80 days Acclimation Temp. 6° C		Dissolved oxygen (mg/l)		Age: 80 days Acclimation Temp. 12° C		Dissolved oxygen (mg/l)		Age: 70 days Acclimation Temp. 18° C		Dissolved oxygen (mg/l)		Age: 4 days Acclimation Temp. 16° C		Dissolved oxygen (mg/l)		Age: 4 days Acclimation Temp. 22° C	
Range	Mean of test	T	M	Range	Mean of test	T	M	Range	Mean of test	T	M	Range	Mean of test	T	M	Range	Mean of test	T	M
1.43	1.43	7	90	1.53	1.53	2	100	1.5—1.6	1.58	3	100	1.4—1.5	1.50	5	96	1.53	1.53	2	100
1.4—1.5	1.46	12	90	1.4—1.6	1.53	7	90	1.6—1.7	1.69	4	100	1.4—1.5	1.50	4	95	1.5—1.6	1.57	3	94
1.4—1.5	1.48	21	100	1.5—1.6	1.58	7	80	1.6—2.0	1.82	6	100	1.53	1.53	1	100	2.1—2.2	1.69	24	25
1.53	1.53	24	30	1.5—1.6	1.60	6	90	1.8—1.9	1.90	6	100	1.7—1.9	1.84	4	90	1.8—2.1	2.02	24	15
1.6—1.7	1.71	24	40	1.6—1.7	1.61	4	100	1.8—1.9	1.92	12	80	1.8—1.9	1.90	24	26	2.0—2.3	2.26	24	34
1.75	1.75	—	0	1.7—1.8	1.78	8	100	1.8—2.1	2.06	12	100	1.7—2.0	1.90	24	29				
1.7—1.8	1.78	—	0	1.7—1.8	1.82	24	20	2.15	2.15	7	90	2.1—2.3	2.29	24	3				
				1.8—1.9	1.89	—	0	2.2—2.3	2.35	24	20								

temperature. The specimens were then placed in the test boxes and the oxygen concentration adjusted to desired levels during the next five hours. Two series of tests were carried out:

Tests under controlled diet

Forty-five fish about 8 months old, electro-fished in the River Kävlingeån were acclimated in a 40 litre aquarium with oxygen saturated water at a fixed temperature (18°) and fed with plankton. During the last 8 days of the acclimation the fish were fed larvae of the mosquito *Chaoborus sp.*; the designated diet for the tests. The fish were kept one month at the acclimation temperature.

Feeding was effected in the following way: 120 mosquito larvae during the first and second days, 160 the third day and 240 larvae daily until the end of the test. The increase was due to the rapid consumption of the initial number of larvae. At the beginning and the end of the experiments the fish were weighed and their length measured.

Tests under repletion diet

Juveniles, 2 months old, hatched and reared in the laboratory at 12° were acclimated at 18° during seven days before the experiment. The fish were fed to repletion with selected plankton during acclimation and the experimental period. At the beginning and the end of the tests the fish were weighed together but their length measured individually.

III. Results

Effects of Lethal Oxygen Levels in Relation to Acclimation Temperature

The survival of larvae and juveniles at low concentration of dissolved oxygen at five temperatures ranging from 6 to 22° is shown in Table 3.

It is evident that there is a reduced resistance to low oxygen concentration which is related to the rise of acclimation temperature of the juveniles, as reported by GRAHAM (*op. cit.*), DOWNING and MERKENS (*op. cit.*) and MOSS and SCOTT (*op. cit.*) for other species. It is most interesting, however, that larvae acclimated at 22°, present a greater resistance to low oxygen concentration than larvae acclimated at 16°.

Larvae died more rapidly than juveniles when exposed to low oxygen levels (Table 3) which agrees with SHEPARD's investigation of *Salvelinus fontinalis* (1955).

Table 4. Growth at various concentrations of dissolved oxygen on a controlled diet (A) and on a repletion diet (B).

	Test period in days	Temp. °C. mean	Water velocity in the test ml/min range	Oxygen concentration		Age in months	Number of fish	Mean weight of fish			Mean total length of fish			No. of mosquito larvae fed (3)
				mean (1)	range (2)			initial (g)	final (g)	gain %	initial (cm)	final (cm)	gain %	
A	26	18.5	300—375	2.37	1.9— 3.0	9	9	1.51	1.90	20.5	5.78	6.20	6.7	5680
	26	18.5	273—375	3.09	2.7— 4.0	9	10	1.35	1.81	25.4	5.61	6.14	8.6	5840
	26	18.3		9.42	9.2— 9.7	9	9	1.26	1.67	24.5	5.35	5.97	10.3	5840
B	20	18.0	300—375	2.88	1.7— 4.2	2	23	0.032	0.091	65.0	1.70	2.39	28.0	
	20	18.0	300—375	3.82	2.2— 6.3	2	34	0.031	0.097	68.0	1.73	2.37	27.0	
	20	18.1		8.98	8.0—10.3	2	31	0.027	0.097	72.1	1.75	2.42	27.6	

1 Daily mean.
2 Over-all range during test.
3 Total number of mosquito larvae eaten by the fish.

The lethal level is distinct. At this limit a slight decrease of oxygen content may increase the mortality greatly (Table 3).

According to CALA *(op. cit.)* the oxygen concentration in River Kävlingeån during periods of heavy pollution is very low. In fact it seems to be lower than the lethal levels of the larvae and juveniles of ide as found in the present tests. The consequences of such periods of oxygen deficit may be catastrophic to the fish population. This may explain the reduction or the disappearance of certain species of fish.

Influence of Oxygen Concentration and Diet on the Growth

The influence of oxygen concentration on the growth of fish was studied by DAVISON *et al.* (*op. cit.*), HERRMANN *et. al.* (*1962.*), STEWART *et al.* (*op. cit.*) and WHITWORTH (*op. cit.*). My results (Table 4) agree with previous reports, although the differences in the relation weight-length are less clear.

The material used in the tests was heterogeneous, but in spite of that both series yielded similar results.

On a controlled diet

During the last two days of the test the fish kept at the lowest oxygen level lost the appetite. Therefore feeding was reduced. The weight differences between fish reared at the three levels of oxygen concentration are not significant, but the length clearly increases with the increase of oxygen tension. However, food and not oxygen was the limiting factor for growth under these conditions as evident from the weight increase of fish at the highest oxygen concentration (Table 4), which was of the same magnitude as at the next lower oxygen level.

On a repletion diet

An increase of weight follows the increase of the oxygen concentration, while relations as regards length are very uncertain.

IV. Summary

The effect of temperature on oxygen requirements and the influence of oxygen concentration on growth at different food intake of *Idus idus* (L.) are discussed.

Juveniles were found to be more resistant to a low concentration of oxygen when reared at high temperatures than at low.

The zone of mortality is delimited by a narrow range of oxygen concentration at all acclimation temperatures. Fish development is stimulated by greater oxygen concentrations.

V. Acknowledgments

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VI. References

CALA, P. 1970 a. On the ecology of the ide *Idus idus* (L.) in the River Kävlingeån, South Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 50: 45—99.

DAVISON, R. C., W. P. BREESE, C. E. WARREN, and P. DOUDOROFF. 1959. Experiments on the dissolved oxygen requirements of cold-water fishes. *Sewage Ind. Wastes* 31: 950—966.

DOWNING, K. M. and J. C. MERKENS. 1957. The influence of temperature on the survival of several species of fish in low tensions of dissolved oxygen. *Ann. Appl. Biol.* 45(2): 261—267.

FLOREZ, F. 1972. The effect of temperature on incubation time, growth and lethality of embryos, larvae and juveniles of the ide, *Idus idus* (L.). *Rep. Inst. Freshw. Res. Drottningsholm* 52: 50—64.

FRY, F. E. J. 1951. A fractionating column to provide water of various dissolved oxygen content. *Canad. J. Tech.,* 29: 114—146.

GARSIDE, E. T. 1959. Some effects of oxygen in relation to temperature on the development of lake trout embryos. *Canad. J. Zool.* 37: 689—698.

GRAHAM, J. M. 1949. Some effects of temperature and oxygen pressure on the metabolism and activity of the speckled trout, *Salvelinus fontinalis. Canad. J. Res.* 27: 270—288.

HERRMANN, R. B., C. E. WARREN and P. DOUDOROFF, 1962. Influence of oxygen concentration on the growth of juvenile coho salmon. *Trans. Amer. Fish. Soc.* 91(2): 155—167.

KINNE, O. and E. M. KINNE. 1962. Rates of development in cyprinodont fish exposed to different temperature-salinity-oxygen combinations. *Canad. J. Zool.,* 40: 231—253.

MOSS, D. D., and D. C. SCOTT. 1961. Dissolved-oxygen requirements of three species of fish. *Trans. Amer. Fish. Soc.* 90(4): 377—393.

SHEPARD, M. P. 1955. Resistance and tolerance of young speckled trout (*Salvelinus fontinalis*) to oxygen lack, with special reference to low oxygen acclimation. *J. Fish. Res. Bd. Can.* 12(3): 387—446.

STEWART, N. E., D. L. SHUMWAY, and P. DOUDOROFF. 1967. Influence of oxygen concentration on the growth of juvenile largemouth bass. *J. Fish. Res. Bd. Can.* 24(3): 475—494.

WHITWORTH, W. R. 1968. Effects of diurnal fluctuations of dissolved oxygen on the growth of brook trout. *J. Fish. Res. Bd. Can.* 25(3): 579—584.

On the dynamics of an exploited population of brown trout (*Salmo trutta,* L.)

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I. Introduction

A study was conducted in order to estimate growth, population size and natural and fishing mortalities in the exploited part of the trout population in a Norwegian lake, Olavatn, where fishing effort and yield were controlled over a period of two years. The estimated parameters were then to be used in a yield equation and the results compared with the observed yield in order to check the validity of the methods used. The study was envisaged as a pilot project, it being thought desirable to process on the computer by a small series before applying similar methods and formulae to trout material collected yearly since 1957 in a neighbouring lake, Øvre Heimdalsvatn. Lake Olavatn was chosen because the several owners of this lake were willing to keep complete records of their fishing in the lake during the period of the study.

Lake Olavatn is situated in Øystre Slidre in southeastern Norway at an altitude of 967 m. The lake has an area of 2.72 km^2, is oligotrophic with soft water, and is mainly surrounded by moor, heathland, bedrock and sparse clusters of birch. There is no permanent human settlement in the catchment area, only a few holiday cabins. Brown trout is the only fish species in the lake.

Early in 1969 an agreement was made with the 11 owners of Lake Olavatn to place the fishery in the lake under complete control throughout the years 1969—70, in order to make possible a preliminary study of the dynamics of the trout population in the lake. In accordance with the agreement, detailed daily fishing journals were kept by the owners, and all tagged fish recaptured were reported.

II. Materials and Methods

All fish lengths mentioned in this paper are total lengths measured from the tip of the snout to the tip of the tail. Mesh sizes of gill nets are measured from knot to knot.

Table 1. Fishing effort, total catch and tagging results. Lake Olavatn 1969—70.

Year	Fishing effort (gill-net nights)	Total catch		Number tagged	Number of recaptures	
		Number	Weight (kg)		Tagged in 1969	Tagged in 1970
1969	1329	1584	480	220	72	—
1970	1617	2397	737	203	55	95

Total fishing effort, catch and tagging data for the two years are shown in Table 1. Gill nets are the most important fishing gear in this lake, as in most Norwegian lakes, and the fishing effort is expressed as the number of gill-net nights. Usually the gill nets are lifted every day. In 1969 1,049 trout were taken on 879 gill-net nights, which gives an average catch of 1.19 trout per unit of fishing effort. Fishing with other kinds of gear, mainly otter, gave 535 trout. Total fishing effort was calculated as $879+535:1.19=1{,}329$ gill-net nights. The same procedure was used in 1970, when on 1,192 gill-net nights 1,767 trout were caught and 630 trout were taken on other kinds of gear.

In both years tagging was done in the last half of June and the first days of July shortly before the fishing season began. Fish for tagging were caught on a chase net or on otter, tagged under water without the use of anaesthetics and thereafter immediately released. Fish that showed any signs of having been damaged by the handling were not used for tagging. Numbered CARLIN tags with double steel thread were used, and the tags were attached below the front end of the dorsal fin in the way commonly used in smolt tagging (see CARLIN 1955).

Experimental fishing, chiefly to secure samples for growth calculations, was done August 21—28, 1969, with nylon gill nets having mesh sizes varying between 26 mm and 45 mm. However, 21 of the 29 nets used had a mesh of 35 mm. Samples of 239 trout were secured. The scale samples were taken in the area between the front of the adipose and the back of the dorsal fin (DANNEVIG and HØST 1931). Celluloid impressions of a number (usually 5—10) of readable scales from each fish were examined and measured under a scale projector.

The calculations were done on an IBM 360/40 computer.

III. Age and growth

The age and the back-calculated growth in centimetres of the 239 trout caught in August 1969 are shown in Table 2. The backcalculations were done on the asumption that the scale radius and the total length of the fish

Table 2. Back-calculated growth. Lake Olavatn 1969.

Age	Number	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8
3+	6	3.6	7.7	13.5	—	—	—	—	—
4+	12	3.6	9.0	14.4	20.3	—	—	—	—
5+	43	4.4	10.5	16.7	22.7	28.1	—	—	—
6+	106	4.1	9.9	15.5	21.3	26.7	30.0	—	—
7+	69	3.7	8.8	14.2	19.0	23.9	28.2	30.6	—
8+	3	4.1	8.4	12.7	16.5	22.4	26.0	29.8	32.5

increase proportionately. For trout smaller than about 10 cm the back-calculated lengths are probably heavily biased owing to allometric growth (KIPLING 1962). Corrections for this are unnecessary for our purpose, however, as fish of these sizes have not yet entered the exploited phase. A more serious matter might be the fact that, as mainly 35 mm gill nets were used for sampling, the material is not a random sample of the exploited part of the trout population (RICKER 1969). However, comparisons (unpublished) of growth values from samples taken on different mesh sizes in Lake Ø. Heimdalsvatn indicate that bias due to selective sampling is of small importance in trout populations with the growth rates and rates of fishing found in these lakes.

As can be seen from Table 2, there is a positive Lee's phenomenon (RICKER 1969) for age groups 5—8. This is very common in Norwegian trout lakes and is probably caused mainly by the size-selective mortality imposed on the trout population by the fishery. The best way to minimize bias from this is to base our growth calculations on SCOTT's method "and build up a growth picture of an hypothetical individual by adding successive yearly increments taken from the final complete year of each age sampled" (RICKER 1958, p. 189). One difficulty is that our small series does not contain fish older than eight years and even of these we have only three. After age seven the growth values have therefore been estimated by means of a WALFORD graph (WALFORD 1946). The results are shown in the first line in Table 3.

Conversion of growth in length to growth in weight is necessary for the yield calculations. RICKER's (1958) method of treating growth in weight as an exponential function was used. An analysis of variance showed that in our material there is no significant variation between length groups in the quotient W: l^3, where W is the weight and l the total length of the fish. The condition factor, $k = \frac{100 \cdot W(\text{in grammes})}{l^3(\text{in cm})}$ was on average 1.01. The coefficients, G, for exponential growth in weight were calculated from the formula $G_n = 3\ (\log_e l_n' - \log_e l_{n-1}')$, (RICKER 1969). The values of G_5 to G_{12} are shown in the second line in Table 3.

Table 3. Growth, gill-net efficiency and fishing mortality. Lake Olavatn 1969.

	l_4'	l_5'	l_6'	l_7'	l_8'	l_9'	l_{10}'	l_{11}'	l_{12}'	l_{13}'	l_{14}'	l_{15}'
Growth (cm)	20.3	25.7	29.0	31.4	34.1	35.4	37.0	37.5	38.0	38.4	38.7	38.9
G	0.70761	0.36243	0.23853	0.24747	0.11223	0.13263	0.04026	0.03975	—	—	—	—
Gill-net efficiency ..	0.04	0.15	0.75	1.00	0.96	0.80	0.65	0.60	0.52	0.50	0.43	—
F	0.05	0.19	0.95	1.27	1.22	1.02	0.83	0.76	0.66	0.64	0.61	—

IV. Population size

The size of the exploited part of the population was estimated by means of the PETERSEN method. Using BAILEY's correction the formula used was $\widehat{N} = \frac{m(c+1)}{r+1}$ (formula (3.7) in RICKER 1958). $\widehat{N}$ is here the estimated number of trout present in the lake at the time of tagging, m is the number of tagged trout, c the number of trout caught between the tagging in 1969 and the tagging one year later, and r the number of recaptures in the sample c.

As the smallest of the tagged fish were not completely vulnerable to the 35 mm nets most commonly used in the fishery, all fish smaller than 28 cm when tagged were omitted. Tagging was done all over the lake to reduce bias due to uneven distribution of the tagged fish. Fishing took place all over the lake.

The resulting PETERSEN estimates are shown in Table 4. The confidence intervals are wide, owing to the small number of tagged fish. As no correction was made for recruitment and as some fish smaller than 28 cm were included in the total catch, $\widehat{N}$ is probably too high. As both the tagging and the subsequent fishing were done at the same time of year in 1969 and 1970, the estimates for the two years will be biased in the same way, and they can be compared. Probably the exploited part of the population contained a few hundred more fish in 1970 than in 1969. As 1,584 trout were killed by fishing between the two tagging periods, the yearly recruitment to the exploited phase was probably of the order of 2,000 individuals.

The material is too small to render it worth while to try more sophisticated corrections of this rough estimate.

Table 4. Estimates of the exploited part of the trout population. Lake Olavatn 1969—70.

Year	Number tagged (≥28 cm)	Recaptures 1969	Recaptures 1970	N	95 % conf. int. for N
1969	159	64	42	3877	2942—4812
1970	118		65	4287	2353—5321

V. Mortality estimates

As tagging was done in two subsequent years, the yearly survival can be estimated according to RICKER (1958), as $\widehat{S}=\frac{r_{12}\cdot m_2}{m_1(r_{22}+1)}$, where $\widehat{S}$ is the estimated rate of survival from July 1969 to July 1970, r_{12} is the number of recaptures in 1970 from the tagging in 1969, r_{22} is the number of recaptures in 1970 of trout tagged in 1970, and m_1 and m_2 are the numbers of fish tagged in 1969 and in 1970. For fish$\geq$28 cm at tagging this gives: $\widehat{S}=\frac{42\cdot 118}{159\cdot 66}=0.4723$. The corresponding coefficient for instantaneous mortality, Z, is $\widehat{Z}=-\log_e\widehat{S}=0.75$.

We could now separate Z into the instantaneous coefficients for fishing mortality (F) and natural mortality (M) by using the unbiased rate of exploitation as estimated from the tagging data. However, the results would still be biased because in Lake Olavatn the fishing mortality operates only from July to October, while the natural mortality is distributed throughout the year. As nothing is known about seasonal variations in the natural mortality, we will assume that it operates at a constant instantaneous rate. As the exact number of tagged trout killed by fishing is known for each month, we can then estimate M by means of the method described by REGIER (1962). REGIER did this graphically, but quicker and more exact results are obtained by using a computer. This method was used and the result controlled by REGIER's graphic method. The estimated natural mortality was $\widehat{M}=0.21$. The estimated fishing mortality in 1969 is $\widehat{F}=\widehat{Z}-\widehat{M}=0.54$.

VI. Yield calculations

We have now sufficient data for calculating the equilibrium yield in Lake Olavatn according to formula (10.3) in RICKER (1958). As the fish will on average reach the length 28 cm in their sixth summer (Table 3, first line) we should start with 2,000 five-year-old recruits and use the G-values in Table 3 and estimated values of F and M. The year should be divided into two periods: (1). July 1—October 1, when all growth takes place and when a fishing mortality of $\widehat{F}=0.54$ is combined with a natural mortality of $\widehat{M}$—0.0525, and (2) October 1—July 1, when only a natural mortality of $\widehat{M}=0.1575$ is operating. This was done on the computer and the resulting equilibrium yield of 498 kg is in good agreement with the actual catch of 480 kg taken in the lake in 1969.

The model seems to be sufficiently realistic to predict an equilibrium yield of the correct magnitude. As the fishing in the lake in 1969 was done

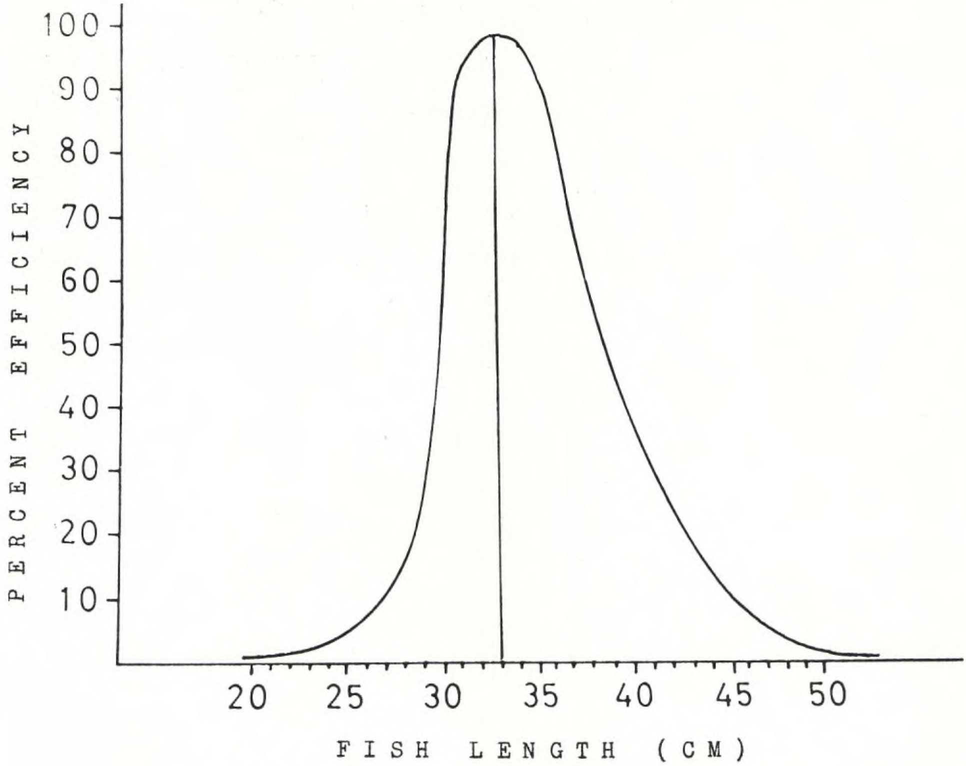

Fig. 1. Selection curve for 35 mm nylon gill nets for trout.

in the same way as in many previous years, the actual yield in 1969 was near the equilibrium yield. However, the constant values of $\widehat{F}=0.54$ for all fish from 28 cm and onwards is very unsatisfactory. $\widehat{F}=0.54$ is only an estimated average value, and the selectivity of the gill nets must result in great differences in fishing mortality during the exploited phase. One of the great advantages of RICKER's flexible model is that we do not need this postulate of a "knife-edge selection", as the selectivity of the fishing gear can easily be included in the model.

No data for the gill-net selection on brown trout have been found in the literature. According to observations in Lake Ø. Heimdalsvatn the selection curve for 35 mm nylon gill nets has the form shown in Fig. 1. As the variance is great, this curve should only be regarded as preliminary, but it will serve our purpose here. From this curve can be taken the approximate relative selection values (relative efficiency of the net) for the different size groups, and these values are shown in the third line in Table 3. The meaning of these values can be illustrated by the following example. For trout in its eight year (between l_7' and l_8') the table shows a relative

Table 5. Computation of equilibrium yield.

Date	G	F	M	G÷(F+M)	$_{e}G\div(F+M)$	Weight of stock (kg)	Average weight of stock (kg)	Yield (kg)
1/ 7—01	—	—	—	—	—	217.9	—	—
	0.70761	0.05	0.0525	0.60511	1.8314	—	308.5	15.4
1/10—01	—	—	—	—	—	399.1	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—02	—	—	—	—	—	340.9	—	—
	0.36243	0.19	0.0525	0.11993	1.1274	—	362.7	68.9
1/10—02	—	—	—	—	—	384.4	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—03	—	—	—	—	—	328.4	—	—
	0.23853	0.95	0.0525	—0.76397	0.4658	—	240.7	228.7
1/10—03	—	—	—	—	—	152.9	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—04	—	—	—	—	—	130.7	—	—
	0.24747	1.27	0.0525	—1.07503	0.3413	—	87.7	111.4
1/10—04	—	—	—	—	—	44.6	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—05	—	—	—	—	—	38.1	—	—
	0.11223	1.22	0.0525	—1.16027	0.3134	—	25.0	30.5
1/10—05	—	—	—	—	—	11.9	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—06	—	—	—	—	—	10.2	—	—
	0.13263	1.02	0.0525	—0.93987	0.3907	—	7.1	7.2
1/10—06	—	—	—	—	—	4.0	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—07	—	—	—	—	—	3.4	—	—
	0.04026	0.83	0.0525	—0.84224	0.4308	—	2.5	2.1
1/10—70	—	—	—	—	—	1.5	—	—
	0	0	0.1575	—0.1575	0.8543	—	—	—
1/ 7—08	—	—	—	—	—	1.3	—	—
	0.03975	0.76	0.0525	—0.77275	0.4671	—	1.0	0.8
1/10—08	—	—	—	—	—	0.6	—	—
	—	—	—	—	—	—	—	465.0

efficiency value of 1.00. For trout in its seventh year the corresponding figure is 0.75 or 75 per cent. This means that the catchability of trout in the different age groups must be proportional to these values for gill-net selection. As F is proportional to the catchability, F must be proportional to these values for gill-net selection. Hence our problem is to find a factor, Q, by which to multiply the selection values in order to get estimates of the true F-values. This can be done from the tagging data.

Of 159 trout tagged in 1969, an estimated number of $159 \cdot \widehat{S} = 75$ survived after one year and 84 were dead. Of these 64 were reported as recaptured, while 20 must have died from other causes than fishing. We have then:

$$\frac{\text{Number of deaths due to fishing}}{\text{Number of deaths due to natural mortality}} = \frac{64}{20} = 3.2$$

If we choose too high a value for Q, the fishing mortalities will become too high and the ratio between the two groups of dead fish will obviously be greater than 3.2. If too low a value for Q is tried, the ratio will be smaller than 3.2. By means of iterations we found Q=1.27. Accordingly the

Table 6. Number of fish of different age groups surviving on July 1.

Age	$Z(=F+M)$	$S(=e^{-Z})$	Number of survivors
5+	—	—	2000
	0.40	0.6703	—
6+	—	—	1341
	1.16	0.3135	—
7+	—	—	420
	1.48	0.2276	—
8+	—	—	96
	1.43	0.2393	—
9+	—	—	23
	1.23	0.2923	—
10+	—	—	7
	1.04	0.3535	—
11+	—	—	2
	0.97	0.3791	—
12+	—	—	1
	0.87	0.4190	—
13+	—	—	—
			Total: 3890

gill-net selection values were multiplied by 1.27 to obtain the new F-values, and these are shown in the last line in Table 3.

In Table 5 is shown the calculation of the equilibrium yield with these corrected F-values. As the 35 mm gill nets also take some 4+ trout, we have to begin the calculations with 2,594 of these on July 1 in year 1. By the prevailing mortalities these will be reduced to 2,000 trout of age 5+ on July 1 in year 2. From the growth curve the total weight on July 1 of the four-year-old fish is estimated as 217.9 kg, which is our starting point. The calculated equilibrium yield is 465 kg, and is again very near the observed catch in 1969.

The PETERSEN estimates of the population sizes in 1969 and 1970 have only been used for a rough estimate of recruitment and have not been used to build up the model. We may therefore check the validity of the model by comparing the PETERSEN estimate of the 1969 population of trout$\geq$28 cm with the number of fish of this size surviving on July 1 as calculated from the model. This calculation is shown in Table 6. The model leaves a population of 3,890 trout five years old and older, while the PETERSEN estimate was 3,877 trout.

The model seems to give a useful description of the trout population in Olavatn in 1969, but the very close fits between calculated and observed yields and between the PETERSEN and the model estimates of population size should not, of course, be taken as an indication of the precision of our estimates. The broad confidence limits in the PETERSEN estimate, the rough estimate of recruitment, the rough estimates of gill-net selectivity and the circumstance that a considerable part of the catch was taken on other gear than gill nets should warn us that the close fits must partly be due to luck.

VII. Prediction of yields after changes in mesh size and fishing effort

With fixed G-values, RICKER's model can easily be used to predict changes in yield due to changes in mesh and/or fishing effort.

In 1969 a fishing effort of 1,329 gill-net nights resulted in a fishing mortality of $F=1.27$ for trout of the size most efficiently caught by the 35 mm gill nets (trout of the modal length). This fishing mortality for trout of modal length we will call F_m. Provided the gill nets do not come so close to one another that they compete, F_m is proportional to the fishing effort. Therefore under average 1969 conditions in Olavatn 1,000 gill-net nights would make $F_m = \frac{1.27 \cdot 1{,}000}{1{,}329} = 0.96$, and an F_m of 2.00 would require $\frac{1{,}329 \cdot 2.00}{1.27} = 2{,}093$ gill-net nights.

When gill-net selectivity is known, we can therefore compute the equilibrium yield in Lake Olavatn for different combinations of mesh sizes and fishing efforts. In Fig. 2 are shown curves giving the equilibrium yields for 4 different mesh sizes with F_m varying from 0.25 to 4.50 and the corresponding fishing efforts. The form of the curves indicates rather abrupt drops in yield if the fishing effort is smaller than the optimal, while a greater effort than necessary has a smaller effect. At the prevailing (1969) growth rate a change to 29 mm nets will reduce the equilibrium yield substantially.

However, our assumption of G-values that are independent of the fishing mortalities is far from realistic. On the contrary, the rather slow growth in Lake Olavatn indicates that a reduction of the trout density would result in faster growth. Observations from Lake Ø. Heimdalsvatn indicate that this density-dependence of growth has far-reaching consequences for yield calculations in lakes where trout is the only fish species. Realistic yield models for populations of this kind must therefore incorporate the density-dependence of trout growth.

VIII. Summary

The dynamics of a population of brown trout in a mountain lake in S.E. Norway were studied on material collected in the years 1969—70. Brown trout was the only fish species in the lake, and fishing effort and yield were controlled during the two years.

Instantaneous natural mortality was estimated as $M=0.21$ by means of tagging in two years.

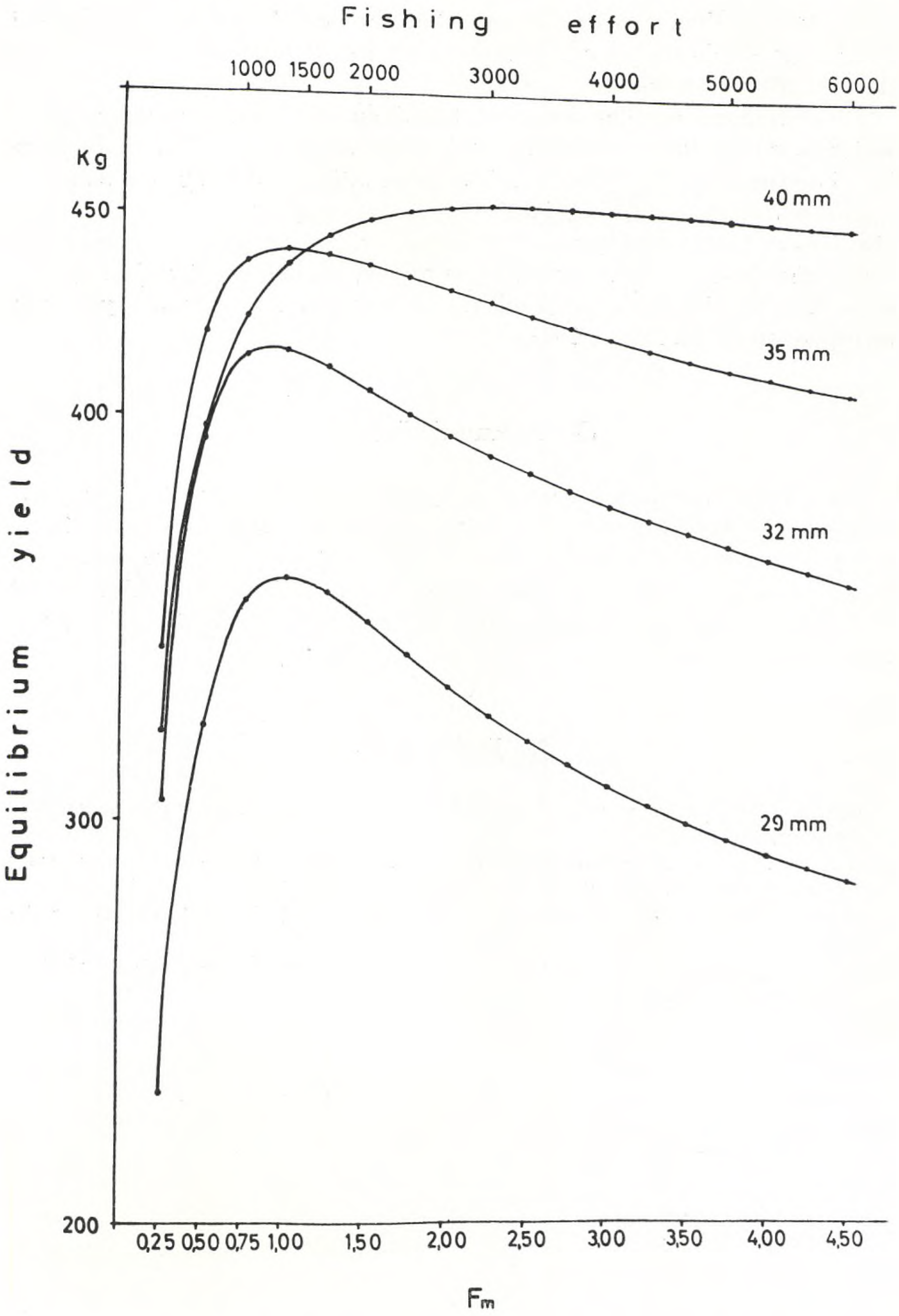

Fig. 2. Equilibrium yield — fishing effort for four different mesh sizes.

RICKER's method was used to calculate the equilibrium yield. Corrected values for the instantaneous fishing mortality, F, were worked out from data on gill-net selection.

The estimated equilibrium yield based on the 1969 population parameters was close to the observed yield in 1969. An estimate of population size based on the model was close to a PETERSEN estimate of the population.

Theoretical curves for equilibrium yield at varying amounts of fishing effort were constructed for gill-net fishing with four different mesh sizes. The author believes these curves to be of very limited use for yield predictions because the density-dependence of trout growth has not yet been incorporated in the calculations.

IX. Acknowledgments

The author is greatly indebted to Professor Ø. Nissen of the Computer Centre of the Agricultural College of Norway for help with the computations, and to the owners of Lake Olavatn for their help and assistance during the two years of the study. Financial support was received from Direktoratet for jakt, viltstell og ferskvannsfiske and from the Agricultural Research Council of Norway.

X. References

CARLIN, B. 1955. Tagging of salmon smolts in the River Lagan. *Rep. Inst. Freshw. Res., Drottningholm* 36: 57—74.

DANNEVIG, A. and P. HØST 1931. Sources of error in computing l_1—l_2 etc. from scales taken from different parts of the fish. *J. Cons.* 6(1): 64—93.

KIPLING, C. 1962. The use of the scales of the brown trout (Salmo trutta L.) for the back-calculation of growth. *J. Cons.* 27(3): 304—315.

REGIER, H. A. 1962. On estimating mortality coefficients in exploited fish populations given two censuses. *Trans. Amer. Fish. Soc.* 91(3): 283—294.

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

— 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. *J. Fish. Res. Bd. Can.* 26(3): 479—541.

WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. *Biol. Bull.* 90(2): 141—147.

Experiments with whitefish fry in enclosures in nature

By THOROLF LINDSTRÖM

Introduction

A field experiment — in the sense in which the term is used here — may be undertaken for different purposes. Though it will always interfere with a natural situation it need not necessarily upset the ecology, and so produce an unnatural situation. If well planned, it may make it possible to analyse the factors important for the ecology of a species as precisely as could be done through a laboratory experiment. The present experiment was prompted by the studies of young rainbow trout in an enclosure in a stream (NORTHCOTE 1969).

The purpose of the present experiment is, however, more restricted than was that of the studies referred to. It does not give much new information about the factors controlling the movements of young whitefish in Lake Sällsjön, Jämtland, (*Coregonus nasus cf.* SVÄRDSON 1970) as it mainly consisted of an attempt to fence off a small part of the lake to allow better observation. Even so, it cannot escape the criticism that the walls were not as invisible as they should have been. Certain surfaces reflect light, and the netting at both ends of the box did not leave water movement and plankton circulation completely undisturbed. The absence of direct sunshine in some of the series and the size of the boxes, in relation to the size of the fry, are, however, factors that might reasonably be expected to minimize the disturbing influences. The experiment may be useful as an intermediate link in the study of whitefish fry behaviour and the factors controlling this behaviour.

The lake experiments

General remarks

Two types of boxes were used, one (Fig. 1 A) for a stone-covered shoreline and the other (Fig. 1 B) for the lower reaches of a brook. Acrylic sheats were used for the walls and the bottoms, the ends being covered with netting. The former type was the larger, measuring 100×40 cm at the bottom and 150×40 cm in the top area, the upper part being extended into a "balcony" at one end of the box. In the middle a dark-blue plate was inserted a little above the bottom so that in effect the box had three sections with

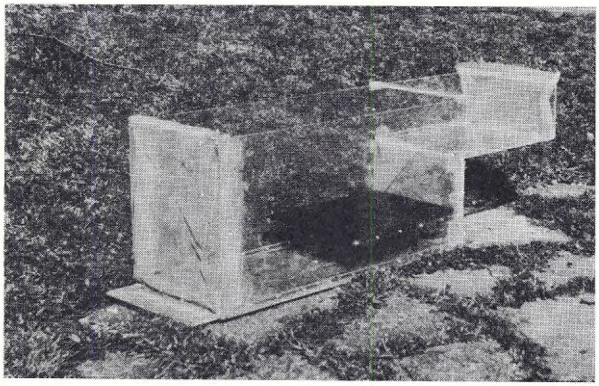

Fig. 1 A. Box of acrylic and nylon netting, used along a stone-covered shoreline.

water depths of 40 cm, 30 cm (the dark-blue plate section) and 10 cm (the balcony) when the box was in the lake. The ends were covered with nylon netting, mesh size 1×1 mm. In some experiments the box was filled with lake water pouring in over the upper rim of the box to allow as free access as possible for plankton.

The majority of the whitefish fry (10—20 mm long) kept swimming superficially or midwater, but in the balcony, with its very small water depth, they often came close to the bottom. Certainly weak and dying animals appeared close to the bottom and kept out of sight in the thin rim of pebbles covering the junction of the netting and the bottom plate. When closely watched, the fry were never observed to enter the space below the dark-blue plate, and they probably did not do so at any time. Water circulation through the box was not very important, as the experiments had to be carried out in completely calm places. Temperature differences between the sections were almost nil (the thermometers were marked in whole degrees centrigrade only).

Section choice in the box

The whitefish fry were caught just before an experiment and were 10—20 mm long. They were released in the middle section and cursorily suveyed every 10 or 15 minutes to ascertain the position of the majority of the fry. An experiment was concluded after 1—4 hours and the position of the fry at the end of the experiment was noted. In some other experiments their tracks were followed more closely, but this involved increased disturbance from the observer's presence. Most of the experiments showed that the majority of the fry preferred the deepest section, even when the "balcony" was pointed out into the lake with stones piled up to its base. When the balcony pointed out into the lake but with the same total distances to the bottom stones as in the other sections, the result was "undecided" indicating

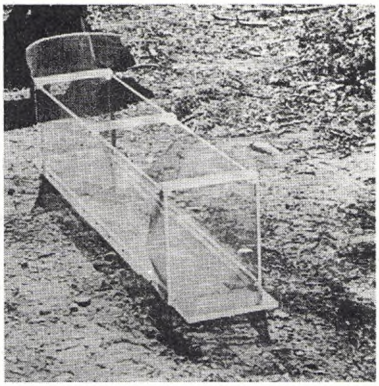

Fig. 1 B. Box of acrylic and nylon netting used in the lower reaches of a brook.

that vision gives the fry impulses to section choice. Otherwise no effect was noted from, *e.g.,* the angle of the box in relation to the shore line or the sun or the time of day (morning, afternoon). When the sun was shining directly into the box, the depth distribution may have been affected but hardly the section choice. A few experiments showed deviating results.

Experiments in slowly running water

The box (Fig. 1 B), was placed in the lowest reaches of a brook on sandy bottom with a water depth of 10—20 cm in the box. It was placed parallel to the direction of the current in the brook and the water passed in through one end, covered with netting (mesh size 1×1 mm), and out through the other end, covered in the same way. The bottom size of the box was 20×100 cm, the junction between the netting and the bottom was covered with a narrow rim of pebbles, and sometimes stones up to the size of a hen's egg were distributed in different patterns over the whole of the bottom. The water velocity in the central surface region was about 10—15 cm/sec. as estimated from very light vegetation debris floating downstream.

In the full strength of the current, the 10—15 mm-long whitefish fry were rapidly swept to the downstream netting; they wriggled vigorously — a movement recalling the coiling in the egg just before hatching — and managed to get down to the bottom, where they could stay a little longer among the pebbles. This coiling is undoubtedly a very energy-consuming movement, only used in such critical situations as this or when the environment is drained of water. The fry travelling along the walls or the bottom of the box could head the current anywhere in the box for several minutes, and ahead of a stone or obstruction of suitable shape they could (though not at the downstream side) rest for a long time.

Pelagically operating gear

To catch fry moving upwards from a deep spawning site (FILIPSSON and LINDSTRÖM 1971) a cone-shaped funnel of pliable cellulose acetate (C.A.B.) was hung out in the pelagic part, over the spawning site. A door was intended to lead the fry up into a chamber of netting above the funnel. No catch has been obtained so far. A new device is about to be constructed at the laboratory with netting rolling down from above and forming a cylinder enclosing a column of water, to be strained later.

Some comments on the habitat studies in which the acrylic box method is included

If the hypothesis that light and temperature are very important as proximate factors guiding the whitefish fry to optimal habitats is to be tenable, it is necessary that differences should exist between the North Swedish lakes, where the ice cover lasts seven months or more, the temperature does not reach 15°C until August and the light conditions are those of the 63rd — 65th parallels, and Lake Huron, where the whitefish fry biology was studied by FABER (1970) and RECKAHN (1970). The occurrence of the fry close to the shore when the bottom drops of rapidly outside points in the Swedish lakes indicates a different habitat choice from that obtaining in Lake Huron even if in the Swedish lakes the outer limits of the habitat are poorly studied. (The inner limits of the habitat in the Swedish lakes as described in 1970 and in the present study may occasionally be crossed, as when abundant whitefish fry, 17 mm in mean length, were observed on June 7 in Lake Sällsjön in a very gently shelving bay among sparse vegetation of *Carex lasiocarpa* over a total depth of only 2—3 dm. The bottom material, consisting of debris from timber-barking activities, was very dark, and the temperature was 10—12°C. It is likely that the light conditions at this locality were responsible for this exceptional habitat choice.)

The experiments in slowly running water were carried out with a view to providing an explanation of how it is that the fry are able to cope with the environment in running water even though their swimming abilities allow them to stand a water velocity of only 7 cm/sec (LINDROTH 1957, River Indalsälven). The fry in the present experiment were slightly older (1—2 weeks after hatching), the temperature lower (4—5°C) and they belong to a population which does not spawn in running water. Still these fish displayed a behaviour which could bring some of them to microhabitats void of current, when the velocity of the central surface region was double the velocity critical for fry from River Indalsälven belonging to *Coregonus lavaretus* with spawning sites in running water. Discussing the latter population, LINDROTH concludes that there is no need to argue a behaviour pattern different from that of lake spawning populations. A behaviour that includes an avoidance of strong currents may give rise to a delayed downstream migration of a minor portion of the fry at least, as shown by LINDROTH in River Indalsälven and by the present author in Lakes Uddjaur and Storavan, *C. peled* (1970). The observations do not strongly encourage further research on differences between Swedish species of Coregonus in behaviour and performance of fry in running water although the observations include Swedish whitefish species with widely different gill raker counts (*cf.* LINDROTH 1959).

The drastic differences in environment between Lake Huron and the North Swedish lakes are, on the other hand, concurrent with differences in fry behaviour during the first weeks after hatching and strongly prompt experimental studies on the differences in reaction of the fry to proximate factors, particularly light and temperature. Also, field studies should be carried out on the differences between optimal habitats of the fry in the two different environments. Those differences in behaviour are further substantiated by the present field experiments with newly hatched fry of a species with gill raker counts similar to those of the species in Lake Huron at temperatures ranging from 5 to 12°C.

References

FABER, D. J. 1970. Ecological observations on newly hatched lake whitefish in South Bay, Lake Huron. p. 481—500. *In* Lindsey, C. G. (Ed.). Biology of coregonid fishes, Univ. Manitoba Press, Winnipeg.

FILIPSSON, O. och T. LINDSTRÖM 1971. Om småsikens lek. *Fauna och flora* 66(3): 121—122. (In Swedish.)

LINDROTH, A. 1957. A study of the whitefish in the Sundsvall Bay district. *Rep. Inst. Freshw. Res. Drottningholm* 38: 70—108.

— 1959. Anteckningar om sikungars beteende. *Sv. Fisk. Tidskr.* 68 (3): 27—28. (In Swedish.)

LINDSTRÖM, T. 1970. Habitats of whitefish in some north Swedish lakes at different stages of life history. p. 461—479. *In* Lindsey, C. G. (Ed.). Biology of coregonid fishes, Univ. Manitoba Press, Winnipeg.

NORTHCOTE, T. 1969. Lakeward migration of young rainbow trout (*Salmo gairdneri*) in the upper Lardeau River, British Columbia. *J. Fish. Res. Bd. Can.* 26(1): 33—45.

RECKAHN, J. 1970. Ecology of young lake whitefish (*Coregonus clupeaformis*) in South Bay, Manitoulin Island, Lake Huron. p. 437—460. *In* Lindsey, C. G. (Ed.) Biology of coregonid fishes, Univ. Manitoba Press, Winnipeg.

SVÄRDSON, G. 1970. Significance of introgression in coregonid evolution. p. 33—59. *In* Lindsey, C. G. (Ed.) Biology of coregonid fishes, Univ. Manitoba Press, Winnipeg.

Some effects of temperature on eel (*Anguilla*) behaviour

By LENNART NYMAN

I. Introduction

The current shift from fossil to nuclear fuel in the power-producing industry has rapidly accelerated the amount of water used for cooling purposes. These hot-water discharges have considerable effect on the aquatic environment since they bring about changes in the entire ecosystem by favouring species with higher temperature requirements and greater tolerance to fluctuations than those of the original fauna.

In Sweden the nuclear power plants are to be located primarily on the coasts and thus the waste heat is discharged into a fairly cold and oligotrophic environment. Among the so-called warm-water fish most likely to be attracted to these sites is the European eel (*Anguilla anguilla* (L.)) the commercially most important species. The possible threats both to the normal spreading of young yellow eels in the Baltic region as well as the emigration from the area of silver eels posed by above all the more southerly locations of these power plants have necessitated investigations of eel ecology to help predict and, if possible, counteract these effects.

The present paper deals with some easily observable effects of temperature influence on selected parts of the ecology of the European eel. This eel genus comprises 17 species all of which breed in tropical waters (BRUUN 1963). Some of these species feed in temperate freshwater regions and are thus subjected to a wide range of temperatures during their life span.

Little is known about influence of temperature on spawning and subsequent embryonic development in the eel during the pelagic phases of its life in the Central Atlantic. By analogy with other marine fish, however, it appears evident that this period is controlled within a narrow temperature range, probably close to 20 degrees centigrade, which was experimentally determined to be optimal for normal sexual development (BOËTIUS and BOËTIUS 1967). This temperature indicates a spawning depth of 100—200 metres in the supposed spawning area in the Sargasso Sea (DEELDER 1970).

During the pro- and post-larval phases temperature is probably not a directive factor since eel larvae are more or less pelagic and are carried by oceanic currents. Little is known about the more active elver stage, but, during the second metamorphosis when elvers turn into eels and some migrate to freshwater, there is evidence pointing at temperature acting as some kind of trigger mechanism attracting some of the young eels to enter rivers (S.

VALLIN, pers. comm., WIDERBERG, 1941, TIDEMAN 1957, 1962, ALM, 1932, HULT, 1942).

It is a well-known fact that the activity of eels and silver eels is greatly influenced by temperature. SINHA and JONES (1967 a) showed that British eels do not feed during the winter months (October to March) and the Japanese do not feed cultured eels when temperatures drop below 17°C. BOËTIUS and BOËTIUS (1967) found that the respiratory rate and the heart beat rate had a maximum at 25°C, which agrees well with practical experiments in pond culture where optimal growth occurs around 25°C.

The activity of the maturing eel is closely connected with the temperature as evidenced by catches in the southern Baltic (THUROW 1959). However, there is also another aspect of high water temperatures, especially during the summer months, since a long warm summer prolongs the vegetative season and speeds up the maturing processes, thus allowing more yellow eels to be transformed to silver eels. This connection was first appreciated by JACOBSON and JOHANSEN (1922) who were able to predict the size of the silver eel catch late in the year from the deviation from normal temperatures during the preceding summer. This method was later verified by several authors (*e.g.* ROSÉN 1930, HULT and SVÄRDSON 1943, JENSEN 1960, 1961).

It was the objective of this paper to analyse what implications a change in water temperature might have for small yellow eels in freshwater, especially easily observable phenomena like choise of bottom substrate, general activity, feeding and aggression.

II. Materials and Methods

A total of 90 young yellow eels, ranging from 13 to 37 cm in length, were employed in these studies. Most of the small specimens were obtained from an eel trap (in freshwater) in Sjælland, Denmark, the majority of the larger specimens emanated from River Lagan, Sweden. Because of the small size of the fish no attempt was made to determine sex.

Three aquaria were used in this study, one (A) was used for a general survey of reactions to changes in temperature, another (B) was employed to investigate reactions to a stable low (8.4—10.4°C) water temperature with a minimal choice of bottom material, and the last aquarium (C) which offered a broad variety of bottom materials and topography was employed to study the behaviour at comparatively high (21—24°C) temperatures. Below follows a more detailed description of each aquarium and the various types of temperature regulators used.

Tank A: 148×57 cm, water depth 40 cm. Bottom material 10 cm thick, particle sizes forming a gradient from loose mud to rocks slightly more than 10 cm in diameter. The temperature regulator comprises a control unit, a

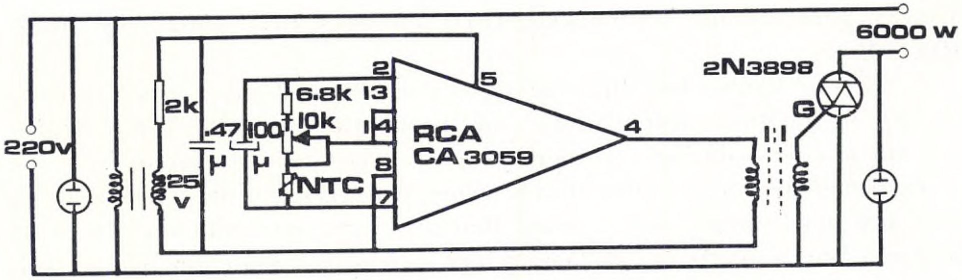

Fig. 1. Schematical outline of the temperature regulator.

thermistor and a connecting unit. The control unit allows selection of any temperature within the 5—30°C range. When the selected temperature is reached a control lamp for heat is switched off automatically. It is also possible to use the unit as a thermometer by adjusting the indicator needle until the lamp is switched off. The meter then indicates the water temperature with a confidence of ±0.1 degrees centigrade. The thermistor consists of an NTC resistance with a thermal time constant of 5 sec, and is cast into the pointed end of a thin glass rod, 75 mm in length. The thermistor (ITT, type F-14) was obtained at AB Multikomponent (Solna, Sweden). The connecting unit allows the simultaneous use of four heaters with a maximum output of 6,000 watts. A schematical outline of the temperature regulator is shown in Fig. 1.

Complete mixing of the water as well as oxygen saturation was achieved by allowing air to bubble up from below the immersed heaters. Homothermy of within 0.5 of a degree was obtained in this way. Cold fresh water was added from a tap throughout the course of the investigation to help keep the water clean, and the water surface was held constant by using a drain pipe.

Tank B: 104×88 cm, water depth 40 cm. Bottom material consisting of mixed sand, gravel and small stones (less than 2 cm in diameter). Bottom topography gently undulating. For the study of substrate selectivity at low temperatures rocks roughly 10×10×10 cm were spread on the bottom.

Cooling of water was achieved by employing an ordinary cooling unit powered by a 7.5 hp motor with a capacity of 14,000 cal at —4°C. The entire unit was delievered by AB Celer (Stockholm, Sweden). This unit provided a constant inflow of cold water during the hot season.

Tank C: 85×42 cm, water depth 10 cm. Only half the total area of this tank was below the water surface. Underwater topography varied with caves, rocks, sand, mud and dense vegetation — mainly *Vallisneria spiralis*. Tank located in constantly heated room, diurnal temperature fluctuating between 22.5 and 24, nocturnal from 21—22.5. Oxygen saturation by air pump.

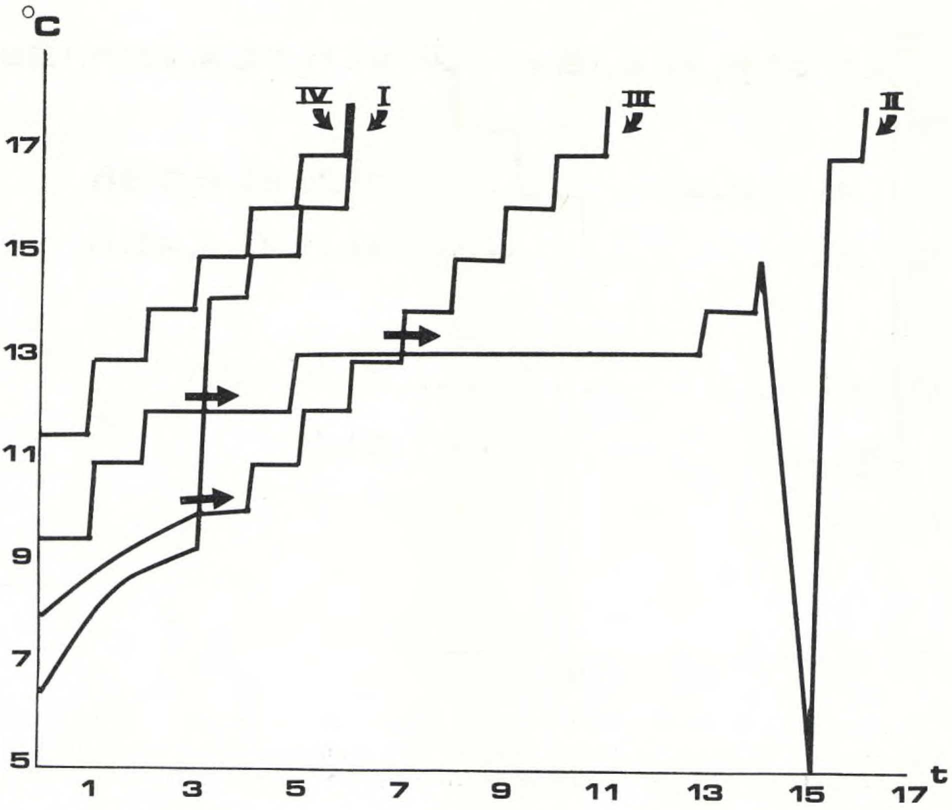

Fig. 2. Variability pattern and duration of the four experiments carried out to study habitat selectivity. Water temperature in degrees centigrade is given on the y axis and time indicated by 24-hour periods on the x axis. Roman numeral indicate each experiment.

III. Results and Discussion

The yellow eel stage is the only period in the life of the European eel where a non-migratory phase may be observed. This period is also used mainly for feeding and fattening. The main objectives of this study were to investigate whether a change in temperature alone would determine which substrate the eel would choose for hiding, and also, whether temperature alone could influence its activity patterns and in what way.

It is a well-known fact that eels are inactive during the coldest months of the year in northern Europe (*e.g.* SINHA and JONES 1967 a, b). To exclude any possibility that this inactive phase would be due entirely to light conditions these experiments were carried out mostly in the winter-time when ambient water temperatures were below those when feeding has been reported (above 10°C) and when light conditions varied almost between the

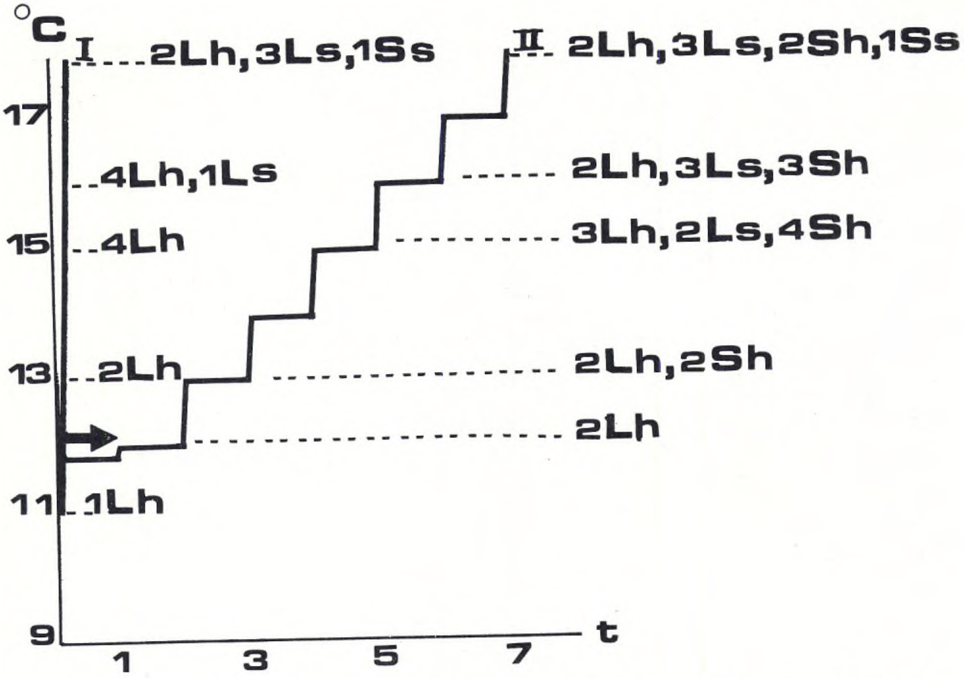

Fig. 3. a) activity of small (S) and large (L) yellow eels when subjected to increasing temperatures. "h" stands for "head" and "s" for "swimming" indicating whether the eels are partly burrowed in the bottom or free swimming. Other symbols as in Fig. 1.

two extremes at this latitude (59°20′ north). However, when the last experiment was carried out in early June the water temperature at the point of water intake had reached 11.5°C.

Habitat selectivity

Four series of experiments with variable temperatures were carried out in tank A. The duration and magnitude of each series is indicated in Fig. 2. Notice also the variability of time given for acklimatization. As described earlier tank A offered a broad variety of bottom material ranging from mud to rocks.

To summarize the results obtained within the 5—18°C interval the following pattern was observed: Between 5—8°C all eels were inactive and completely hidden in the mud. Some clumping of individuals was observed. From 8°C a gradual migration in the sediments took place — from mud to rocks the size of a fist. This migration was the first sign of any activity. At 9°C 10—20 % of the eels protruded their heads from between the rocks. This percentage increases gradually up to 13°C when roughly 60 % of all

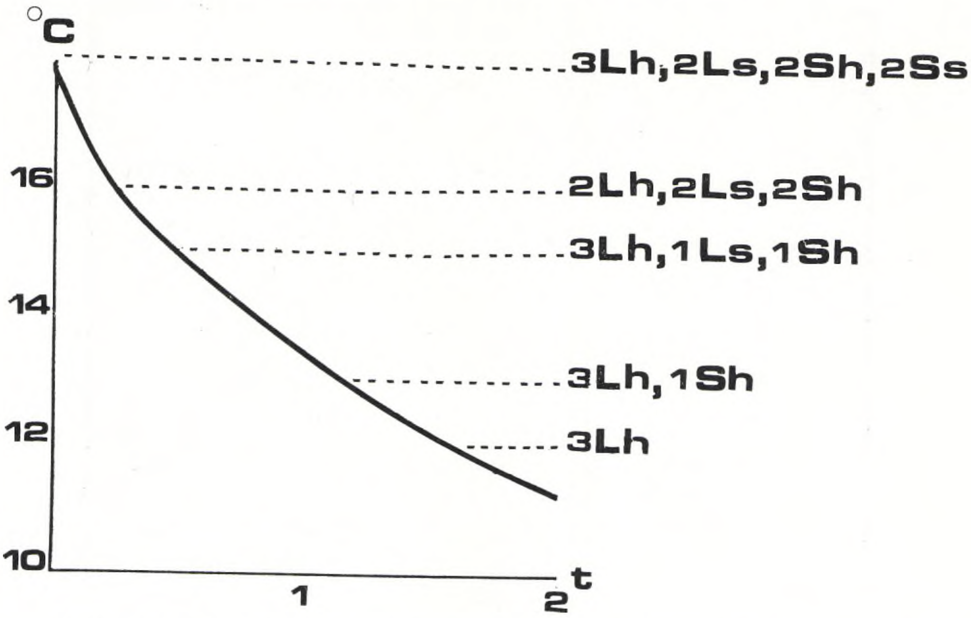

Fig. 3. b) activity of yellow eels when subjected to a lowering of the temperature. Symbols same as in Fig. 3a.

heads are visible. Already at 11°C a few individuals may emerge as much as half the body length from the substrate, this observation occurs with increasing frequency at rising temperatures and also at night. At 14°C a remarkable shift in habitat and activity apparently takes place. Now several free-swimming specimens were noted, especially at night, which clearly illustrates the mainly nocturnal habits of this species. Those eels completely emerged are found resting mainly on mud and sand, whereas those still more or less hidden tend to favour rocky bottom. At 16°C all eels are normally either free-swimming or resting on the bottom, mainly on mud or sand. Those partly hidden still favour rocks. This pattern was not changed at 18°C when the experiments in this tank were discontinued.

The duration of acklimatization seemed of great importance. The drastic drop in temperature during the latter part of experiment II (the heaters were unintentionally switched off) forced all eels back to muddy habitat where they were completely concealed. A rapid increase in temperature from 5 to 17°C in two hours caused a delayed reaction in the activity pattern as compared to the conditions observed at a rate of increase of 1 degree centigrade per 24 hours. Thus all eels were hidden at 11°C, but at 14.5°C 60 % of them protruded their heads again, all of them among rocks. The first free-swimming specimen was observed at 16.5°C, as compared to 14°C under "normal conditions". At 17°C 60 % of all eels were either resting on

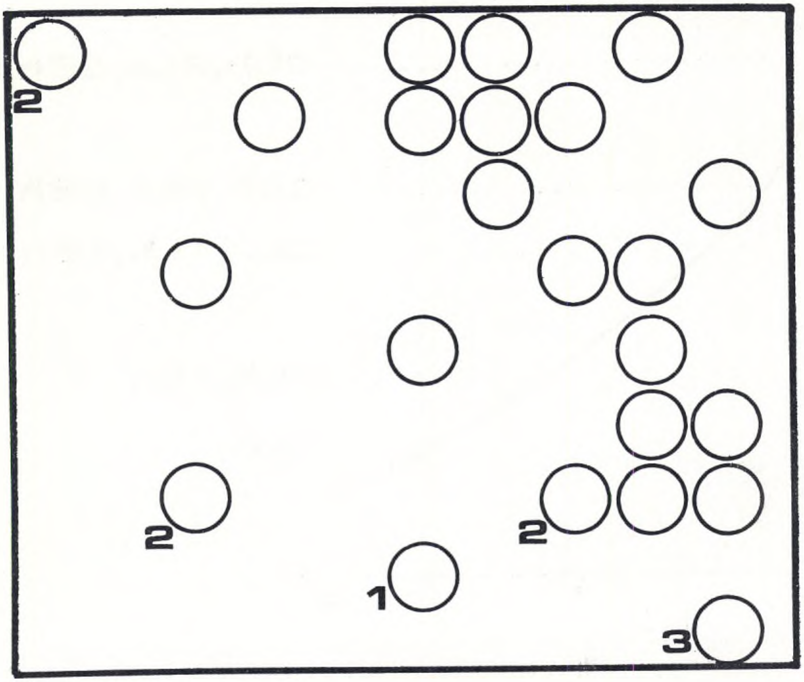

Fig. 4. Spreading of 10 yellow eels released at the surface (after 5.5 hours). Open circles indicate position of 23 rocks spread at random.

sandy or muddy bottom or free-swimming. This retardation in reaction rate was even more noticeable in experiment I when a 5 degree rise from 9 to 14.2 in one hour brought about that only 3 heads became visible, and subsequent electro-fishing revealed 4 specimens still hiding in the mud. After 24 hours of recovery from the shock all specimens seemed acklimatized as 2 were now resting on mud, 1 was swimming and all seven other fish were spread evenly among the rocks heads protruding. Thus a fairly simple correlation between substrate selectivity, temperature and acklimatization time is indicated in these young yellow eels when they are given a wide choice of substrate types. A quite different pattern was indicated when the eels were subjected to a constant low or high temperature or when possibilities for substrate selectivity were minute.

The eels used in these studies were not tagged to allow individual classification, but, there seemed to be a tendency for small eels to have higher temperature optima than larger specimens, at any rate the larger eels appeared less influenced by the temperature fluctuations. Thus small eels disappeared first when the temperature was lowered and under reversed conditions displayed a delayed return in comparison with the larger spe-

Table 1. Clumping of eels.

Exp. I.	Date	27/10	28/10	30/10	3/11	electrofishing	4/11	9/11	13/11	19/11
10 eels	°C	10.3	10.4	10.1	9.7		9.4	9.1	8.8	10.4
		3	6	7	9		4	6	6	7
		2	2	3	1		3	4	3	2
		2	2	—	—		2	—	1	1
		2	—	—	—		1	—	—	—
		1	—	—	—		—	—	—	—

Exp. II.	Date	20/11	23/11	25/11	26/11	30/11	1/12	2/12	4/12	8/12
10 eels	°C	10.0	9.8	8.9	9.2	8.8	9.4	9.0	9.2	8.4
		2	6	6	6	7	7	8	8	8
		2	3	2	1	2	2	1	2	2
		1	1	1	1	1	1	1	—	—
		1	—	1	1	—	—	—	—	—
		1	—	—	1	—	—	—	—	—
		1	—	—	—	—	—	—	—	—
		1	—	—	—	—	—	—	—	—
		1	—	—	—	—	—	—	—	—

cimens. To test the validity of this observation three experiments were carried out (in November 1971) in tank A.

In each test 5 small (13—16 cm) and 5 larger eels (25—35 cm) were employed. These two size groups were enough different to allow direct classification as soon as the heads emerged from the bottom material. Temperature variability and reaction patterns are plotted in Fig. 3 a and b. The reactions to temperature changes are clearly much less pronounced in the larger specimens.

The bottom substrate of tank B consisted of coarse sand and gravel on top of which a number of rocks were distributed at random. Water temperatures throughout the two experiments ranged from 8.4 to 10.4°C. Ten eels were released at the surface. After 5.5 hours they had spread according to Fig. 4. All eels were visible and were tightly pressed up against the rocks rather than burrowed in the gravel. Despite a rather constant temperature the distributional pattern changed gradually until after 7 days nine of the ten eels were tightly joined up between a couple of rocks, the single remaining specimen also hiding behind a rock (see Table 1, Exp. I). The typical pattern at low temperatures with many eels congregating in one spot, usually with most of their bodies parallel to one another, was evident also from the second experiment (Exp. II), which lasted over a 19-day period, at the end of which 8 eels were joined up in the manner described (Table 1).

Crowding of eels has been previously reported (*e.g.* by SMITT, 1895). It might be assumed that this behaviour is an adaptation to cold since relatively less heat is emitted the larger the heat-radiating body. This explanation is often used to explain the large bodies of Arctic animals. Clumping of elongate animals during hibernation is common among snakes and lizards (C. ANDRÉN, pers. comm.).

When after seven days of experiment I all eels were recaptured by electro-fishing and then released again, a new centre was formed, but at another location.

When the temperature was kept below 7°C and all rocks besides one were removed all eels congregated below that rock and lay motionless with only minute signs of active respiration. This state lasted for two months after which the experiment was interrupted. Such a state of lethargy has previously been believed to occur only at a temperature below 2°C (DANNEVIG, 1945).

Tank A was used also for another experiment. Only coarse sand and gravel were employed as bottom substrate to see whether absence of rocks and mud would prevent formation of a clump of eels. This experiment was carried out in late autumn allowing the water temperature to follow ambient lake temperature. It could be observed that with decreasing temperature fewer heads were visible, and, that the first sign of clumping occurred just below 10°C. At 7.9 only two heads were still visible above the gravel and at 6.4°C, six days later, no head emerged and subsequent electro-fishing revealed eight eels in a clump.

In tank C the water temperature was never below 21°C. Only three eels were present in the aquarium at any one time because of the small water volume. A wide range of habitats was nevertheless possible to achieve by concealing rocks and spots of dense vegetation. All eels were very active during both day and night, and when scared hid among rocks, never in sand or gravel.

Feeding

It was prevously said that eels do not feed during the winter. In fact eels do not seem to take the bait until the water temperature reaches at least 10°C (BRUUN, 1963), and Japanese eels (*Anguilla japonica*) apparently stop feeding when the temperature drops below 14°C (OKADA, 1960). In the present investigation the eels did not start feeding or searching for food until the temperature had reached 14°C. Then even small eels attacked freshly killed fish by taking a mouthful of flesh and rotating around their long axis to tear it off. This way of foraging is described in detail by DEELDER (1970). Small prey, like invertebrates and fish fry were seized by using a method reminiscent of a vacuum, since the prey seemed more or less sucked into the mouth of the eel.

The reason why these eels did not feed at a temperature below 14°C may be due to a too short acklimatization time. Feeding was observed both at day and night.

Aggression

When in tank A the temperature had reached 17°C aggression between eels was commonly observed. Direct fighting often occurred when eels came too close to one another, either by gripping each other mouth to mouth if confronted head on, or, by one eel biting the "tail" of the eel in front of him. Aggressive behaviour among eels was described by LARSEN (1970) who mentioned that two eels could not be kept together in a small tank without fighting. LARSEN attributed this to strong territorial behaviour and the observations in tank C at temperatures above 21°C clearly demonstrated the validity of his findings.

When a 22 cm eel was released in tank C it selected the central cave system as its permanent hiding place where it returned whenever frightened. Three days later another eel, 17 cm in length, was released in the same aquarium. The smaller of the eels was attacked almost instantly and selected a more distally located cave as its home. When after three more days a third eel (14 cm) was liberated there was only one uninhabited rock system left, a small rock roughly equally distant from the caves of both other eels. This place was also selected by the last eel, even though it could not conceal more than half its body beneath the rock. It was obvious that the last eel was not at all satisfied with its hiding place, since it was roaming the aquarium far more than the others. Whenever this eel came within sight of any of the other two it was attacked and driven back. However, when the first eel was foraging both smaller eels escaped without even attempting to defend their own territories. Thus it seems obvious that yellow eels, at least during part of this stage, display strong territorial behaviour. This behaviour is evidently triggered by the water temperature, at least in young specimens, and although in these experiments (tank A) aggression was not observed below 17°C it may be assumed that under natural conditions this level is reached at an even lower temperature, due to a slower rise of temperature and thus far more time for acklimatization. Also, the size of a territory appears dependent on the size of the fish.

It is easy to realize the importance of territorial behaviour in this case. An active dispersal of the feeding and fattening yellow eels after the inactive crowding during the winter months must be favourable for a maximal exploitation of food resources as well as reducing predation, and the most frequently found mechanism in nature for achieving these aims is territorial behaviour.

IV. Conclusions

The present study has indicated that yellow eels may be highly selective with regard to structure of the bottom substrate, not only during hibernation but also during the more active periods. When confronted with a wide selection of bottom material eels seem to prefer mud at water temperatures below 8—9°C. In the absence of suitably located muddy bottoms they prefer rocks roughly the size of a fist, and rocky bottoms are apparently superior for hiding at temperatures in the 9—24 degree range. Crowding of eels was observed at temperatures below 8°C, where several specimens frequently formed a clump. Clumping occurred in mud, among rocks or in sand/gravel in the order here given according to availability. Clumping of individuals at low temperatures is probably a way of diminishing the heat emittance, since a large body emits relatively less heat than a small one — a fact frequently used to explain the large bodies of Arctic animals. Also, clumping has been observed during hibernation among other elongate animals, *e.g.* snakes and lizards.

When the water temperature rises above 8—9°C eels seem to migrate from mud to rocks (if present) and with increasing temperature an increasing number of them protrude their heads from out of the bottom substrate. Also, with increasing temperature a territorial behaviour becomes evident and at about 17°C direct aggressive measures were observed when two eels came close to one another. When temperatures rose above 20°C the territorial behaviour became even more pronounced. The size of each territory, however, appears dependent on the size of the fish — larger eels always defeated small ones — and also, on density of prey (LARSEN 1970).

Foraging was observed at temperatures above 14°C, which agrees well with SATTLER's (1954) observations that eels enter the littoral zone after hibernation when the water temperature is approximately 15°C.

The difference in reaction rate between small and large specimens, small eels displaying a delayed activity pattern at low temperatures and reacting more rapidly to a lowering of the temperature, agrees well with ALM's (1932) opinion that ". . . the small eels are most sensitive to temperature. If the temperature is not very high only the larger and older eels start to migrate (upstream) while only at a higher temperature also smaller eels start to move, thus increasing the total number of migrating eels" (author's transl.).

The same view was arrived at by SÖRENSEN (1951) who demonstrated a dissimilarity between small and larger eels with respect to sensitivity to light, current and temperature conditions. SÖRENSEN found that larger eels are less sensitive to low temperature than elvers the activity of which decreased rapidly under adverse temperature conditions.

The observations here discussed seem to indicate that elvers and young yellow eels during their pre-territorial period may be attracted by the hot-water discharges of thermal power plants. Among older yellow eels there is also evidence pointing at attraction, however, this force may be counteracted by the territorial behaviour, even though the hotwater could provide a bigger than normal food supply, thereby possibly diminishing the size of the territories. Anyway, the higher temperature should provide a higher yield of catchable eels by increasing the activity of them, also the growth rate might increase yielding a higher productivity.

Silver eels being migratory non-feeders could again be attracted by the high temperature of the discharges, but, since these eels migrate downstream and head for marine areas they are probably less vulnerable to attraction than either of the earlier forms. Thus, it appears that measures should be taken primarily to counter-act the possible accumulation of ascending elvers and possibly young yellow eels, *e.g.* by employing electric fences. If no such diversion is technically or economically feasible, the elvers could either be collected and transported outside the area of influence or some kind of compensation for obstructed spreading in the Baltic (primarily a problem at Barsebäck in the Sound) should be tried *i.e.* transplantation of elvers collected west or southwest of this area, for instance in Denmark, Norway or Great Britain. Parallel to such transplantations it should be investigated whether this state of attraction is permanent or just implies a delayed immigration.

V. Summary

Irrespective of season of the year young yellow eels could be forced to perform a series of activity patterns when the water temperature was artificially manipulated. Besides changing preference for bottom substrate they displayed both crowding behaviour (at low temperatures) and intraspecific aggression (at high temperatures). Foraging was also initiated by a rise in temperature and a couple of degrees higher, when aggressive actions developed, a strong territorial behaviour became evident. Also, there was a discrepancy between small and larger yellow eels, larger specimens being less sensitive to temperature fluctuations.

Some biological implications of these findings as well as the possible impact of thermal discharges to eel migrations are discussed.

VI. Acknowledgments

Thanks are due especially to Professor G. Svärdson who initiated my investigations in this field and also to Dr. L. Westin who critically read and commented on the present paper. I am also indebted to Mr. P.-U. Allmo who constructed the temperature regulator system.

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VII. References

ALM, G. 1932. Ålyngeltillgång och ålyngelinplanteringar. *Svensk Fisk. Tidskr.* 41(1): 2—5. (In Swedish.)

BOËTIUS, I. and J. BOËTIUS 1967. Studies on the European eel, *Anguilla anguilla* (L.). *Medd. Danm. Fisk. og Havunders.* 4(11): 339—405.

BRUUN, A. F. 1963. The breeding of the north Atlantic freshwater eel. *Adv. Mar. Biol.* 1: 137—169.

DANNEVIG, A. 1945. Ålens reaksjon på miljøforandringer. *Naturen* 12: 366—372. (In Norwegian.)

DEELDER, C. L. 1970. Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus) 1758. FAO, EIFAC 70/Gen-6, 74 p.

HULT, J. 1942. Ålyngeluppsamlingsstationen vid Trollhättan. *Svensk Fisk. Tidskr.* 51(12): 237—238. (In Swedish.)

— and G. SVÄRDSON 1943. Ålfångst och vattentemperatur. *Ostkusten* 15 (10): 18—19. (In Swedish.)

JACOBSEN, J. P. and A. C. JOHANSEN 1922. On the causes of the fluctuations in the yield of some of our fisheries. II. The eel fisheries. *Medd. Kom. Havunders.* VI (9): 32 p

JENSEN, Å. J. C. 1960. Dansk prognos om höstens blankålfiske. *Svensk Fisk. Tidskr* 69(10): 141. (In Swedish.)

— 1961. Die Schwankungen des Aalbestandes und der Aalfischerei in den dänischen Küstengewässern. *Z. Fisch.* 10(8—10): 635—641.

LARSEN, K. 1970. Småvandsfiskeri og krebseavl. J. Fr. Clausens Forlag, Aschehoug. Copenhagen, 254 pp. (In Danish.)

OKADA, Y. 1960. Studies on the freshwater fishes of Japan. *J. Fac. Fish. Univ. Mie,* 4: 1—860.

ROSÉN, N. 1930. Om ålen på vandring. *Fiskaren* 1(1): 2—4. (In Swedish.)

SATTLER, K. 1954. Iakttagelser rörande ålen i Flensburgerfjorden. *Svensk Fisk. Tidskr.* 63(8/9): 124—125. (In Swedish.)

SINHA, V. R. P. and J. W. JONES 1967 a. On the food of the freshwater eels and their feeding relationships with the salmonids. *J. Zool., London,* 153: 119—137.

— 1967 b. On the age and growth of the freshwater eel (*Anguilla anguilla*). *J. Zool., London,* 153: 99—117.

SMITT, F. A. 1895. Skandinaviens Fiskar. II. Norstedt & Söners Förlag, Stockholm. p. 567—1239. (In Swedish.)

SÖRENSEN, I. 1951. An investigation of some factors affecting the upstream migration of the eel. *Rep.Inst. Freshw. Res. Drottningholm,* 32: 126—132.

TIDEMAN, M. 1957. Åluppsamlingen vid Norrköping år 1956. *Svensk Fisk. Tidskr.* 66(1): 12—14. (In Swedish.)

— 1962. Uppsamlingen av smååI i Norrköping år 1961. *Svensk Fisk. Tidskr.* 71(1): 17—18. (In Swedish.)

THUROW, F. 1959. Über Fangerträge und Wachstum des Aales in der westlichen Ostsee. *Z. Fisch.* 8(7—8): 597—626.

WIDERBERG, J. 1941. Om fångst och utplantering av ålyngel. *Svensk Fisk. Tidskr.* 50(12): 267—272. (In Swedish.)

A new approach to the taxonomy of the "*Salvelinus alpinus* species complex"

By LENNART NYMAN

I. Introduction

The genus *Salvelinus,* the chars, comprises a series of holarctic species some of which offer delicate taxonomic problems. Within this genus there are two species which are considered to have rather well defined limits, (the lake trout, *S. namaycush,* and the brook trout, *S. fontinalis*) the other two, however, viz. the Dolly Varden (*S. malma*) and the Arctic char (*S. alpinus*), cover a great variety of systematic opinions, most of which emphasize the occurrence of multiple species within these taxa. The various problems concerning the systematic positions within this group are referred to as the "*Salvelinus alpinus* complex". There are several parallels to the complexity of char systematics among other salmonid fish, *e.g.* among whitefish and ciscoes, and the reasons for this situation are quite obvious. Many of the genera are circumpolar in distribution, and, since they are either anadromous or completely bound to freshwater there are numerous possibilities for a disjunct geographical distribution, further enhanced by the fluctuations of the last period of glaciations. Thus geographical barriers may have prevented contact between different populations for a considerable amount of time, resulting in many cases in genetical divergence to the extent that reproductive isolating mechanims evoled capable of maintaning the two incipient species intact when they came in contact again after the breakdown of the barriers. In some cases, however, the build up of the isolating mechanisms was not completed and as a consequence hybridization occurred. The gene flow resulted in various stages of introgression, so obviously this is not only a problem of phenotypical sibling species but also one of distinguishing integrades between these species. That this is in fact so was elegantly shown by SVÄRDSON (1949, 1958, 1970) who used the gillraker count as hereditary parameter in the genus *Coregonus.*

The *Salvelinus alpinus* complex has been commented on by several authors. REGAN (1914) grouped all chars other than lake trout and brook trout into one species, *S. alpinus,* whereas the other extreme may be represented by BERG (1948) who distinguished 11 species of this genus in the Soviet Union. JORDAN *et al.* (1930) recognized 14 species of what we today consider the genus *Salvelinus,* and others on the slightly splitting side are *e.g.* WENT and TWOMEY (1957), VLADYKOV (1954) and TUUNAINEN (1970).

Far more numerous are those who consider only two relevant species (*S. alpinus* and *S. malma*) in the area studied by the present author, *viz.* North America and northern Europe. Among those are MARTIN (1939) and BEHNKE 1968, 1972). Some have gone even further and describe *S. malma* as a subspecies of *S. alpinus* (TSUYUKI *et al.* 1966, DYMOND 1947).

A few russian authors even claim that *S. alpinus* and *S. malma* are synonymous (SAVVAITOVA 1966, CHERNENKO 1969). Thus there is a considerable degree of controversy as to taxonomic nomenclature in the genus *Salvelinus*. How, then, can we deal with this intricate problem, if, according to the biological species concept, all sympatrically living and reproductively isolated populations are to be treated as full species. Two schools of thought have evolved as a result of this controversy. One school suggests (VLADYKOV 1954, WALTERS 1955) lumping of all populations into *S. alpinus* so as to prevent a proliferation of scientific names. Their view is well formulated by BEHNKE (1972): "Certainly from a fisheries management point of view, sympatric populations with ecological and life history distinctions should be treated as distinct species. Because of the problem with scientific nomenclature, however, I believe in some instances, we will have to accept a classification permitting two reproductively isolated populations of *Salvelinus alpinus* to occur in some lakes".

The other school has focused attention on the fact that all these sympatric sibling species need not be unique biological innovations, but rather combinations of a few ancestral species which had attained reproductive isolation allopatrically and as a secondary event came in contact due to a changing environment (SVÄRDSON 1958, 1961, SVÄRDSON and NILSSON 1964). Because the ancestral species most probably were marine rovers as are many of the populations in the high Arctic today, a circumpolar distribution of the same few species may be accounted for. The problem in the genus *Salvelinus* is thus mainly a problem of variation, primarily of morphological characteristics but also of varying degrees of introgression, as stated above.

The central problem then is one of finding a set of parameters capable of distinguishing the ancestral species, not only from lake to lake but from continent to continent. It is the intention of this paper to offer a new approach to the taxonomy of the so called *Salvelinus alpinus* complex. This is achieved by employing gene frequency data of a previously described enzyme polymorphism (NYMAN 1965), in cases of sympatry combined with growth analysis of otoliths. Also, certain other proteins are investigated to indicate the amount of qualitative hereditary divergence.

II. Materials and Methods

A total of 3,003 Arctic char were examined electrophoretically. Specimens were obtained from Swedish and Norwegian localities during the period

Table 1. Arctic char sampling stations.

No.	Locality	Approx. lat. N	Year sampled	Fry [1]	Adults	Total number sampled
1	Blue Hill Pond (Nfld., Canada)	48°30′	1969	—	×	13
2	Sand Hill River (Labrador, Nfld.)	52°30′	1969	—	×	48
3	Shona Lake (Baffin Island, Can.)	63°41′	1969	—	×	37
4	Frobisher Bay (off Baffin Island)	63°43′	1969	—	×	29
5	Godthåb District (Greenland)	64°10′	1969	—	×	133
6	Godthåb District (Greenland)	64°10′	1970	—	×	57
7	Keyhole Lake (Victoria Island, Can.)	69°23′	1969	—	×	210
8	Kuujjua River (Victoria Island, Can.)	71°15′	1969	—	×	23
9	Lake Vättern (Sweden)	58°—59°	1965, 1966, 1971	×	×	232
10	Lake Unden (Sweden)	58°45′	1967	×	—	50
11	Lake Tinnsjøen (Telemark, Norway)	59°45′	1967	×	—	108
12	Lake Brossen (Sweden)	60°45′	1968	—	×	98
13	Lake Näckten (Sweden)	62°45′	1967, 1971	×	×	117
14	Lake Håckren (Sweden)	63°15′	1971	×	—	14
15	Lake Ottsjön (Sweden)	63°15′	1967, 1968, 1969, 1970	×	×	270
16	Lake Torrön (Sweden)	63°45′	1967	×	—	96
17	Lake Kvarnbergsvattnet (Sweden)	64°30′	1967	×	—	100
18	Lake Kvesjøen (Nord-Trøndelag, Norway)	64°30′	1967	×	—	56
19	Lake Kultsjön (Sweden)	65°	1969	—	×	28
20	Lake Överuman (Sweden)	66°15′	1971	×	×	32
21	Lake Hornavan (Sweden)	66°15′	1967	—	×	50
22—23	Lake St. Rösjön (Sweden)	61°30′	1971	×	×	212
24—25	Lake St. Blåsjön (Sweden)	64°45′	1970, 1971	×	×	394
26—27	Lake Ankarvattnet (Sweden)	64°45′	1969	—	×	54
28—29	Lake Övre Björkvattnet (Sweden)	65°45′	1967, 1970, 1971	—	×	88
30—31	Lake Yraf (Sweden)	66°15′	1971	×	×	454
						Total 3,003

[1] age group O+ and 1+

1965—1972, from North America in 1969 and 1970 and Greenland in 1969 and 1970. Data on the various localities and fish samples are given in Table 1. The approx. locations of the populations sampled are indicated in Fig. 1, where the numerals refer to those given in Table 1. For supplementary data see also the description of each population in the Results section. Two specimens of *S. malma* were obtained in British Columbia. From these two fish blood, slime, muscle, liver, kidney, heart and spleen were removed and analysed electrophoretically.

Blood was procured in a variety of ways after it had been shown that freezing and thawing did not interfere with esterase kinetics to the degree that classification could not be made. Thus blood was collected both from fresh and frozen specimens, in heparinized and non-heparinized capillary tubes as well as absorbed directly on pieces of filter paper. The stability of the tertiary structure of this enzyme is well illustrated by the sample from Lake Brossen (Sweden) which had been kept in a frozen state since 1968 and when analysed in 1972 displayed the degree of accuracy indicated in Fig. 2 B.

The electrophoresis equipment employed is described in detail elsewhere (NYMAN 1967 b), to summarize it is type employing horizontal starch gel slabs allowing simultaneous analysis of approx. 45 specimens. Esterase classification was achieved by utilizing a variety of substrates: naphthyl acetate (α, β), naphthyl propionate (α, β), naphthyl bytyrate (α), naphthyl caprylate (α) and naphthyl laurate (α). All these substrates were dissolved in distilled water and acetone. Inhibition studies were carried out by exposing the gels to a variety of concentrations of several inhibitor substances. The esterase classification procedure is described elsewhere (NYMAN 1972). For routine classification of esterase phenotypes α-naphthyl acetate and Fast Red TR (diazonium salt) were used. Incubation was performed in .2 molar buffer of mono- and dibasic sodium phosphate (BURSTONE 1962). Optimal staining intensity was reached in approx. 25 minutes. In the comparative study of *S. alpinus* and *S. malma* esterase, lactate dehydrogenase, peroxidase, alkaline phosphatase, haemoglobin and total protein (Amido Black) were examined. The staining techniques employed are based on recipes published elsewhere (NYMAN 1967 a, b).

Most otolith examinations were performed by O. FILIPSSON whose method is thoroughly described in a recent paper (FILIPSSON 1967).

III. Results

Fig. 2 A shows a diagrammatic picture of the esterase polymorphism encountered in Arctic char blood. This polymorphism was first described in a sample from Lake Vättern (NYMAN 1965) and a year later supplemented by another sample of the same spawning population to make a total of 100 specimens (Nyman 1967 b). The phenotypical distribution of this sample assuming a one-locus two-allele polymorphism in a panmictic population agreed well with the expected distribution according to the CHW (CASTLE—HARDY—WEINBERG) equilibrium. Thus the first test of the supposed hereditary mechanism proved valid.

Before studying the biological significance of the polymorphism a few

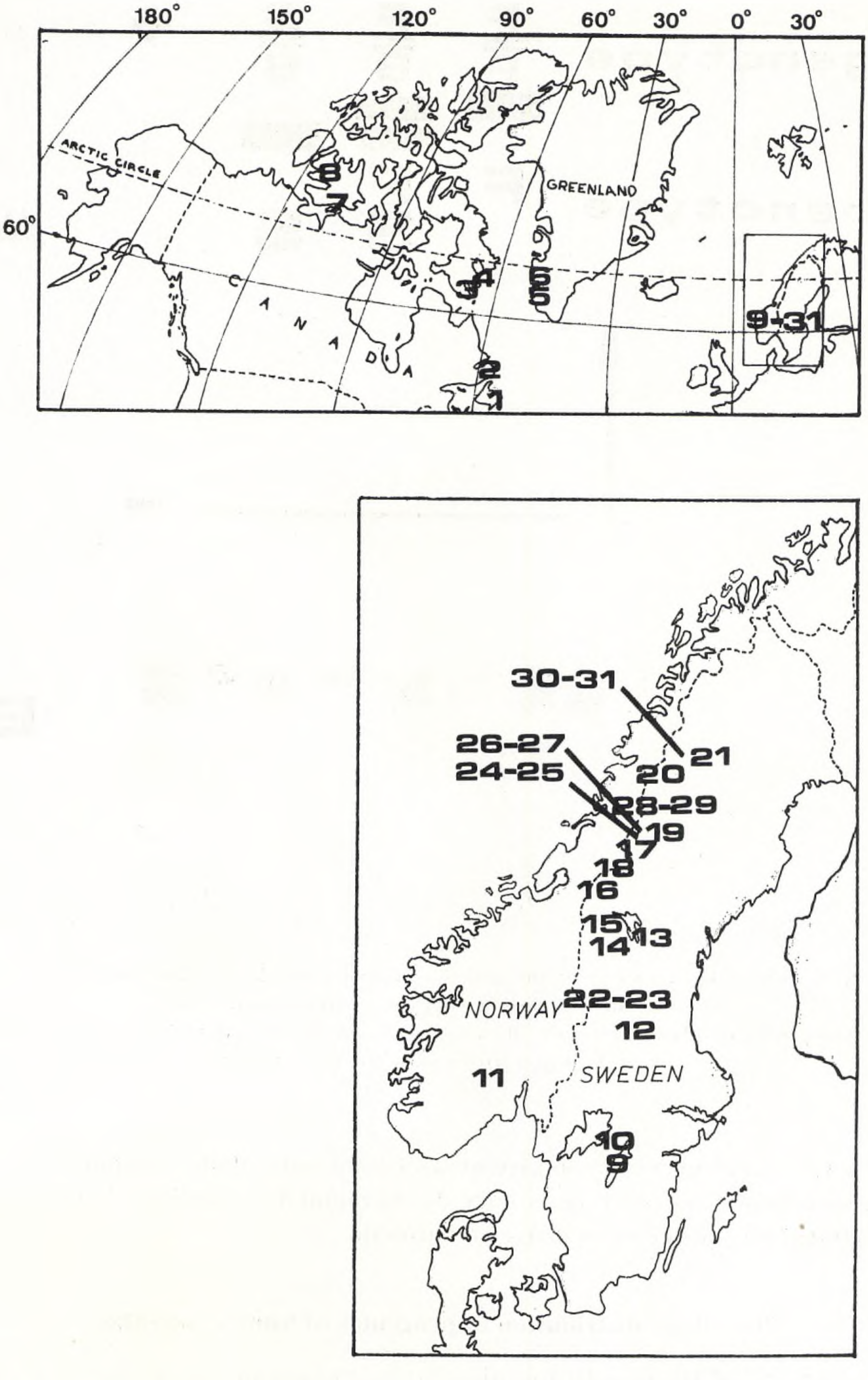

Fig. 1. Approx. locations of the 31 populations sampled. Numerals refer to those given in Table 1.

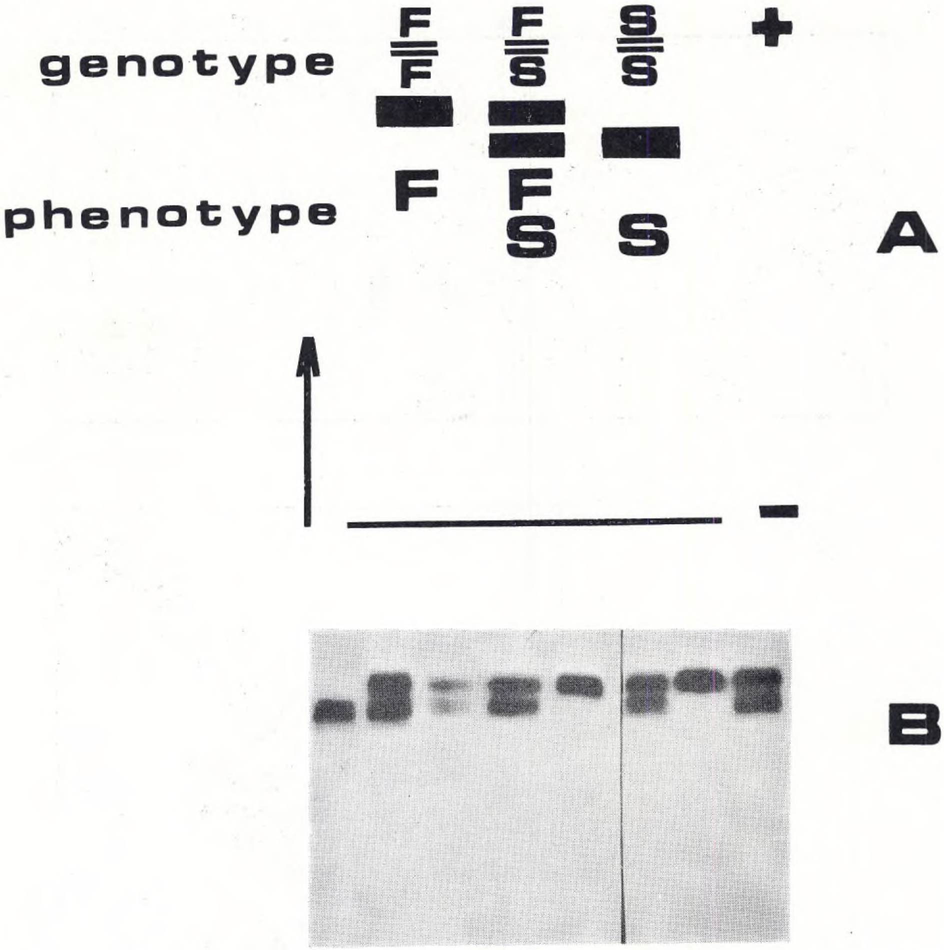

Fig. 2. A) Schematical outline of the genetical background of the three allelic combinations of plasma esterase in Arctic char.

B) Zymograms of plasma esterase phenotypes from Lake Brossen. These samples have been kept in a frozen state for several years.

more tests were necessary to give evidence not only of the mechanism itself but also prove its strict hereditary background by showing that it is independent of size of fish, sex, age and growth.

Phenotype distribution in progenies of known parentage

In the fall of 1969 upstream migrating spawners of Arctic char were collected at a counting fence on the outlet of Lake Ottsjön. Three pairs of randomly chosen males and females ranging from 700—1,450 gr were col-

Table 2. Phenotype distributions in progenies of known parentage.

Pair 1

		female		male
	P	F/S	×	F/S

expected ratio of phenotype classes in F_1 1 : 2 : 1

		obs	exp
F_1	F	12	13
	F/S	27	26
	S	13	13
		52	

χ^2(1 d.f.) = 0.12
probability of worse fit 0.70—0.80

Pair 2

		female		male
	P	F/S	×	F/S

expected ratio of phenotype classes in F_1 1 : 2 : 1

		obs	exp
F_1	F	12	12.75
	F/S	27	25.50
	S	12	12.75
		51	

χ^2(1 d.f.) = 0.17
probability of worse fit 0.60—0.70

Pair 3

		female		male
	P	F/S	×	F/F

expected ratio of phenotype classes in F_1 1 : 1 : 0

		obs	exp
F_1	F	26	26.50
	F/S	27	26.50
	S	—	—
		53	

χ^2(1 d.f.) = 0.02
probability of worse fit > 0.90

lected and the spawn of each pair was kept separate and was taken to the Semlan Rearing Station (province of Jämtland, Sweden) for incubation and wintering. Each fish and pair was tagged individually and put in deep freeze. During the fall of 1970 approx. 50 fish of each progeny were collected at the Salmon Research Institute at Älvkarleö, where the eggs had been kept from the eyed stage. The fry averaged 10.2 cm. All 156 fry were kept in deep freeze until December 2, 1970, when they were thawed out with their parents. Blood was collected from all fish and analysed simultaneously. In Table 2 the observed distributions of esterase phenotypes in the three progenies as well as their parents are presented. These distributions agree extremely well with the expected Mendelian distributions attributed to a genetic background of two condominant allelic genes. Thus the hypothesis of the genetics of the polymorphism is well substantiated.

Examination of independence of sex of gene frequency distributions

If there are sex correlated differences in the distribution of the two alleles responsible for the esterase polymorphism in Arctic char a disproportion of either sex will cause results which deviate considerably from the true situation as evidenced by a 1: 1 ratio of males to females. Fig. 3 A and B indicate samples of two populations (A=Lake Yraf, B=Lake Blåsjön) where the left bar represents the female sample in each case. The frequency of the F-allele in sample A (which is taken from the dwarf from — *tita*) is 0.31 in the females (26) and 0.27 in the males (69). The length of the bars indicates the 95 % confidence intervals. In sample B, which is taken from the normal char the corresponding figures are 0.16 (28) and 0.17 (59). There is thus no indication of sex linkage in this polymorphism.

Independence of age of fish

Another possible cause of variability of gene manifestation would be an ontogenetic difference. This possibility is, however, more or less eliminated by the artificial hybridization reported in section 1, further data given below emphasize the validity of this judgment. Fry belonging to age group 0+ are compared with large spawners of the same populations in Fig. 3 C and D, where C stands for Lake Vättern and D for Lake Näckten. Both samples give almost identical results for young and sexually mature specimens.

Independence of size of fish

In samples where age data are lacking length measurements may be employed to test independence of size. Samples taken from the Godthåb District (Greenland) in 1969 (E) and from Keyhole Lake (Victoria Island, NWT, Canada) — illustrate the lack of discrepancy between small and large specimens of the same populations (Fig. 3. E—F).

Independence of growth

Finally, growth data of allopatric populations or sympatric populations which do not overlap in growth pattern, may provide additional evidence

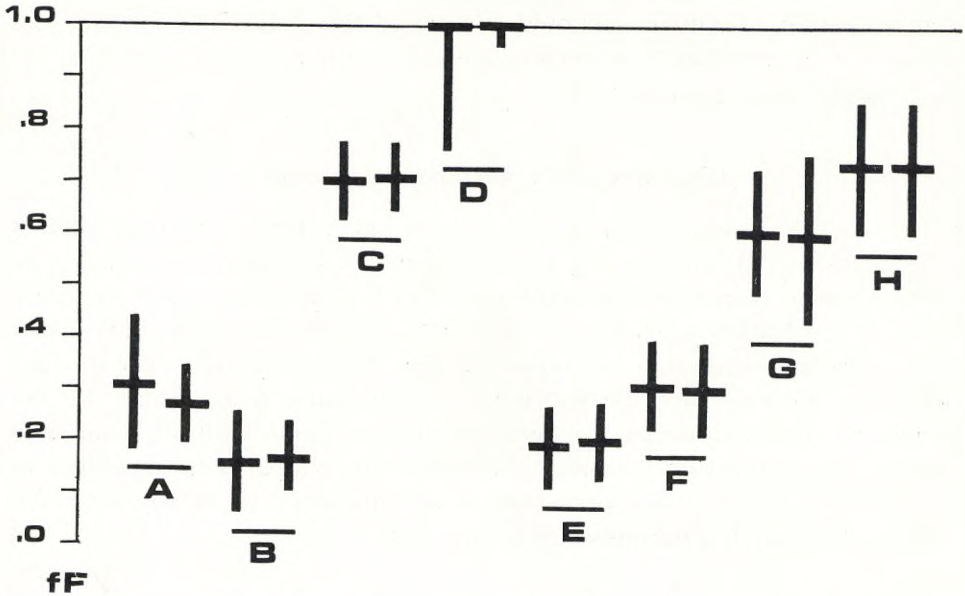

Fig. 3. Demonstration of gene frequency independence of sex, A—B, age, C—D, size, E—F, and growth, G—H. For further reference consult the text.

of independence of growth capacity, *i.e.* disclaim any possibility that a certain allele is correlated to a superior growth. Samples G and H (Fig. 3) represent samples of the allopatric char in Lake Brossen and the normal char in Lake Övre Björkvattnet, and the sub-samples drawn from specimens with superior and inferior growth capacity indicate they are virtually identical.

The results stated above thus verify the hypothesis that the esterase polymorphism in the plasma of Arctic char is controlled by two allelic codominant genes at one locus, and, that the polymorphism is independent of sex, ontogeny, size and growth capacity of the fish.

Esterase classification

Both alleles were equally insensitive to high and low concentrations (p/=3.00—5.00)[1] of eserine sulphate and p-hydroxymercuribenzoate, whereas dichlorvos and di-isopropylfluorophosphate inhibited both in low concentrations (p/=5.00). These properties are characteristic of carboxylesterases (AUGUSTINSSON 1961). Comparisons of enzyme reaction rates indicate this esterase has a selective affinity for short-chain naphthyl esters, and especially the alpha isomer of naphthyl propionate. These results agree

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[1] negative logarithm of the molar concentration of inhibitor solution.

well with studies on other salmonids (Nyman 1970, 1972). Thus the plasma esterase of Arctic char is a carboxylesterase with a selective affinity for alpha-naphthyl propionate.

Gene frequency variation of samples

The gene frequency distribution of all 31 population samples are plotted to indicate the variability of gene frequencies. The statistical significance of these values is indicated by plotting the 95 % confidence intervals which take into account the size of the samples (Fig. 4). The horizontal bars which are the same length indicate observed gene frequency (fF) whereas the confidence intervals are illustrated by vertical bars. Samples 22—31 are grouped in pairs. Each pair is derived from the same body of water and reflects the significant genetical divergence of sympatric populations of Arctic char. All five cases of sympatry are discussed in detail under the headline **Sympatric populations of Arctic char.**

Allopatric char populations

The term allopatric is here not used in the strict sense of the word, but refers either to a known case of allopatry, or, where data are lacking to cases with no deviations in zygotic proportions from those expected under Castle—Hardy—Weinberg equilibrium (CHW). The latter case refers to the fact that samples taken from population mixtures where the contributing populations differ with respect to gene frequencies will produce a heterozygote deficiency (Li 1955). Also it could be observed in the samples taken from sympatric populations that the growth usually varied between the two populations and gene frequency calculations of small and large fish thus tended to display differing frequencies.

Thus a further indication of allopatry is the absence of any size-correlated frequency difference and population samples without such deviations have been referred to this headline.

The distributions of esterase phenotypes in the various allopatric populations and agreement of expected values assuming a one-locus, two-allele polymorphism in panmictic populations are presented in Table 3. The respective probabilities of computed chi-square values indicate no deviations from expected values, *i.e.* all populations sampled are in a state of relative equilibrium.

Sympatric populations of Arctic char

I have just shown that in allopatric populations of Arctic char there is no correlation between growth rate and a certain frequency of the gene 'F'. This situation is exemplified by "C" in Fig. 5 when growth is plotted on

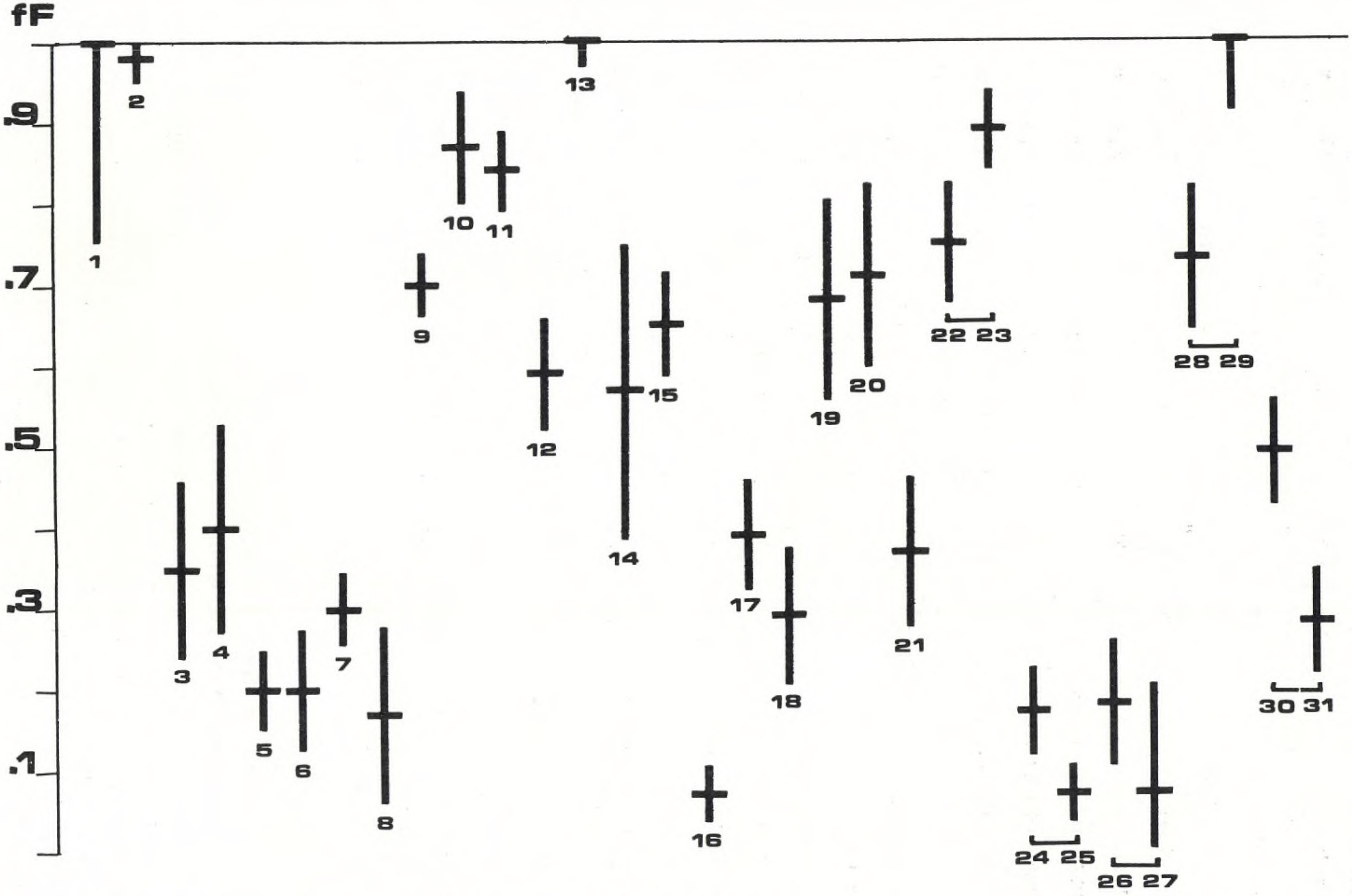

Fig. 4. Gene (EstF) frequencies and 95% confidence intervals of the 31 population samples. Populations 22—31 represent the five sympatric species pairs.

1=Blue Hill Pond (Canada), 2=Sand Hill River (Canada), 3=Shona Lake (Canada), 4=Frobisher Bay (Canada), 5=Godthåb District (Greenland), 6=Godthåb District (Greenland), 7=Keyhole Lake (Canada), 8=Kuujjua River (Canada), 9=Lake Vättern (Sweden), 10=Lake Unden (Sweden), 11=Lake Tinnsjøen (Norway), 12=Lake Brossen (Sweden), 13=Lake Näckten (Sweden), 14=Lake Håckren (Sweden), 15=Lake Ottsjön (Sweden), 16=Lake Torrön (Sweden), 17=Lake Kvarnbergsvattnet (Sweden), 18=Lake Kvesjøen (Norway), 19=Lake Kultsjön (Sweden), 20=Lake Överuman (Sweden), 21=Lake Hornavan (Sweden), 22—23=Lake St. Rösjön (Sweden), 24—25=Lake St. Blåsjön (Sweden), 26—27=Lake Ankarvattnet (Sweden), 28—29=Lake Övre Björkvattnet (Sweden), 30—31=Lake Yraf (Sweden).

Table 3. Agreement of observed and expected values in allopatric populations.

No.	Locality Est	F/F	F/S	S/S	Total	fF	χ^2(1 d.f.)	Probability of worse fit
1	Blue Hill Pond	13	—	—	13	1.0	—	—
		13	—	—				
2	Sand Hill River	46	2	—	48	0.98	0.005	>0.90
		46.1	1.9	—				
3	Shona Lake	3	20	14	37	0.35	1.27	0.25—0.50
		4.5	16.8	15.6			1	
4	Frobisher Bay	4	15	10	29	0.40	0.18	0.50—0.75
		4.6	13.9	10.4				
5	Godthåb District (1969) ..	7	40	86	133	0.20	0.71	0.25—0.50
		5.3	42.6	85.1				
6	Godthåb District (1970) ..	2	19	36	57	0.20	0.25	0.50—0.75
		2.3	18.2	36.5				
7	Keyhole Lake	20	87	103	210	0.30	0.08	0.75—0.90
		18.9	88.2	102.9				
8	Kuujjua River	—	8	15	23	0.17	1.09	0.25—0.50
		0.7	6.5	15.8				
9	Lake Vättern	108	107	17	232	0.70	1.87	0.10—0.25
		112.4	98.2	21.4				
10	Lake Unden	38	11	1	50	0.87	0.04	0.75—0.90
		37.8	11.3	0.8				
11	Lake Tinnsjøen	77	28	3	108	0.84	0.06	0.75—0.90
		76.2	29.0	2.8				
12	Lake Brossen	31	53	14	98	0.59	1.31	0.25—0.50
		33.8	47.5	16.7				
13	Lake Näckten	117	—	—	117	1.0	—	—
		117	—	—				
14	Lake Håckren	4	8	2	14	0.57	0.37	0.50—0.75
		4.5	6.9	2.6				
15	Lake Ottsjön (excluding 3 progenies)	44	57	11	112	0.65	1.47	0.10—0.25
		46.9	51.1	13.9				
16	Lake Torrön	—	14	82	96	0.07	0.59	0.25—0.50
		0.5	13.0	82.5				
17	Lake Kvarnbergsvattnet .	16	45	39	100	0.39	0.25	0.50—0.75
		14.8	47.4	37.8				
18	Lake Kvesjøen	4	24	28	56	0.29	0.14	0.50—0.75
		4.6	22.9	28.6				
19	Lake Kultsjön	13	12	3	28	0.68	0.01	>0.90
		12.9	12.2	2.9				
20	Lake Överuman	16	14	2	32	0.71	0.23	0.50—0.75
		16.1	13.2	2.7				
21	Lake Hornavan	6	25	19	50	0.37	0.11	0.50—0.75
		6.9	23.3	19.9				

the x-axis. Allopatry is thus indicated by a line parallel to the x-axis. In certain water systems there are wellknown cases of two or three types of char living sympatrically. In many cases these forms may be separated by differing colouration or size of spawners, other sympatric pairs may differ in feeding or spawning ecology but be morphologically similar to a degree that prevents classification of individual specimens. Since a hereditary character like the enzyme polymorphism described above is not correlated to the external morphology of the fish, but reflects the specific requirements of a homeostatic system subject to certain selection pressures derived from

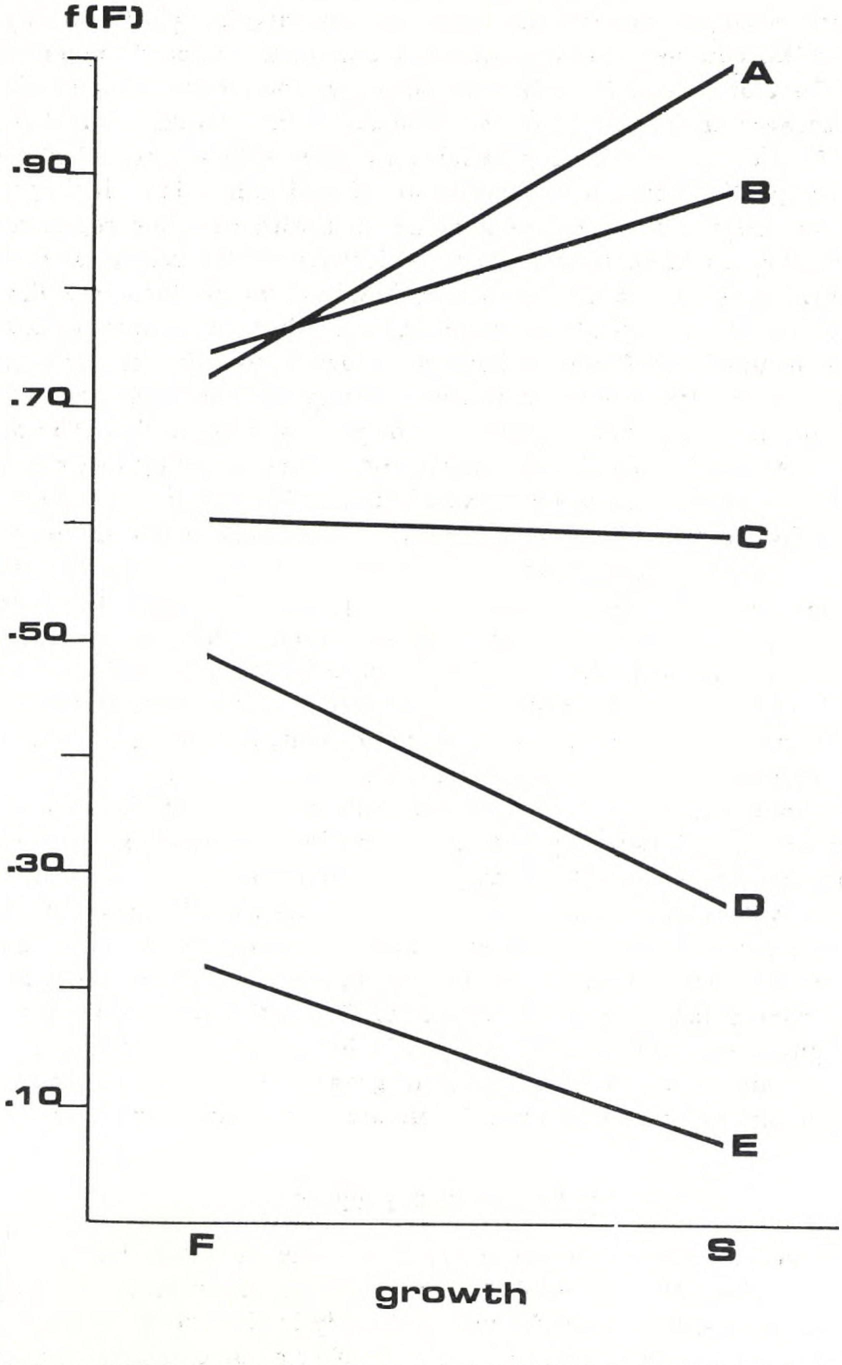

Fig. 5. Gene (EstF) frequency discrepancy of fast and slow growing fish in samples from lakes with sympatric chars. A=Lake Övre Björkvattnet, B=Lake St. Rösjön, D=Lake Yraf and E=Lake Blåsjön. The gene frequency independence of growth in allopatric populations is exemplified by C=Lake Brossen.

a specific ecological pattern the problem of phenotypical plasticity may be more or less eliminated. If it is assumed that these sympatric populations of fish have originated from different ancestral species the inherent differences between their gene pools would make them unequally suitable for the various ecological niches of a lake. In lakes with diversified biotopes direct competition between two species would tend to be minute if they were originally designed to fit different niches and with complete reproductive isolation they could go on living sympatrically until the ecological pattern is broken. In certain bodies of water, however, where there are limited possibilities for ecological differentiation or where a former ecological balance is upset, or finally, where reproductive isolation is incomplete, a gene flow of varying magnitude could swamp the borderlines of two incipient species and produce populations displaying introgression. The problem of assessing the magnitude of introgression among sibling fish has been treated by SVÄRDSON (1970) and LINDSEY *et al.* (1970). In the present sample we have five cases of sibling populations of Arctic char. These sibling pairs represent the whole range of problems encountered among sympatric chars: One lake (22—23) is characterized by two populations where the average weight of spawners differ as much as 20—30 grams in the "tita" as opposed to approx. 700 grams in the large char. Mature fish of the small char of age group 7 may thus be only slightly longer than 1+ specimens of the larger form. In this lake there is consequently no difficulty separating the spawners of the large form from those of the small one.

In the next example (28—29) there is little difference in size of the two char populations, however, growth rate and different otolith shape are not overlapping (FILIPSSON 1967, NILSSON and FILIPSSON 1972). The following two lakes with sympatric populations (26—27 and 24—25) have gone even further in morphological convergence, and the presence of a small char is indicated by a wide range in size per age group. Also, the smaller char is usually darker and has a more blunt head. The last case (30—31) features two populations which overlap completely in morphology, gonad development, size and to a large degree also in growth rate. These four different stages of sibling species differentiation are treated independently below.

Lake St. Rösjön (22—23)

As stated above there are two chars in this tiny (less than 1 square kilometre) and shallow (max. depth 3—5 metres) lake (ANDERSSON, GUSTAFSON and LINDSTRÖM 1971). They differ considerably in size and growth rate and the maximum weight attained by the two differ as much as 50 grams and 3,600 grams. A sample of spawners of the big char, averaging som 700—800 grams, was collected in September 1971. These fish, 33 specimens, had a gene frequency (fF) of 0.76. Samples of small char, averaging some 20 grams

(9—16 cm) were classified according to gonad development and general colouration, and those with silvery appearance and still not sexually mature were considered con-specific with the large char. Small fish that were either fully mature or displaying the typical features of the dwarfed char — blunt nose and big eyes (ANDERSSON *et al.* 1971) were classified as tita. A few samples of small char were also aged employing otoliths and those with a size of 13—16 cm and 6 years older or more were grouped with the dwarfs. These groupings brought the totals of presumed large char to 69 and the presumed dwarfs to 73. In Fig. 4 (22—23) the confidence intervals (95 %) of the two population samples are given and the lack of overlap indicates they belong to different spawning populations. In Table 4 the agreement of observed and expected values assuming CHW equilibrium is calculated and the P-values indicate a good correlation, giving further evidence to the theory of two different gene pools. A heterogeneity test of allele frequencies displayed a probability of less than 0.005 that they belong to the same population. Using the relationship $\frac{f^{T} - f^{Total}}{f^{T} - f^{N}}$ to calculate the proportion of young fish of the 'big size population' in the combined samples of small char yielded a value of only 6 % as opposed to 20 % if those small fish actually classified as belonging to the large char are counted. This discrepancy would probably indicate that either the gene frequency of the large char is lower than recorded or the gene frequency of the "tita" is even higher.

Lake Övre Björkvattnet (28—29)

The differential morphological and ecological characteristics of the two chars in this lake have been described in detail by NILSSON and FILIPSSON (1972). The 88 fish examined in the present study are completely segregated as to growth rate (Fig. 6) and equally well separated on a gene frequency basis (Fig. 4 and Table 4). A calculation of the heterogeneity of allele frequencies of the two populations gives a probability of less than 0.0001 that they belong to the same gene pool.

Lake St. Blåsjön (24—25)

The two populations in this lake overlap in size and growth but most of the specimens with slow growth are rather well separated from the remainder of the specimens. The gene frequency of this group was 0.07. If the other extreme in growth rate, viz. the fastest growing specimens in each age group, comprising roughly 25 % of the total sample, was used as an estimate of the other char in the lake the gene frequency rose to 0.17, significantly higher than the frequency observed among the specimens with poor growth rate (Table 4). By using the relationship stated in the previous

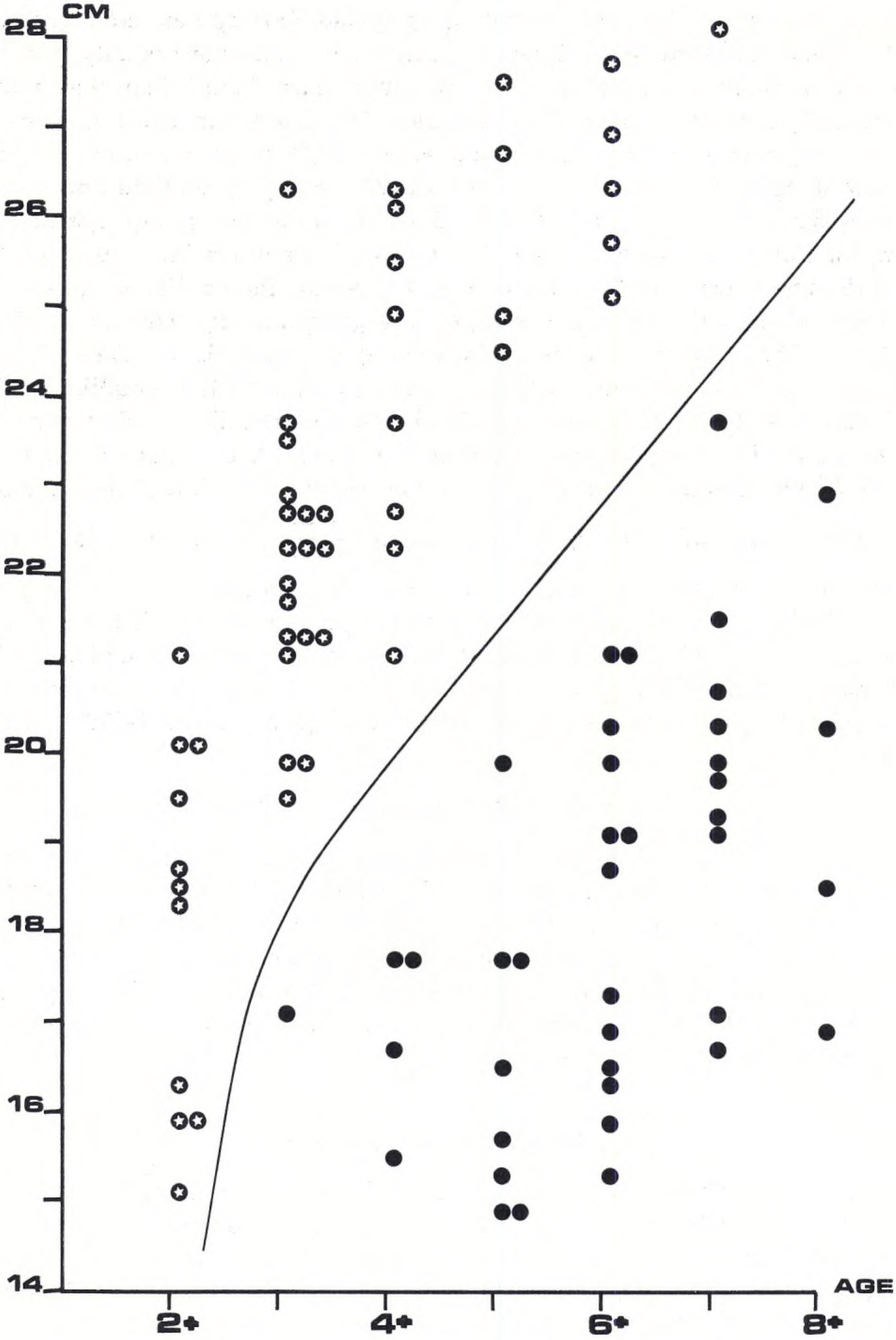

Fig. 6. Complete segregation of growth patterns in the sympatric chars of Lake Övre Björkvattnet.

Table 4. Chi-square analysis of heterogeneity of allele frequencies in populations of Arctic char.

N=normal char, T(tita)=dwarf char

No.	Locality	Est	F/F	F/S	S/S	Total	fF	χ^2(1 d.f.)	Probability of worse fit
22—23	Lake St. Rösjön	N	39	25	5	69	0.75	—	—
			38.4	26.1	4.4	—	—	0.12	0.50—0.75
		T	59	12	2	73	0.89	—	—
			57.8	14.3	0.9	—	—	1.74	0.10—0.25
Heterogeneity of allele frequencies:								9.04	<0.005

No.	Locality	Est	F/F	F/S	S/S	Total	fF	χ^2(1 d.f.)	Probability of worse fit
24—25	Lake St. Blåsjön	N	2	29	67	98	0.17	0.33	0.50—0.75
			2.8	27.4	67.8	—	—	—	—
		T	—	14	92	106	0.07	0.56	0.25—0.50
			0.5	13.1	92.5	—	—	—	—
Heterogeneity of allele frequencies:								9.48	<0.005

No.	Locality	Est	F/F	F/S	S/S	Total	fF	χ^2(1 d.f.)	Probability of worse fit
26—27	Lake Ankarvattnet	N ...	2	13	32	47	0.18	—	—
			1.5	13.9	31.6	—	—	0.23	0.50—0.75
		T ...	—	1	6	7	0.07	—	—
			0.0	0.9	6.1	—	—	0.01	>0.90
Heterogeneity of allele frequencies:								0.41	0.50—0.75

No.	Locality	Est	F/F	F/S	S/S	Total	fF	χ^2(1 d.f.)	Probability of worse fit
28—29	Lake Övre Björkvattnet	N	24	22	2	48	0.73	—	—
			25.5	19.0	3.5	—	—	1.20	0.25—0.50
		T	40	—	—	40	1.0	—	—
			40	—	—	—	—	—	—

Heterogeneity of allele frequencies:

	F	S
N	70	26
T	80	—

to permit employing the formula used above an approx. value is obtained by substituting the Est S freguency of T (0) for *1*.

Thus:

	F	S	Total
N	70	26	96
T	79	1	80
	149	27	176

$$\chi^2 = \frac{(70\times1-26\times79-88)^2\,176}{96\times80\times149\times27} =$$

=20.47 (1 d.f.) The real chi-square value is thus even higher than this value and gives a P of less than 0.0001.

Table 4 continued

No.	Locality	Est	F/F	F/S	S/S	Total	fF	χ^2(1 d.f.)	Probability of worse fit
30—31	Lake Yraf	N	24	64	27	115	0.49	—	—
			27.3	57.5	30.3	—	—	1.49	0.10—0.25
		T	6	41	48	95	0.28	—	—
			7.4	38.2	49.4	—	—	0.51	0.25—0.50
Heterogeneity of allele frequencies:								18.01	<0.0001

example (Lake St. Rösjön) a proportion of 40 % dwarfs is indicated (gene frequency of the total sample is 0.13). This figure implies that some 50 specimens of the dwarf (roughly 33 % of the total of this population sample) overlap the growth distributional pattern of the normal char.

Lake Ankarvattnet (26—27)

The sample analysed from this lake is the only one where the two populations sampled do not display significant gene frequency differences. This situation is likely the result of the very small sample of the dwarf char (7). The gene frequencies of the normal and the dwarf char, respectively, are, however, virtually identical to those of the corresponding populations in nearby Lake Blåsjön (see above), so nothing contradicts the hypothesis that the same chars are present in this lake also.

Lake Yraf (30—31)

The presence of two sympatric populations of char in the lake was evidenced by a recent investigation (NYMAN and FILIPSSON 1972). The material used in that study is included in the present paper and the results condensed. These two chars overlap almost completely in growth and size and would have been considered a fairly normally distributed population of allopatric char, had it not been discovered that the fast growing specimens had a significantly higher gene frequency than the specimens with poor growth (Fig. 4, Table 4). Two samples were obtained in this lake, the first — January 1971 — was taken on standard gillnets with limited mesh size variation (Fig. 7), the second sample (Aug.—Oct. 1971) was taken by so called "survey nets" — 36 m in length and consisting of 12 sections with a mesh size varying from 150 to 20 mm stretched mesh. The second sample thus displayed a far better size and growth distribution of the various age groups (Fig. 8). The two samples were divided subjectively roughly equally distant from the mean size of each age group to provide samples of sufficient size

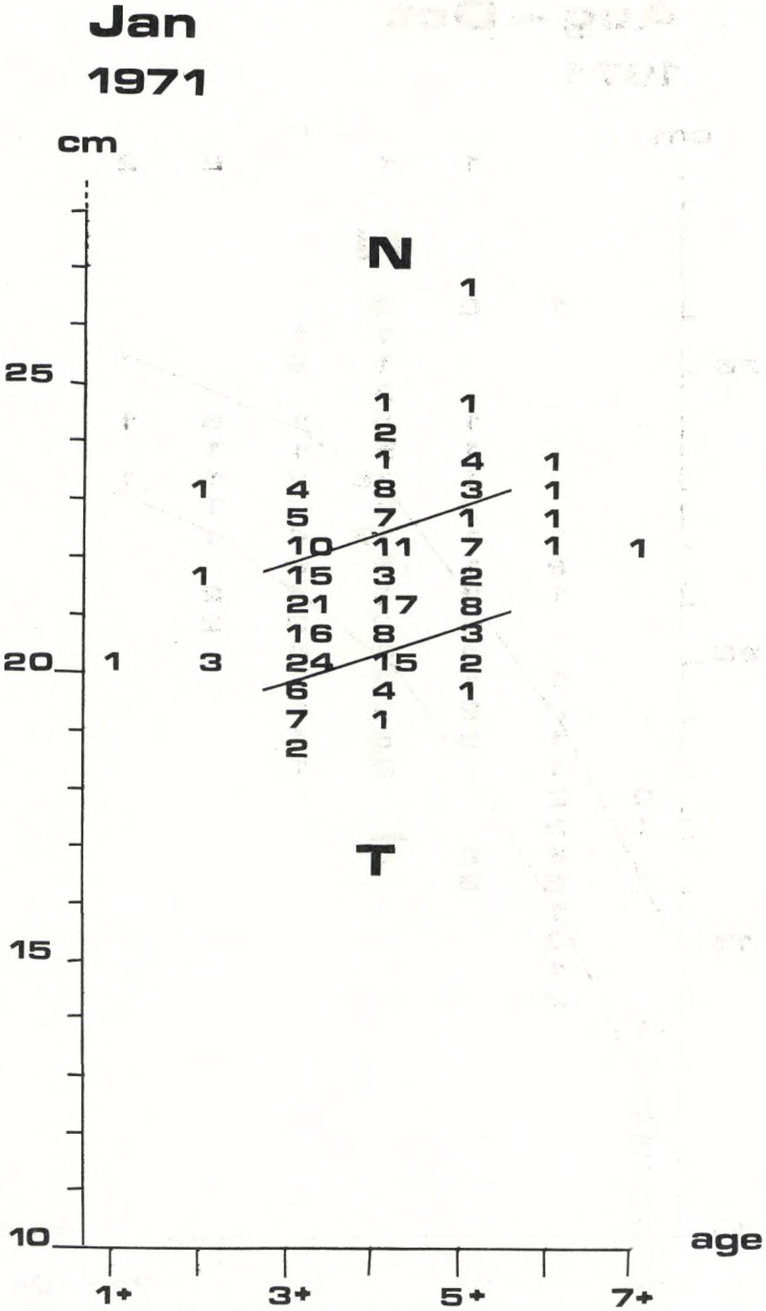

Fig. 7. Size and growth distribution of chars in the samples from Lake Yraf. Those fish above the top line are treated as "normal" char (N), those below the lower line are termed dwarf char (tita=T).

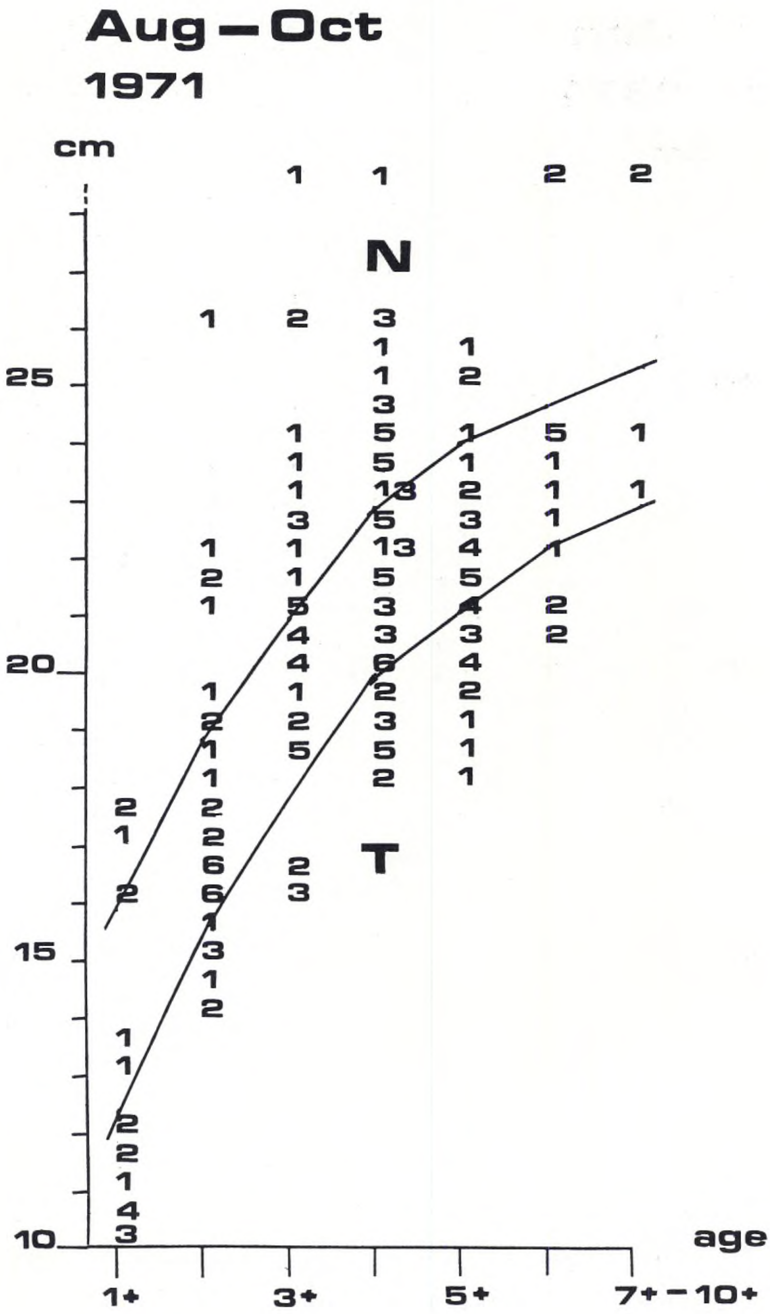

Fig. 8. Wording same as in Fig. 7.

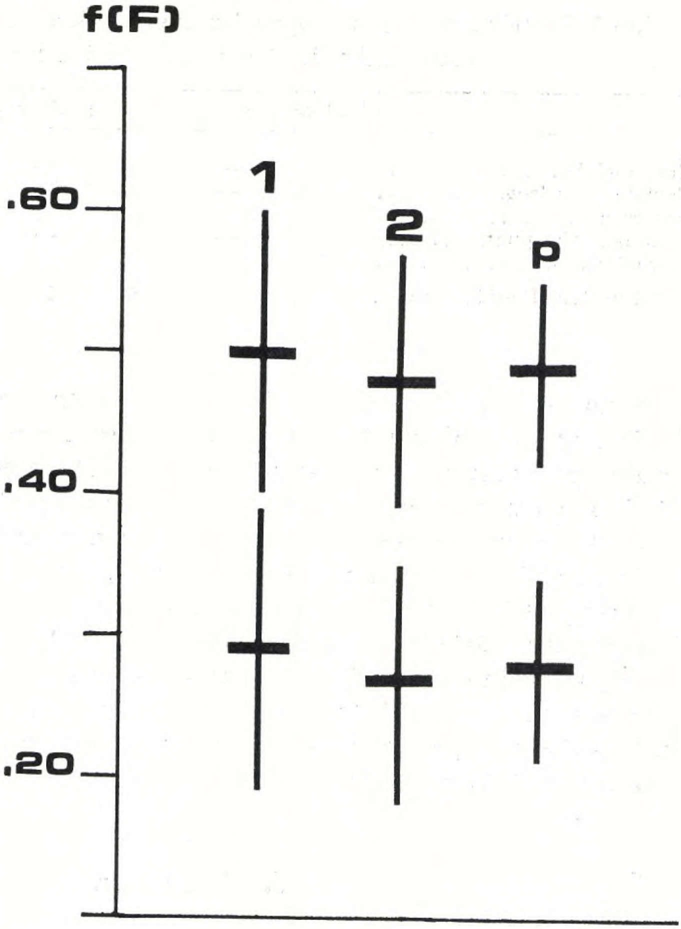

Fig. 9. 95 % confidence intervals of the two samples from Lake Yraf and of the pooled samples.

for meaningful statistical treatment. The portion above the line dissecting the faster growing portion of each sample was termed N for normal char and the portion below the lower line was termed T for "tita" (dwarf char).

The reason why two samples were taken from this lake was the limited size distribution of the first sample, and the almost overlapping confidence intervals (Fig. 9). The second sample broadened the gap between the two confidence intervals and pooled values gave a probability of less than 0.0001 that the two samples were drawn from the same population.

S. alpinus contra *S. malma*

A variety of protein systems were examined electrophoretically in various tissues of the two Dolly Varden char available and compared to five specimens of Arctic char from Keyhole Lake (No. 7, Table 1). The systems analysed are presented in Table 5.

Table 5. Protein systems employed for the examination of genetic divergence between Arctic char and Dolly Varden char.

	Blood	Slime	Muscle	Liver	Kidney	Heart	Spleen
haemoglobin	×	—	—	—	—	—	—
lactate dehydrog.	×	—	×	×	—	—	—
esterase	×	×	×	×	×	×	×
alkaline phosphat.	—	—	×	—	—	—	—
peroxidase	×	×	×	×	×	×	—
total protein (Amido Black)	×	×	×	×	—	—	—

In no case was there any dissimilarity between the two species of char, indicating they belong to the same "species complex" characterized by relatively minute genetical divergence. These findings agree with TSUYUKI *et al.* (1966) who reported that the muscle myogen pattern of the two species were almost superimposable. Since the two other chars in this geographical region, *viz.* the lake trout and the brook trout, display qualitative differences in their protein patterns (TSUYUKI and ROBERTS 1965, NYMAN 1965, 1967 a, TSUYUKI *et al* 1966) it may be concluded that the Dolly Varden char is more closely related to the Arctic char than to either of the other two. Of special interest is the fact that both Dolly Varden char were Est^F homozygotes. This implies the same physiological role of this allele as was postulated by NYMAN and SHAW (1971) in normal Arctic char and brook trout.

IV. Discussion

When all nineteen allopatric population samples of "normal" char or char with excellent growth are plotted in a diagram where the frequency of Est^F is on the x-axis and the latitude (N) on the y-axis, almost every population falls within the zone marked in Fig. 10. This situation emphasizes the hypothesis put forward by NYMAN and SHAW (1971) which postulates a negative correlation between latitude and frequency of that particular allele. These authors indicated the prescence of a difference in enzyme reaction rate between the two different molecular forms of serum esterase in char, the Est^S allele being superior at low temperatures. A further indication that this hypothesis may be valid is obtained from the natural distribution of the brook trout (more southerly than in char), which has a monomorphic serum esterase most probably coded by the same allele as the Est^F allele in char. This is, however, only true for allopatric populations of normal or large char. I mentioned above that there are exceptions also among allopatric normal char from this rule, and three of the four cases may quite easily be accounted for. Population "6" which emanates from Lake Näcken

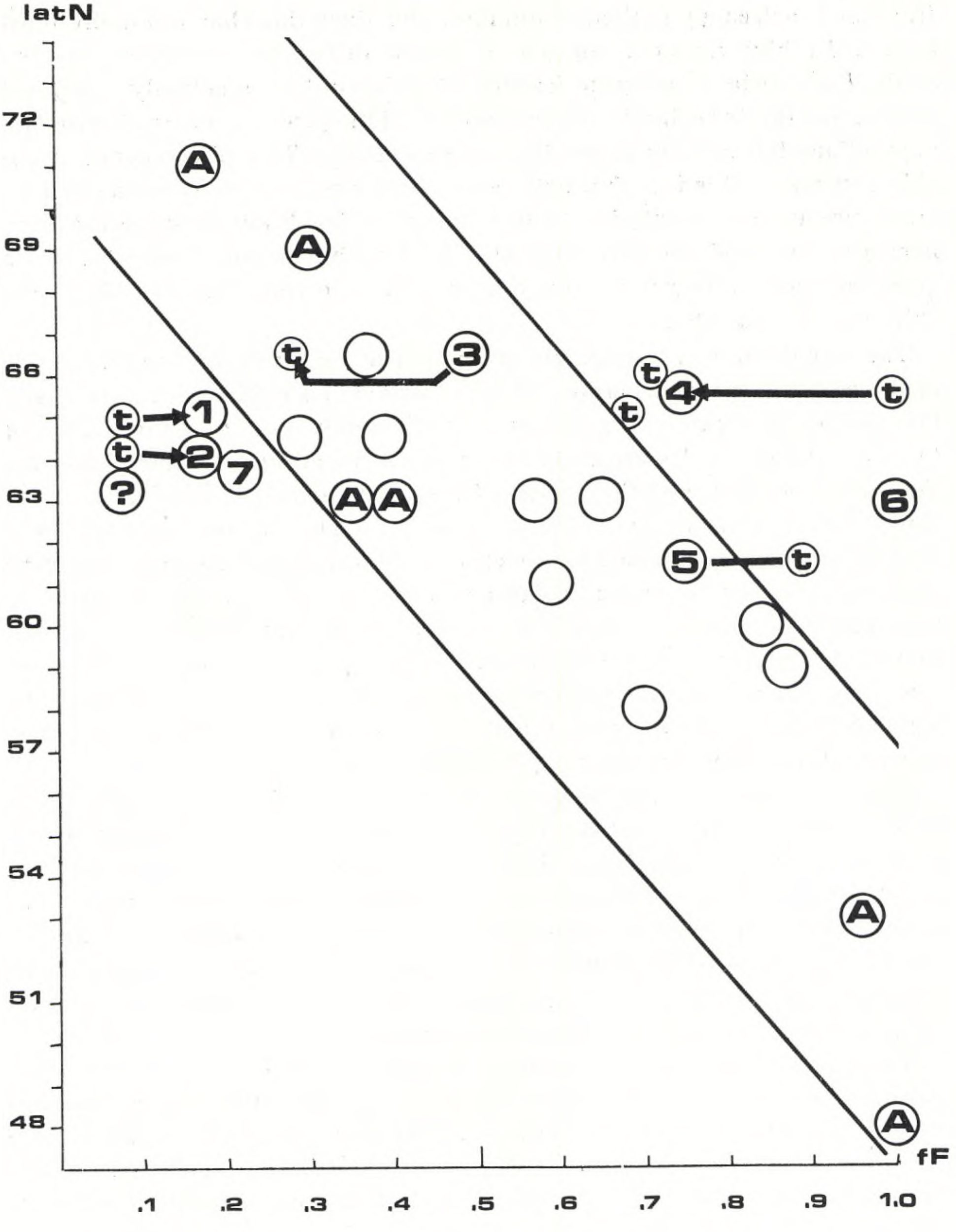

Fig. 10. Distribution of char population samples with regard to latitude (y-axis) and gene frequency (x-axis). "A" indicates samples from North America and "t" stands for "tita" (dwarf char). Other symbols are treated in the text.

(No. 13) is extremely limited in number, and since this char originally must have had a high frequency of gene F genetic drift with subsequent fixation of the Est^F allele seems quite feasible. Population "7" is actually composed of two, viz. the Greenland samples with the same gene frequency. Those two populations fall slightly below the theoretical line. This phenomenon probably depends on the fact that both populations are derived from an environment directly fed by glaciers, which means a far lower temperature than normally recorded on this latitude. The fourth example, indicated by a question mark, reflects the situation in Lake Torrön (No. 16). This case will be discussed later.

The dwarf chars (t), allopatric or sympatric, evidently fall on either side of the normal char distribution. This is taken as an indication that actually two species of dwarf chars are present. Evidently the adaptative value of the two esterase alleles are different in the three groups of char suggesting three different homeostatic systems. Of special interest is the fact that the North American samples, be they taken from anadromous or landlocked populations of normal char, follow exactly the same latitude correlated gene frequency cline as the Scandinavian population samples. It may be expected, however, that future investigations will indicate a slightly different inclination of the gene frequency / latitude cline in populations from Scandinavia, since this region is warmer than areas on the same latitude in North America. This phenomenon would tend to make the inclination roughly intermediate between those of the American populations and the x-axis.

This fact plus the lack of qualitative differences in protein patterns is rather strong evidence that the normal char of North America (and Greenland) — anadromous or landlocked — is con-specific with the normal char of Scandinavia. Whether the aberrant population in Lake Torrön, which was taken from fry hatched at a rearing station, reflects that only a very limited number of parents with atypical genetic setup were used, or, really is the indication of a fourth species, *i.e.* the second species of normal char, is an open question. Further sampling is utterly necessary.

The really interesting part of these results, as I see them, is the situation observed in sympatric populations. In cases 1, 2 and 4 the normal char has a gene frequency outside the normal distribution. In all these lakes there is little or no difference in size of the sympatric chars, a fact that normally favours hybridization. It is thus reasonable to assume that these aberrant normal char have been subject to intogression by the dwarf char, which would mean that the gene frequency of the normal chars would change in the direction of that of the dwarfs. This is also the case. In case 3 is seems that the direction of gene flow has been toward the dwarf, since that population has a higher frequency than expected whereas the normal char is precisely where it "should be". Case 5 is also interesting since it typifies a case where both sympatric species are located where they are supposed to be when existing allopatrically. This case refers to Lake St. Rösjön (Nos 22—23) where it is very unlikely that any introgression should take place due to the extreme difference in size and growth rate of the two species.

There is evidence from one of the samples — Lake Yraf (Nos 30—31) — that the rate of gene flow between the two sympatric chars is a slow process, since a sample of spawners was virtually identical to the dwarf in gene frequency, and in this lake introgression seems to have had the most pronounced impact on the dwarf. Small samples of pelagic fish indicated these were predominantly normal char, which appears the normal ecological distinction between two sympatric chars (NILSSON and FILIPSSON 1972).

The systematic position of *Salvelinus malma* (Dolly Varden) appears quite clear from this and other studies. As stated in the Results section the lack of qualitative differences in the protein patterns studied, which would have been an indication of the same degree of genetical divergence as that observed *e.g.* between brook trout and Arctic char, illustrates that Dolly Varden belongs in the *S. alpinus* complex. Exactly where it belongs is indicated by the sympatric occurence of Dolly Varden and Arctic char in southern Alaska (DELACY and MORTON 1943, MCPHAIL 1961) which implies they are genetically separated.

Since the normal Arctic char of Alaska probably belongs to the same species as the char of *e.g.* Victoria Island (anadromous and landlocked), the Dolly Varden probably represents a fourth species of char within the *S. alpinus* complex. It should also be mentioned that no qualitative variation in protein patterns has so far been detected in *any* of the 31 Arctic char populations studied. These results agree with those of SAUNDERS and MCKENZIE (1971) who showed the con-specific properties of *S. aureolus, S. oquossa* and *S. alpinus.*

To summarize the opinions of the present author it appears that the material here presented comprises four species of char, all of which belong to the *S. alpinus* complex.

Three species have been found in Scandinavia, two of which are dwarfs with usually a littoral or benthic way of life, whereas the normal char lives a more pelagic life. This is true of lakes only. It is not known whether either of the dwarfs still occur as anadromous populations. In North America at least two species appear to be present, *viz.* the normal char, which appears conspecific with the normal char in Scandinavia, and the Dolly Varden char, anadromous as well as landlocked, which represents a more predaceous form. Although the present author did not have the possibility to sample any positive dwarf char from North America, there are other data suggesting the presence of such forms (*e.g.* MCPHAIL 1961, SAUNDERS and POWERS 1969). Whether these dwarfs are conspecific with either of the Scandinavian forms has as yet not been proved, anyway they imply the presence of at least three species of char in North America as well.

How do the results presented above correspond to the two modern schools of char taxonomy? **Behnke** (1972) states that: "The widespread distribution of sympatric char in European lakes would suggest that 2 or 3 species invaded these lakes in postglacial times. Taxonomic comparisons, however, do not support this assumption". **Behnke** found, using morphological criteria (which clearly may be modified by environmental conditions) that usually the two sympatric chars of a given lake appeared more closely related to one another than to chars of other lakes. As to **Behnke**'s sample of sympatric chars from Sweden, three of his populations are included in the present study, *viz.* Nos. 24—25, 26—27 and 28—29. All three displayed pronounced introgression with a swamping not only of the gene pools but of morphological characteristics as well. The major differences between the two schools of thought are concerned with the time factor and the number of splits of ancestral species producing reproductively isolated populations.

According to **Behnke** (1927 one heterogeneous ancestor migrated upstream the postglacial rivers and in each lake system, more or less sympatrically, evolved into two or more reproductively isolated populations. **Behnke**'s view is also embraced by **Lindsey** *et al.* (1970) with regard to the specification of whitefish in North America. Their view postulates a great number of "splits" must have occurred and more or less sympatric speciation. **Svärdson** (1958, 1961, 1970), on the other hand, believes that a limited number of species (3 or 4) existed already during the Anzylus stage (in the Gulf of Bothnia) and independently invaded the freshwater areas after the recession of the ice, and, although they may have been slightly hybridized before entering freshwater, the bulk of mixing of genetic material occurred in the lakes by means of introgression, and is actually still occurring. **Svärdson** thus postulates a limited number of splits in pre-glacial times (allopatrically) and that morphological and genetic convergence is of recent origin and reflects introgression. **Svärdson**'s opinion presupposes the existence of rather unchanged populations in lakes with allopatric chars. The results of the present investigation strongly suggest that the introgression theory of **Svärdson** is the more likely of the two.

V. Summary

Gene frequency data of an esterase polymorphism in Arctic char (*Salvelinus alpinus* (L.)) were analysed in 31 populations of landlocked and anadromous char from North America, Greenland and Scandinavia. Also, two specimens of Dolly Varden char (*Salvelinus malma* (**Walbaum**)) were analysed electrophoretically. On the basis of gene frequency distributions correlated with ecological parameters three sibling species of char within the so called *Salvelinus alpinus* complex could be distinguished in the Scandinavian samples. One of these species, the normal char, appears conspecific with the normal char of North America and Greenland, whereas the other form studied from this region — the Dolly Varden — is considered a distinct species. The variability of sympatric chars is believed to have resulted from introgression in recent times after the ancestral species had evolved their reproductive isolating mechanisms allpotrically.

VI. Acknowledgments

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VII. References

ANDERSSON, G., K.-J. GUSTAFSON and T. LINDSTRÖM 1971. Rödingen i Rösjöarna på Fulufjäll. *Inform. Inst. Freshw. Res.,* (8) 20 p. (Mimeographed in Swedish.)

AUGUSTINSSON, K.-B. 1961. Multiple forms of esterase in vertebrate blood plasma. *Ann. New York Acad. Sci.* 94: 844—860.

BEHNKE, R. J. 1968. A new subgenus and species of trout, *Salmo (Platysalmo) platysephalus,* from southcentral Turkey, with comments on the classification of the subfamily *Salmoninae. Mitt. Hamburg zool. Mus. Inst.* 66: 1—15.

— 1972. The systematics of salmonid fishes of recently glaciated lakes. Part I. Subfamily *Salmoninae. J. Fish. Res. Bd. Can.* 29(6): 639—671.

BERG, L. S. 1948. Freshwater fish in the USSR and adjoining countries. *Zool. Inst. Akad. Nauk. SSSR,* 4(27): 466 p.

Burstone, M. S. 1962. Enzyme histochemistry and its application in the study of neoplasms. Acad. Press, New York and London, 621 p.

CHERNENKO, YE. V. 1969. Evolution and cytotaxonomy of the family *Salmonidae. Probl. Ichthyol., Amer. Fish. Soc.* 9(6): 781—788.

DeLacy, A. C. and W. M. Morton 1943. Taxonomy and habits of the chars, *Salvelinus malma* and *Salvelinus alpinus,* of the Karluk drainage system. *Trans. Amer. Fish. Soc.* 72: 79—91.

Dymond, J. R. 1947. A list of the fresh-water fishes of Canada east of the Rocky Mountains. *Misc. Pub. Roy. Ontario Mus. Zool.* 1. 36 p.

Filipsson, O. 1967. Åldersbestämning av röding med hjälp av otoliter. *Inform. Inst. Freshw. Res.* (5) 10 p. (Mimeographed in Swedish.)

Jordan, D. S., B. W. Evermann and H. W. Clark 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Columbia. *Rep. U. S. Fish. Comm.* 2. 670 p.

Li, C. C. 1955. Population Genetics. Univ. Chicago Press, Chicago, 366 p.

Lindsey, C. C., J. W. Clayton and W. G. Franzin 1970. Zoogeographic problems and protein variation in the *Coregonus clupeaformis* species complex. p. 127—146. *In* Biology of Coregonid fishes. C. C. Lindsey and C. S. Woods (Eds.). Univ. Manitoba Press, Winnipeg.

Martin, W. R. 1939. The Arctic char of North America. Univ. Toronto, M. A. Thesis 64 p.

McPhail, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *J. Fish. Res. Bd. Can.* 18(5): 793—814.

Nilsson, N.-A. and O. Filipsson 1972. Characteristics of two discrete populations of Arctic char (*Salvelinus alpinus* (L.)) in a north Swedish lake. *Rep. Inst. Freshw. Res., Drottningholm,* 51: 90—108.

Nyman, O. L. 1965. Variation of proteins in hybrids and parental species of fishes. Rep. Swed. Salm. Res. Inst., 13 11 p.

— 1967 a. Protein variation in various populations of Atlantic salmon. *Rep. Swed. Salm. Res. Inst.,* 8 11 p.

— 1967 b. Protein variations in *Salmonidae. Rep. Inst. Freshw. Res., Drottningholm,* 47: 5—38.

— 1970. Electrophoretic analysis of hybrids between salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.). *Trans. Amer. Fish. Soc.* 99(1): 229—236.

— 1972. Plasma esterases of some marine and anadromous teleosts and their application in biochemical systematics. *Rep. Inst. Freshw. Res., Drottningholm,* 51: 109—123.

— and O. Filipsson 1972. Rödingen i Yraf. *Inform. Inst. Freshw. Res., Drottningholm,* (10) 16 p. (Mimeographed in Swedish with English summary).

— and D. H. Shaw 1971. Molecular weight heterogeneity of serum esterases in four species of salmonid fish. *Comp. Biochem. Physiol.* 40 B: 563—566.

Regan, C. T. 1914. Systematic arrangement of the fishes of the family *Salmonidae. Ann. Mag. nat. Hist.* 8(13): 405—408.

Saunders, L. H. and J. A. McKenzie 1971. Comparative electrophoresis of Arctic char. *Comp. Biochem. Physiol.,* 38(3 b): 487—492.

— and G. Powers 1969. The Arctic char, *Salvelinus alpinus* (*Linnaeus*) of Matamek Lake, Quebec. *Can. Nat.* 96: 919—934.

Savvaitova, K. A. 1966. Intraspecific biological forms of *Salvelinus alpinus* (L.) in Kamchatka. *Transl. Ser. Fish. Res. Bd. Can.* (795), 30 p.

Svärdson, G. 1949. The coregonid problem. I. Some general aspects of the problem. *Rep. Inst. Freshw. Res., Drottningholm,* 29: 89—101.

— 1958. Specification in freshwater fish as illustrated by *Coregonus. Proc. XVth Inter. Conf. Zool.,* Sect. II (1): 137—141.

— 1961. Young sibling fish in northwestern Europe. *In:* Vertebrate Specification. Univ. Texas Symp. p. 498—513.

— 1970. Significance of introgression in Coregonid evolution. *In:* Biology of Coregonid fishes. p. 33—59. Lindsey C. C. and C. S. Woods (Eds.). Univ. Manitoba Press, Winnipeg.

— and N.-A. NILSSON 1964. Fiskebiologi. Hallandspostens Boktryckeri, Halmstad, 253 p. (In Swedish.)

TSUYUKI, H. and E. ROBERTS 1965. Zone electrophoretic comparison of muscle myogens and blood proteins of artificial hybrids of *Salmonidae* with their parental species. *J. Fish. Res. Bd. Can.* 22(3): 767—773.

— J. F. UTHE, E. ROBERTS and L. W. CLARKE 1966. Comparative eletropherograms of *Coregonus clupeaformis, Salvelinus namaycush, S. alpinus, S. malma* and *S. fontinalis* from the family *Salmonidae. J. Fish. Res. Bd. Can.* 23(10): 1,599—1,606.

TUUNAINEN, P. 1970. On the relationship of salmon fish. *Transl. Ser. Fish. Res. Bd. Can.* (1,476), 11 p.

VLADYKOV, V. D. 1954. Taxonomic characters of the eastern North America chars (*Salvelinus* and *Cristivomer*). *J. Fish. Res. Bd. Can.* 11(6): 904—932.

WALTERS, V. 1955. Fishes of western arctic America and eastern arctic Siberia. *Bull. Amer. Mus. nat. Hist.,* 106(5): 255—368.

WENT, A. E. J. and E. TWOMEY 1957. Notes on Irish char, *Salvelinus colii* GUNTHER: VI. *Irish Nat. J.* XII(8): 205—206.

Fish predation effects on the species composition of the zooplankton community in eight small forest lakes

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Contents

I. Introduction

Since the fifties, limnologists have been aware of the ability of a fish population to influence its plankton environment through direkt predation. This means not only a reduction in abundance of different species but also a change in the species composition and a change in the size composition within the species.

Several field studies have dealt with this problem. HRBACEK and co-workers were able in some small Elbe backwaters to demonstrate the great importance of the fish population size for the species composition in the plankton community (HRBACEK 1958, 1959, 1962, HRBACEK *et al.* 1961, HRBACEK and NOVOTNA-DVORAKOVA 1965, NOVOTNA and KORINEK 1966).

The same problems have been investigated in an illustrative way in the studies concerning the alewife (*Alosa pseudoharengus*) (BROOKS and DODSON 1965).

The mechanisms involved in the interspecific relations within the plankton community have also been discussed (BROOKS and DODSON 1965, BROOKS 1968, BURNS and RIGLER 1967, STRASKRABA 1965).

The present investigation is a comparison between the plankton fauna (especially the cladocerans) in eight small forest lakes, of which four are treated with rotenone and provided with new fish populations, consisting of new species.

Concomitant investigations of physico-chemical limnology were carried out so that factors other than fish predation could be taken into consideration in the evaluation of the results.

II. The study area

The investigated lakes lie in the central part of the province of Bohuslän in south-western Sweden, approximately 60 km from Göteborg (Gothenburg) (Fig. 1).

All the lakes are located within a small area (3.5 km^2), in which geological and meteorological factors are uniform. The terrain is rather hilly and the rock type is gneiss. The lakes are surrounded by forest (mainly consisting of pine, spruce and oak), which to some extent provides shelter from strong winds. Some basic morphometric data are summarized in Table 1. The lakes are shallow and the littoral zones constitute relatively large parts of the lake area. The bottoms are throughout very uniform, consisting of organic sediment with remains of rotting plants and alloctonous material from the surrounding forest. There is little difference in the sediment composition. The vegetation is sparse in all the lakes. Scattered patches of *Phragmites communis, Nymphaea alba, Equisetum fluviatile* and other rooted plants occur in shallow water.

The application of rotenone took place in 1957—61. The fish species present before and after the rotenone treatment are listed in Table 2.

A few years after the eradication of the fish fauna of lake No 2, the original species (with the exception of perch) managed to reoccupy the water though a ditch from another lake at an exceptionally high spring water.

III. Methods

Field methods

Location of sample sites for water and plankton are shown in Fig. 1.

Samples were taken monthly at all sites during the sampling period (April 1971—April 1972).

Temperature and oxygen were measured with an electrical oxygen meter. Water sampling for laboratory analyses was done with an ordinary RUTTNER sampler. Transparency was measured with a standard 20 cm Secchi disc.

Zooplankton samples were taken in two different ways.

Fig. 1. Location of the investigated lakes and the sampling stations. Sites of plankton and water samples in the limnetic zone ○, and of plankton samples in the littoral zone ●.

Table 1. Morphometric features of eight forest lakes in the province of Bohuslän, southwestern Sweden.

Lake	Elevation (m)	Area (ha)	Max depth (m)	Mean depth (m)	Volume (m^3)
1. Lilla Mörtevattnet	105	4.3	10.0	3.2	137,000
2. Lilla Stockelidsvattnet	130	1.0	6.0	3.0	30,000
3. Stora Stockelidsvattnet	135	1.9	6.0	2.1	40,000
4. Lilla Blackevattnet	140	1.0	4.5	2.0	20,000
5. Lilla Valeklintsvattnet	134	2.1	7.0	2.7	56,000
6. Holmevattnet	142	2.3	5.0	2.1	47,000
7. Stora Valeklintsvattnet	130	4.3	4.5	1.6	70,000
8. Södra Flågvattnet	120	2.3	5.0	2.0	46,000

a. In the pelagial zone sampling was done with a plankton net (mesh 80 μ; mouth area 324 cm^2; net length 60 cm) which was weighted at the bottom to ensure that the mouth was directed upwards during descent. The net was hauled at a constant speed of 0.5 m/sec from the bottom to the surface. Five hauls were made on each occasion.

b. The sampling in the littoral zone within the vegetation was done with a handle plankton net (mesh 65 μ; mouth area 200 cm^2; net length 50). The net was hauled 4×10 m on each occasion. The samples were preserved in formalin (4 ‰).

The use of the plankton net cannot guarantee a complete quantitative evaluation, but is permits relative comparisons when sampling is done within a uniform environment. It is, however, an advantage to use this type of sampling in shallow lakes, where it is capable of giving adequate samples from the entire column of water.

Table 2. Fish species in eight forest lakes in the province of Bohuslän southwestern Sweden.

Fish species	Lake number											
	1	2		3	4		5		6	7		8
		br	ar		br	ar	br	ar		br	ar	
Leuciscus rutilus L.	+	+	+	+	+	—	+	—	+	+	—	+
Perca fluviatilis L.	+	+	—	+	+	—	+	—	+	+	—	+
Esox lucius L.	+	+	+	—	—	—	+	—	+	+	—	—
Anguilla anguilla L.	+	+	+	+	+	—	+	—	+	+	—	+
Salmo trutta L.	—	—	—	—	—	—	—	+	—	—	+	—
Salvelinus fontinalis (MITCHILL)	—	—	—	—	—	+	—	+	—	—	+	—
Salmo gairdneri (RICHARDSON)	—	—	—	—	—	—	—	+	—	—	+	—

br:before rotenone
ar:after rotenone

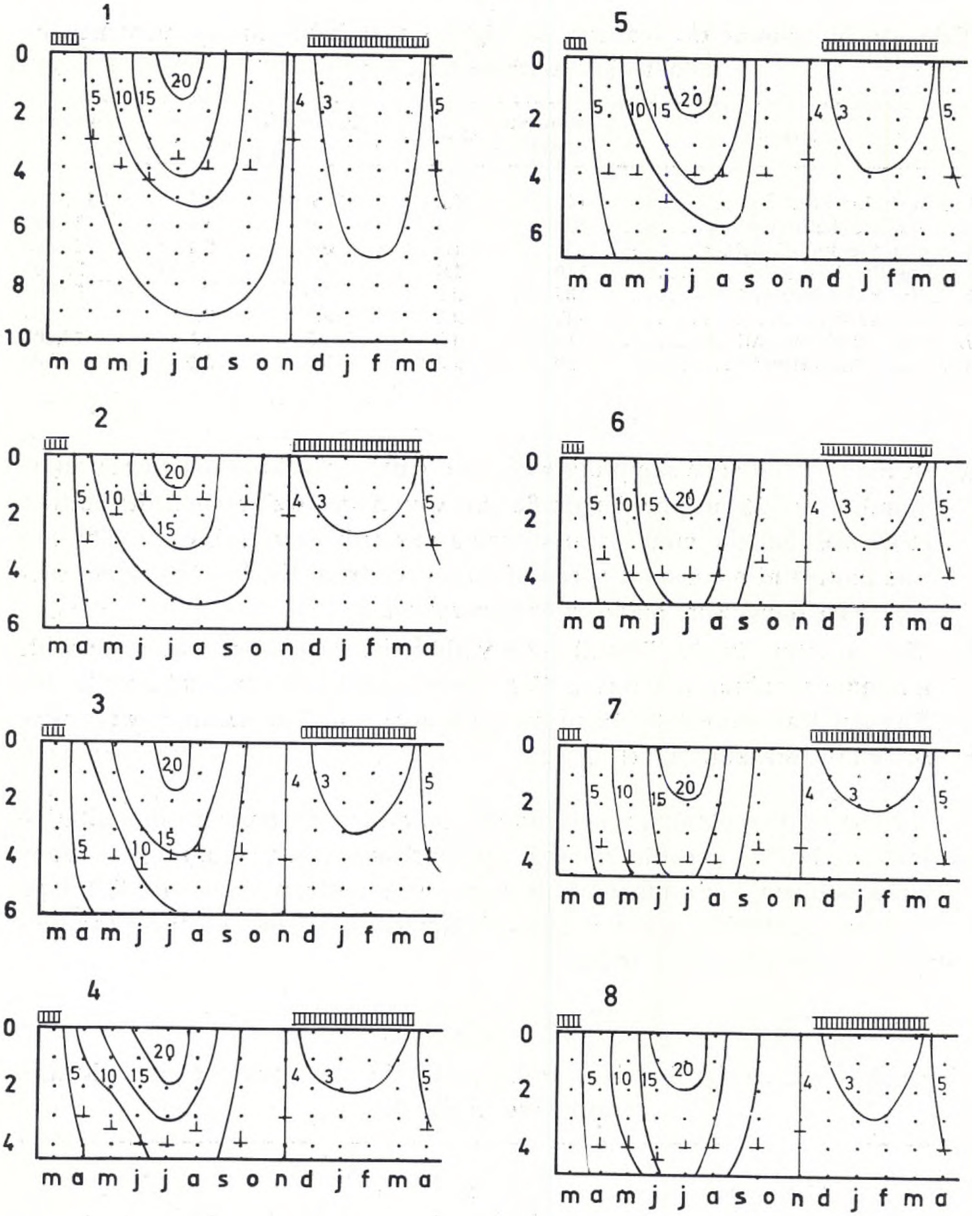


Fig. 2. Isotherms, and light penetration in the investigated lakes (March 1971—April 1972). SECCHI disc ⊥. Ice cover ııııııı.

Laboratory methods

For the identification, counting and measuring of the zooplankton, stereo- and compound microscopes were used. For counting an open chamber and for measuring, an open lined tray was used.

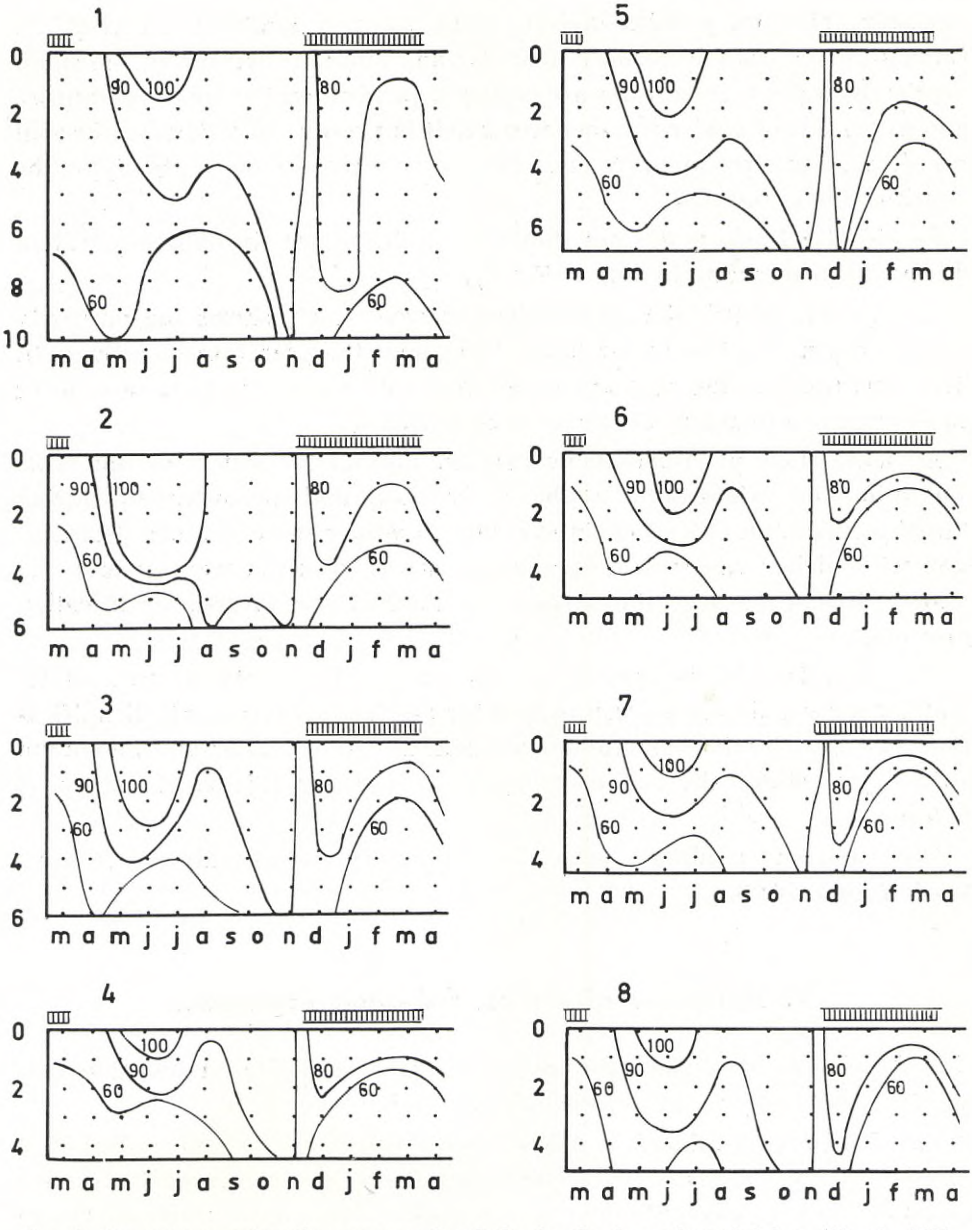


Fig. 3. Percentage saturation oxygen isopleths in the investigated lakes (March 1971—April 1972).

IV. Physico-chemical limnology

Measurements concerning the physico-chemical conditions have been carried out since autumn 1968.

The isotherm patterns for the eight lakes are strikingly similar throughout the year. Thermal profiles indicate weak summer stratification (Fig. 2). Circulation does not occur only in spring and autumn. Because of the small depths the water temperatures are closely dependent on the air temperatures, and in periods of colder summer weather it is possible to get homeothermal conditions and circulation. A short time after a circulation of this type, the stratification is restored.

Secchi disc readings did not shown great differences in light penetration during the year, except in lake 2 (Fig. 2).

The vertical distribution of dissolved oxygen clearly shows the similarity in the oxygen situation in the lakes throughout the year (except in lake 2). The conditions during stagnant situations in winter and summer are never so severe that a total lack of oxygen occurs (Fig. 3).

All lakes show pH fluctuations that are normal for waters of this type. The minimum values occur at the ice break-up and the maximum during the phytoplankton flowerings in summer. In winter there is a pH stratification with higher values in deeper water, where readings were at least 0.2 higher than those near the surface. In summer the inverse stratification prevails.

The variations in the specific conductivity and the total amount of Ca and Mg show a similar pattern to that for the fluctuations of pH. Stratification occurs with minimum values just beneath the ice cover and maximum values just above the sediment layer. In summer this stratification is inverted.

Maximum and minimum values for laboratory water analyses are summarized in Table 3.

V. Rotenone effect on fish-food organisms

The purpose of a rotenone treatment is to eradicate undesirable fish species and thereby create populations more suitable for game fishing.

Fish-food organisms are, however, also sensitive to rotenone (albeit in a physiologically different way). The toxic effects are influenced by several abiotic factors. Exposure to light, oxygen, alkali, heat and turbidity decrease the efficiency. The effects are pH-dependent and the poison strikes harder in acid water than in alkaline (ÖBERG, 1956).

The initial effects on the crustacean zooplankton are catastrophic, almost a complete eradication occurring within 24 hours. The effects on rotifers are also severe; most species disappear immediately after poisoning (ALMQUIST 1959, ANDERSON 1970, BERZINS 1958, HRBACEK and NOVOTNA-DVORAKOVA 1965; KISER *et al.* 1963). According to ALMQUIST and ANDERSON, certain

Table 3. Maximum and minimum values of laboratory water analyzes.

Lake number depth (m)		pH		(Ca+Mg) ppm		Specific conductance µS$_{20}$	
		Min	Max	Min	Max	Min	Max
1	0	5.7	7.1	8.3	9.3	65.5	79.0
	5	5.4	7.0	9.3	11.4	75.0	79.0
2	0	5.7	8.4	8.7	14.0	66.2	100.0
	4	5.9	7.8	12.7	15.7	90.0	98.0
3	0	5.4	7.9	4.8	12.7	47.5	92.0
	4	5.5	7.3	11.3	15.0	83.0	98.5
4	0	4.3	6.9	5.5	9.1	54.0	79.0
	3	5.3	6.2	8.2	11.5	77.1	84.0
5	0	5.2	7.2	6.7	11.0	58.5	93.0
	4	5.8	6.9	10.4	12.5	79.0	91.0
6	0	4.8	7.0	4.5	9.2	46.2	81.0
	4	5.8	6.6	7.8	12.6	73.0	98.5
7	0	5.5	7.3	8.9	10.0	55.0	83.0
	4	5.5	7.1	9.1	14.0	78.0	100.0
8	0	4.7	7.2	6.9	8.1	63.0	84.0
	4	4.9	6.9	7.6	8.8	70.5	86.0

species of the genera *Keratella* and *Kelikottia* are less affected. Phytoplankton seems to be almost unaffected.

The mortality of benthic invertebrates shows a clear dependence on the ability of the animals to escape the poison. Mud-dwelling species and species living in epiphyton have better changes of survival than do other species (ALMQUIST 1959, LINDGREN 1960, ANDERSON 1970).

In general a sufficient number of different species are left after the poisoning, and these build up new populations.

A necessary condition for the restocking of the lakes with fish is the recovery of the plankton and the benthic communities.

HRBACEK and NOVOTNA-DVORACOVA (1965) found that phytoplankton, rotifers and protozoans reappeared first, and within 3—4 months almost every crustacean species was back. ANDERSON (1970) showed that most species of crustacean zooplankton had reappeared within 10 months of the initial eradication. The time required to achieve the pre-rotenone species diversity and abundance is at least three years. Both investigations show a change in the species composition after the recovery, due to alterations in the predation intensity on the plankton community. KISER *et al.* (1963) reported that none of the 42 cladoceran or copepod species disappeared permanently after a rotenone treatment. Adult cladocerans which came into contact with the poison were killed, but the species survive thanks to parthenogenetic summer eggs and ephippial eggs.

Table 4. Limnetic species in eight forest lakes in the province of Bohuslän, southwestern Sweden (Rotifers excluded).

	Lake number							
	1	2 r	3	4 r	5 r	6	7 r	8
Heterocope appendiculata G. O. SARS	+	+	+	+	+	+	+	+
Eudiaptomus gracilis G. O. SARS	+	+	+	+	+	+	+	+
Thermocyclops oithonoides G. O. SARS	+	+	+	+	+	+	+	+
Eucyclops serrulatus FISCHER	+	+	+	+	+	+	+	+
Cyclops strenus FISCHER	+	+	+	+	+	+	+	+
Polyphemus pediculus (LINNÉ)	+	+	+	+	+	+	+	+
Bythotrephes longimanus LEYDIG	—	—	—	—	+	—	+	—
Sida crystallina O. F. MÜLLER	+	+	+	+	+	+	+	+
Diaphanosoma brachyurum (LIÉVEN)	+	+	+	+	+	+	+	+
Holopedium gibberum ZADDACH	+	+	+	+	+	+	+	+
Daphnia longispina (O. F. MÜLLER)	—	—	—	+	+	—	+	—
Daphnia cristata G. O. SARS	+	+	+	—	—	+	—	+
Ceriodaphnia quadrangula (O. F. MÜLLER)	+	+	+	+	+	+	+	+
Scapholeberis mucronata (O. F. MÜLLER)	+	+	+	+	+	+	+	+
Bosmina longirostris (O. F. MÜLLER)	+	+	+	+	+	+	+	+
Bosmina coregoni BAIRD	+	+	+	+	+	+	+	+
Eurycercus lamellatus (O. F. MÜLLER)	+	+	+	+	+	+	+	+
Acroperus harpae BAIRD	+	+	+	+	+	+	+	+
Alona affinis LEYDIG	+	+	+	+	+	+	+	+
Alona quadrangularis (O. F. MÜLLER)	+	+	+	+	+	+	+	+
Alonella nana (BAIRD)	+	+	+	+	+	+	+	+
Chydorus sphaericus (O. F. MÜLLER)	+	+	+	+	+	+	+	+

(r:treated with rotenone)

VI. Results and Discussion

The species and size composition of the cladoceran community

The discussion will mainly treat the structure of the cladoceran communities, since the planktivores prefer cladocerans to calanoid and cyclopoid copepods (BERG and GRIMALDI 1966, BROOKS 1968, IVLEV 1961).

The species composition of the crustacean zooplankton of the investigated lakes is presented in Table 4. The homogeneity in the species distribution is apparent. Only three species diverge in this respect. *Bythotrephes longimanus* is found only in lakes 5 and 7 and *Daphnia longispina* (Fig. 4) only in lakes 4, 5, and 7, while *Daphnia cristata* (Fig. 5) is present in all the other lakes. How can these differences be explained?

Three factors to be considered are:

1. The quality of the lakes (phys.-chem. factors).
2. The rotenone treatment *per se.*
3. The predation.

1. The physico-chemical limnology conditions in the lakes show great similarities during the year, and the differences in the sediment composi-

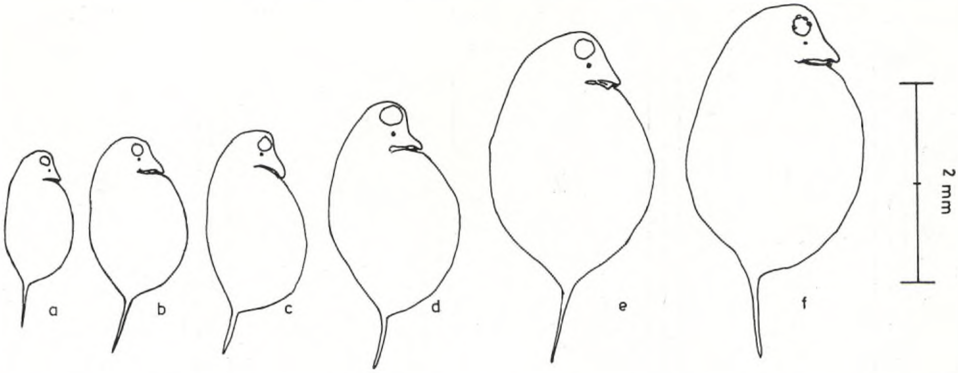


Fig. 4. *Daphnia longispina* (O. F. MÜLLER). Young individuals, a—b. Adult females, c—f.

tion and the vegetation are very small. It is therefore justifiable to assume that the plankton situation in lakes 4, 5, and 7 before the rotenone treatment (before the introduction of new fish species) did not differ significantly from the other lakes.

2. Lake no 2, which has undergone a rotenone treatment but contains the original fish species (with the exception of perch), can serve as a control of possible rotenone effects on the plankton community. The species composition here and in the untreated lakes is completely con-accordant. No visible differences appeared after the regeneration of the plankton fauna.

3. To be able to explain the described species differences and also the differences in the size composition within the plankton community, we must consider the predation, and in connection with this, of course, the fish populations of the lakes. Lakes 2, 4, 5, and 7 were treated with rotenone and

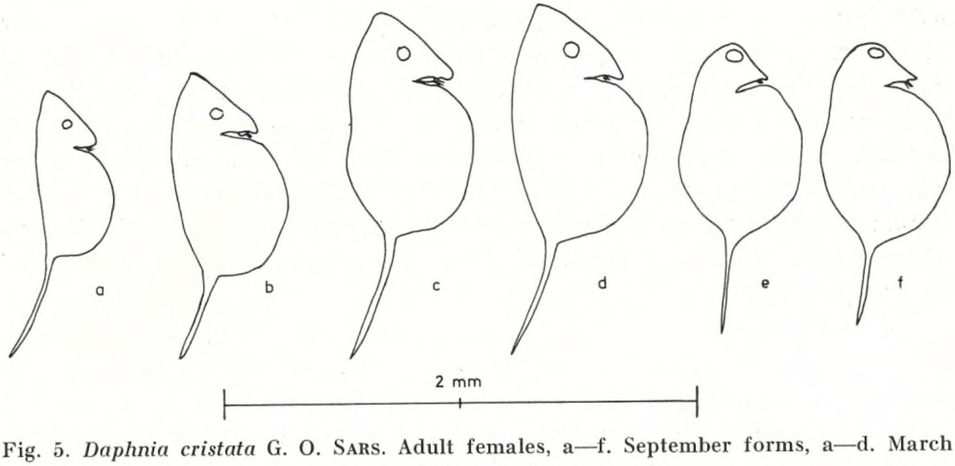


Fig. 5. *Daphnia cristata* G. O. SARS. Adult females, a—f. September forms, a—d. March forms, e—f.

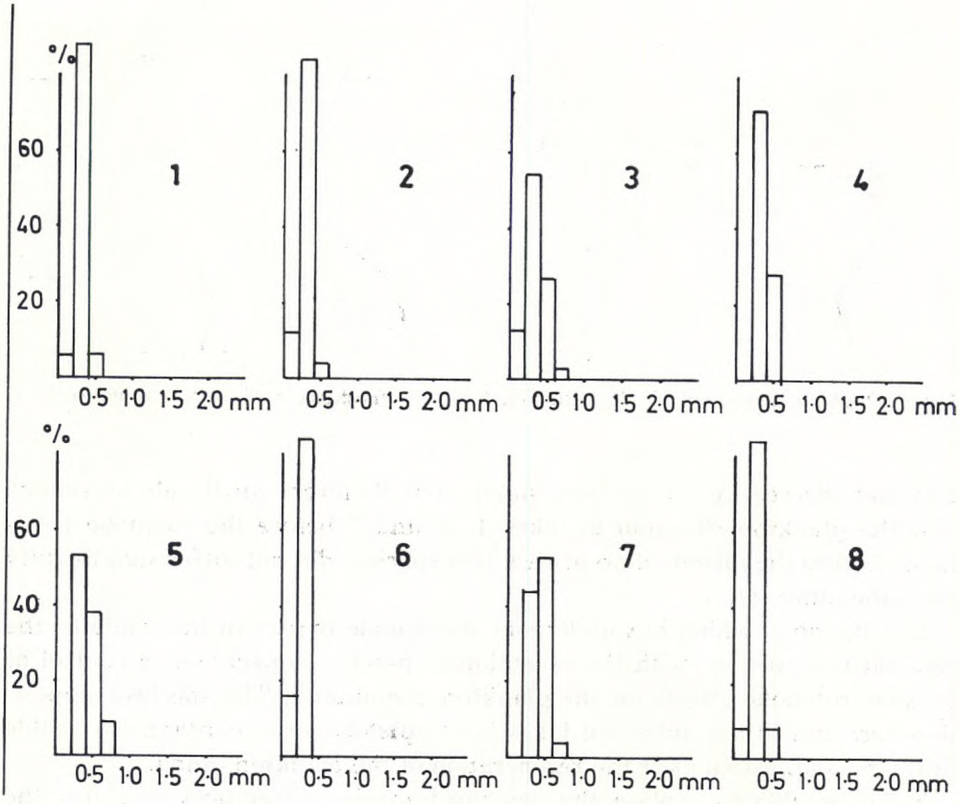
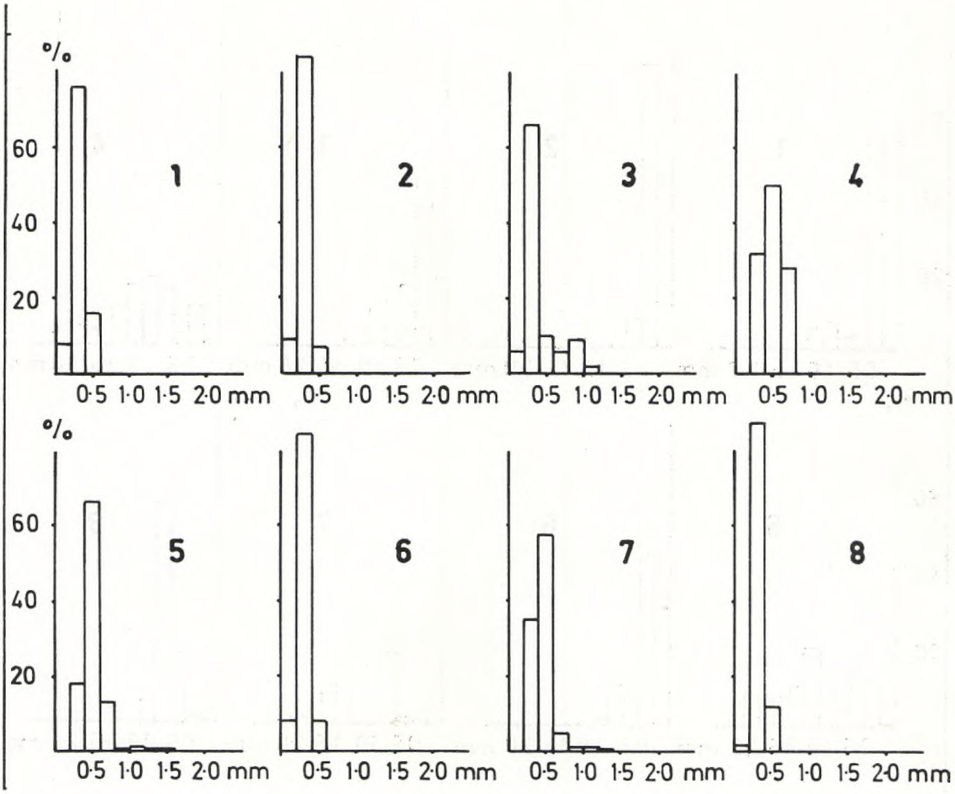


Fig. 6. Size distribution in the cladoceran community. A: 25/1 1972, B: 23/4, C: 29/6 1971).

provided with new species (see above), which owing to lack of suitable spawning places are unable to reproduce in this water. This is not valid for lake 2, where the original species (with one exception of perch) reoccupied the water. The fish populations in the other lakes treated were maintained with regular outputs of fishes. The original species in lakes 1, 2, 3, 6 and 8 were able to spawn and to produce each year great quantities of fry which during their early life are dependent on a plankton diet. The fish populations in these lakes are consequently more dense than in the treated lakes. It has not yet been possible to carry out an objective measurement of the fish-population size.

Most fresh-water fishes are as adults facultative planktivores. Stomach analyses, from all lakes, show that adult perches and roaches often predate on plankton, which the salmonides more seldom do. Only the larger species, *Eurycercus lamellatus, Bythotrephes longimanus* and *Daphnia longispina,* occur in the salmonid diet (STENSON, in prep.).

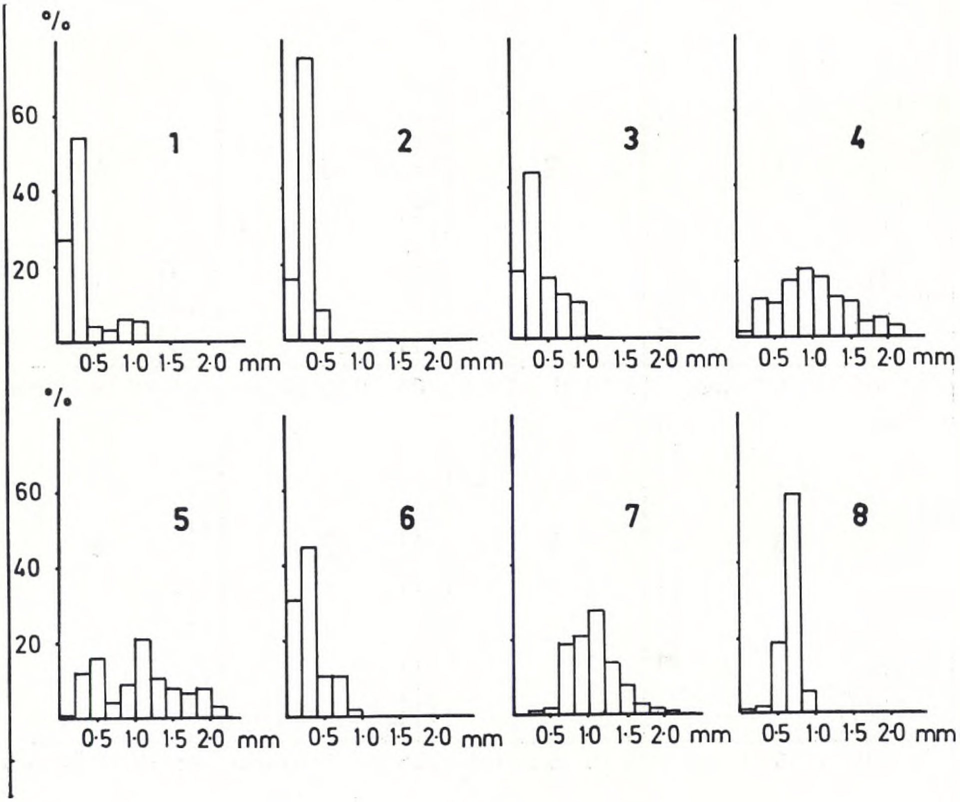


6 B

The presence of the large shoals of fry in the lakes containing the original species, indicate, together with the results of the stomach analyses, that the predation is most intensive in these lakes.

Both obligate and facultative planktivores are highly selective in their choice of prey. From a general point of view we can state that, where the environment permits choice, the largest prey will be selected (Brooks 1968, Brooks and Dodson 1965, Lindström 1955). When the predation is intensive, size-selective predation will eliminate larger individuals and species, allowing smaller forms, which escape predation, to dominate. This would explain why the larger forms *Bythotrephes longimanus* and *Daphnia longispina* are absent in the lakes with intensive predation. *D. longispina* is here replaced by the smaller and less predation sensitive *D. cristata* (Table 4). The absence of *Bythotrephes longimanus* from lake 4 is probably due to morphometric factors; the lake is too small and shallow to contain this species.

Whether or not a plankton species is eliminated through predation depends on the predation intensity, and before a species disappears the mean



6 C

size is suppressed to a critical value, where the number of fertile females remaining is too low to secure the existence of the species.

The predation in the lakes with roach and perch is too intensive to permit the existence of *Daphnia longispina* (mean length 1.4 mm) but not too intensive to eliminate *D. cristata* (mean length 0.85 mm).

After introduction of planktivores in a fish-free lake where *Daphnia pulex* was the dominant herbivore, the mean size of *Daphnia* decreased from 1.4 mm to 0.8 mm within four years. Too low a number of individuals reached the length 1.2 mm, which was the critical length in this case, needed for reproduction. *D. pulex* was eliminated and replaced by the species *D. galeata* and *D. retrocurva* (GALBRAITH 1967).

When the predation pressure decreases, the larger forms can return and, thanks to their greater effectiveness in collecting nanoseston, eliminate smaller forms (BROOKS and DODSON 1965).

High predation pressure results in a decrease of the size and elimination of certain larger forms. This process is illustrated in Fig. 6, where the size

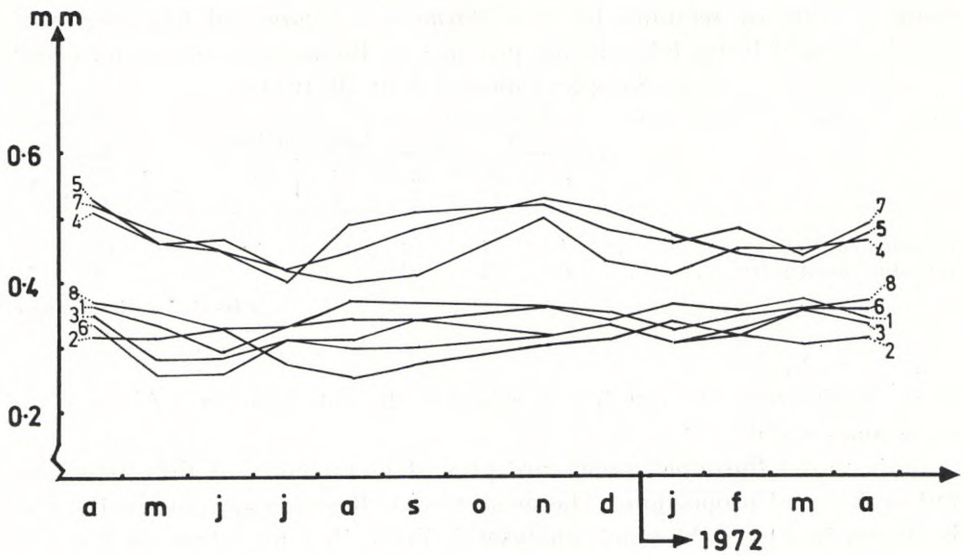


Fig. 7. Mean size of *Bosmina* spp (April 1971—April 1972).

distribution within the cladoceran community on three occasions during the year is shown. Fig. 6 A (January 25, 1972) shows an "under ice" situation, when the cladoceran number is low, consisting mainly of *Bosmina spp* and a few *Daphnia cristata.* After the break-up of the ice, Fig. 6 B (April 23, 1971), the hatching of ephippial eggs begins and the number of species and individuals increases while the size distribution changes somewhat in an upward direction. The last figure, Fig. 6 C (June 29, 1971), shows the situation during the summer, when the differences between the lakes with intensive predation and the lakes with low predation intensity are clearly indicated.

The succession of two *Daphnia* species which is shown in this work is also demonstrated in char lakes — whitefish lakes in northern Sweden (LÖTMARKER 1964, NILSSON and PEJLER unpubl.). The latter investigation also shows how the larger *Heterocope saliens* in the char lakes is replaced by *H. appendiculata* in the whitefish lakes.

Relations between *Bosmina coregoni* and *B. longirostris*

Special attention has been paid in this work to the relations between the two species *Bosmina coregoni* and *Bosmina longirostris.*

The succession of these species has been studied by several authors (*e.g.* MINDER, 1938), in connection with cultural enrichment of lake water. The eutrophication has been stated as the reason for the shift from *B. coregoni*

Table 5. Numeric relations between *Bosmina coregoni* and *Bosmina longirostris* in eight forest lakes in the province of Bohuslän, southwestern Sweden. (Samples collected June 29, 1971).

	Lake number							
	1	2 r	3	4 r	5 r	6	7 r	8
Bosmina coregoni	1	1	3	15	19	1	13	8
Bosmina longirostris	6	21	22	1	1	9	2	7

(r:treated with rotenone)

to *B. longirostris.* The question is whether the eutrophication *per se* could cause such a shift.

Both of the *Bosmina* species are present in all lakes at the same time, but in different proportions. The mean size of *Bosmina spp* during the year is shown in Fig. 7. Stomach analyses indicate that predation on *Bosmina* above all by roach and also by perch is intensive (STENSON, in prep.). Since the predation is size-dependent, the larger species, *Bosmina coregoni,* will be suppressed, but when the predation is of low intensity, as in lakes 4, 5, and 7, the smaller species will be completely eliminated by the larger one.

Consequently, the relations between the numbers of *B. coregoni* and *B. longirostris* (Table 5) seem to be dependent on the fish density or the intensity of the predation.

The enrichment of a water can create conditions necessary for high phyto-zooplankton abundance, thereby facilitating the existence of obligate planktivores or otherwise modifying the fish population, with a change in the predation intensity as a result. Size-selective predation will then eliminate the larger *B. coregoni* and allow the smaller *B. longirostris* to dominate (BROOKS 1969). This theory that the shift may be caused by size-selective predation is supported by the results of this investigation.

VII. Summary

1. The crustacean plankton fauna of 8 small forest lakes in the province of Bohuslän, S.W. Sweden, were investigated, especially with regard to effects of size-dependent predation.
2. Four of the lakes were treated with rotenone. Three of these lakes were restocked with new fish species, the fourth having been reoccupied by the original species.
3. The physico-chemical limnology conditions in the lakes showed great similarities throughout the year and the differences in the sediment composition and vegetation were very small.

4. The lake treated with rotenone but containing the original fish fauna had exactly the same zooplankton species composition as the untreated lakes.
5. In the lakes with low predation intensity (*i.e.* those with the new fish species) the larger zooplankton species *Bythotrephes longimanus* and *Daphnia longispina* were present. These species were eliminated in the lakes with high predation intensity and *D. longispina* was here replaced by the smaller species *D. cristata*.
6. A clear difference, in the size distribution of the cladoceran community, between the lakes with high predation intensity (those with the original fish species) and the lakes with low predation intensity (those with the new fish species) is demonstrated.
7. The larger *Bosmina coregoni* replaced the smaller *B. longirostris* when the predation intensity decreased.

VIII. Acknowledgments

This investigation was carried out at the Department of Zoology, University of Gothenburg. I am greatly indebted to Professor Gunnar Svärdson, who initiated the investigation and lent his support to it. I wish to express my thanks to Professor Anders Enemar for his kind help and encouragement, and to the members of Trollhättans Flug- och Spinnfiskeklubb for their extensive help with the field work.

The investigation was financially supported by grants from the Fishery Board of Sweden and from the Faculty of Mathematics and Science, University of Gothenburg.

IX. References

ALMQUIST, E. 1959. Observations on the effect of rotenone emulsives on fish food organisms. *Rep. Inst. Freshw. Res. Drottningholm* 40: 146—160.

ANDERSON, R. S. 1970. Effects of rotenone on zooplankton communities and a study of their recovery patterns in two mountain lakes in Alberta. *J. Fish. Res. Bd. Can.* 27(8): 1335—1356.

BERG, A. and E. GRIMALDI. 1966. Ecological relationships between planktophagic fish species in the Lago Maggiore. *Verh. int. Ver. Limnol.* 16: 1065—1073.

BERZINS, B. 1958. Om fiskevård med rotenon. *S. Sveriges Fisk. Fören., Årsskr.* 1957: 41—53. (In Swedish.)

BROOKS, J. L. 1968. The effects of prey-size selection by lake planktivores. *Syst. Zool.* 17: 272—291.

— 1969. Eutrophication and changes in the composition of the zooplankton. *In* Eutrophication. Nat. Acad. Sci. Washington D.C.: 236—255.

— and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150: 28—35.

BURNS, C. W. and F. H. RIGLER 1967. Comparisons of filtering rates of *Daphnia* in lakewater and in suspensions of yeast. *Limnol. Oceanogr.* 12: 492—502.

GALBRAITH, M. G. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Trans. Amer. Fish. Soc.* 96(1): 1—10.

HRBACEK, J. 1958. Typologie und Produktivität der teichartigen Gewässer. *Verh. int. Ver. Limnol.* 13: 394—399.

— 1959. Density of the fish population as a factor influencing the distribution and speciation of the species in the genus *Daphnia*. *Proc. XVth Int. Congr. Zool.:* 794—796.

— 1962. Species composition and the amount of the zooplankton in relation to the fish stock. *Rozpravy CSAV, rada MPV* 72(10): 1—116.

— M. DVORAKOVA, V. KORINEK and L. PROCHAZKOVA. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh. int. Ver. Limnol.* 14: 191—195.

— and M. NOVOTNA-DVORAKOVA. 1965. Plankton of four backwaters related to their size and fish stock. *Rozpravy CSAV, rada MPV* 75(13): 1—65.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn. 302 p. (Transl. from Russian).

KISER, R. W., J. R. DONALDSON and P. R. OLSON. 1963. The effects of rotenone on zooplankton populations in freshwater lakes. *Trans. Amer. Fish. Soc.* 92(1): 17—24.

LINDGREN, P. E. 1960. About the effect of rotenone upon benthonic animals in lakes. *Rep. Inst. Freshw. Res. Drottningholm* 41: 172—184.

LINDSTRÖM, T. 1955. On the relation fish size—food size. *Rep. Inst. Freshw. Res. Drottningholm* 36: 133—147.

LÖTMARKER, T. 1964. Studies on planktonic crustacea in thirteen lakes in northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 45: 113—189.

MINDER, L. 1938. Der Zürichsee als Eutrophierungsphänomen. *Geol. Meere Binnengewässer* 2(2): 284—299.

NOVOTNA, M. and V. KORINEK. 1966. Effect of the fishstock on the quantity and species composition of the plankton of two backwaters. Hydrobiol. Stud. 1 Prague: 297—322.

STRASKRABA, M. 1965. The effect of fish on the number of invertebrates in ponds and streams. *Mitt. int. Ver. Limnol.* 13: 106—127.

ÖBERG, K. 1956. Försök med rotenon i olika pH-värden. *Svensk Fisk. Tidskr.* 65(8/9): 117—119. (In Swedish.)

The predatory impact of eel (*Anguilla anguilla* L.) on populations of crayfish (*Astacus astacus* L.)

By Gunnar Svärdson

Contents

I. Introduction

In his book on the Swedish fauna (1855), the zoologist Sven Nilsson of Lund University wrote about the feeding habits of the eel: "the most favoured food is crayfish eggs and young, which he finds in their holes under stones and in the river banks when they moult. He seeks for them with such eagerness, that, when he has been introduced into a water rich in crayfish, he reduces or exterminates them within a few years. Such has been the case in Lake Vänern and in the rivers running into that lake" (author's translation). A German version of this section on the eel was published a few years later (Nilsson 1860).

The knowledge summarized by Nilsson was also widely appreciated by the fishermen in those days (Lloyd 1854, Cederström 1895). Later, however, this information faded away. Steffenburg (1872), writing a monograph on the crayfish, made his best to prove that the eel was not so destructive to crayfish as was generally said among the people living around the big lake Vänern. His principal argument, repeated by many writers up to this very day, was the well-known fact that eel and crayfish do live sympatrically in many lakes.

The native crayfish (*Astacus astacus* L.) was struck by a disease, caused by the fungus *Aphanomyces astaci,* Schikora, from the year 1907 and onwards (ARWIDSSON 1920). The disease is still spreading within Sweden. It brought the crayfish production down to only a fraction of the former height. All the best producing lakes were ruined. The owners of fishery rights lost a good and regular annual income. At the same time, and at an increasing rate, the demand for crayfish, as a delicacy, followed the general rise in standard of living.

After some reconnaissance, an American species, *Pacifastacus leniusculus* (DANA), was found which seemed able to serve as a substitute for *Astacus* (SVÄRDSON 1959a, 1959b, 1964, 1965). After introductory experiments had shown that the species was acceptable in flavour, capable of reproducing in the new country and resistant to the disease (UNESTAM 1969, 1972) the Fishery Board of Sweden imported some 70,000 specimens from Lake Tahoe, Nevada in 1969. These crayfish were sold to private lake owners but some were also planted into Lake Hjälmaren. This lake has "free water" which means that any Swedish citizen may fish outside the near shore area.

The eel, however, has also become a delicacy and is nowadays in short supply. Its price is rising. Many rivers have become barred by dams or by pollution, obstructing the ascending young eels. The significant commercial eel fishery in the Baltic Sea has been threatened by a diminishing supply of silver eels. Commercial eel fishermen ask for more eel plantings in fresh water.

In spite of the warnings (SVÄRDSON 1967, 1968) that NILSSON's old statement was still valid, the management has continued according to the principle "both eel and crayfish in the same water". These unwise actions culminated in 1970—72 when large numbers of young eels were released into Lake Hjälmaren, where the *Pacifastacus* had been introduced in 1969. Both plantings were supported by state funds. The eel cannot enter Lake Hjälmaren on its own and the size of the eel population in this lake is therefore up to human decision at present time.

This conflict over an old theme prompted the present review in the hope that a better understanding could be achieved and the fate of *Pacifastacus* might improve.

II. Materials and Methods

The principal material for this review is local written records of all kinds. Moreover personal communication with numerous contributors has been included.

In some sections hitherto unpublished material from the files of the institute has been utilized. These "lake surveys" were initiated by the late professor GUNNAR ALM when the institute started to operate in 1932. Accordingly most Swedish lakes were supposed to be surveyed by the local fishery con-

Table 1. Chronological distribution of the lake surveys used for studies on interaction of eel and crayfish.

Year	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928
Surveys	2	1	—	—	—	1	2	—	—	—
Year	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938
Surveys	—	15	76	139	132	126	116	111	241	206
Year	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
Surveys	124	100	61	57	27	25	13	9	9	18
Year	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
Surveys	36	—	1	—	1	—	18	—	1	1
Year	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
Surveys	—	2	—	—	—	—	—	—	—	—

Total number of lake surveys 1,671.

sultant of the various districts. Some basic limnological information should also be gathered and the people fishing the lake were supposed to be asked about the fish fauna. If possible, the lake was to be fished by the fishery consultant himself.

These lake surveys were partly a failure and the major objective could not be fulfilled. Some districts were lagging in reporting, and some of the information was fragmentary.

Since the abundance of eel in a lake is rather fluctuating, the lake surveys nowadays prove of interest mainly as historical documents. Crayfish populations are not stable either. Most of the lake surveys on file at the present institute were performed 1932—40 (Table 1). Since that time the hydroelectric activity, pollution and spread of the *Aphanomyces* disease have greatly changed the conditions of many lakes. For the purpose of the present paper, however, this lack of actuality is irrelevant.

Only a small minority of the lake surveys give information about the yield. According to instructions, the average yield for the last five years should be noted. Most fishery consultants have chosen to express the yield verbally, especially concerning the eel. Phrases like "much fewer than they used to be" "catch good until the X dam was built", "you may get some on a line of 100 hooks", "two specimens caught in the last twenty years" etc. are often met with. Crayfish are also often reported in the same vague manner.

The credibility of the lake surveys is no better than the knowledge of the local fishery right owners. In one case, a small lake near Stockholm, the eel was reported in the survey as non-existing. Later, the present institute made a rotenone treatment of that particular lake and two big eels were found dead. The last specimens of eel in a lake may be hanging on for extremely long periods. Eels, planted in lakes with no outlets, have been found up to some 50 years later, and one specimen, kept in an aquarium, was known to be 88 years old (SVÄRDSON 1949).

The full information available from the 1,671 lake surveys will be given elsewhere. Below some general trends concerning the distribution and habitat are given in condensed form in comparison with older regional reports of a similar kind.

The section on case histories (*vide infra*) is based mainly not on the lake surveys. The case histories are drawn from books, papers, letters and communication with private persons and the fishery officers of the various districts.

The kind cooperation of all concerned is cordially acknowledged. Without their help this review could never have been written.

III. The geographical distribution of eel and crayfish in Sweden

LUNDBERG (1899) published a map on the distribution of eels in Sweden (Fig. 1). It can be seen that eels penetrate widely into the Baltic basin and reach far inland. LUNDBERG noted that eels are most abundant on the western slope of southern Sweden. After the spawning grounds of the eel in the Atlantic were discovered and the spread of elvers into the Kattegatt was realized, this phenomenon seemed less puzzling than it did to the earlier writers.

The distribution of the eel is not stable. It fluctuates according to human activities. Mostly this activity interferes with the accessibility of lakes to ascending eels. The building of dams and the polluting industries on the river mouths constitute obstacles. The eel planting activity of man, starting already in the further eighteenth century (GYLLENBORG 1770) was strongly advocated by TRYBOM (1881, 1893) and later became almost a routine management.

The crayfish distribution in Sweden was pictured by ALM (1929, Fig. 2) Omitted on the map are some scattered populations along the northern Baltic coast, all of which are known or supposed to have been initiated by man. The crayfish distribution is more stable than that of the eel but the crayfish plague (*Aphanomyces*) has caused great losses. The early timetable of *Aphanomyces* spread was mapped by ARWIDSSON (1920) and ALM (1929). It is important, however, to note that experience has shown that crayfish are not completely exterminated by the disease. After a few years stray specimens are normally seen and they are supposed to have survived in small creeks, ditches or somewhere upstream, when the *Aphanomyces*-disease swept over the lake. In small lakes the population may recover, with or without the help of man, but larger lakes are often affected by new outbreaks every 6—10 years.

In Table 2 the information from the lake surveys is condensed. The rivers

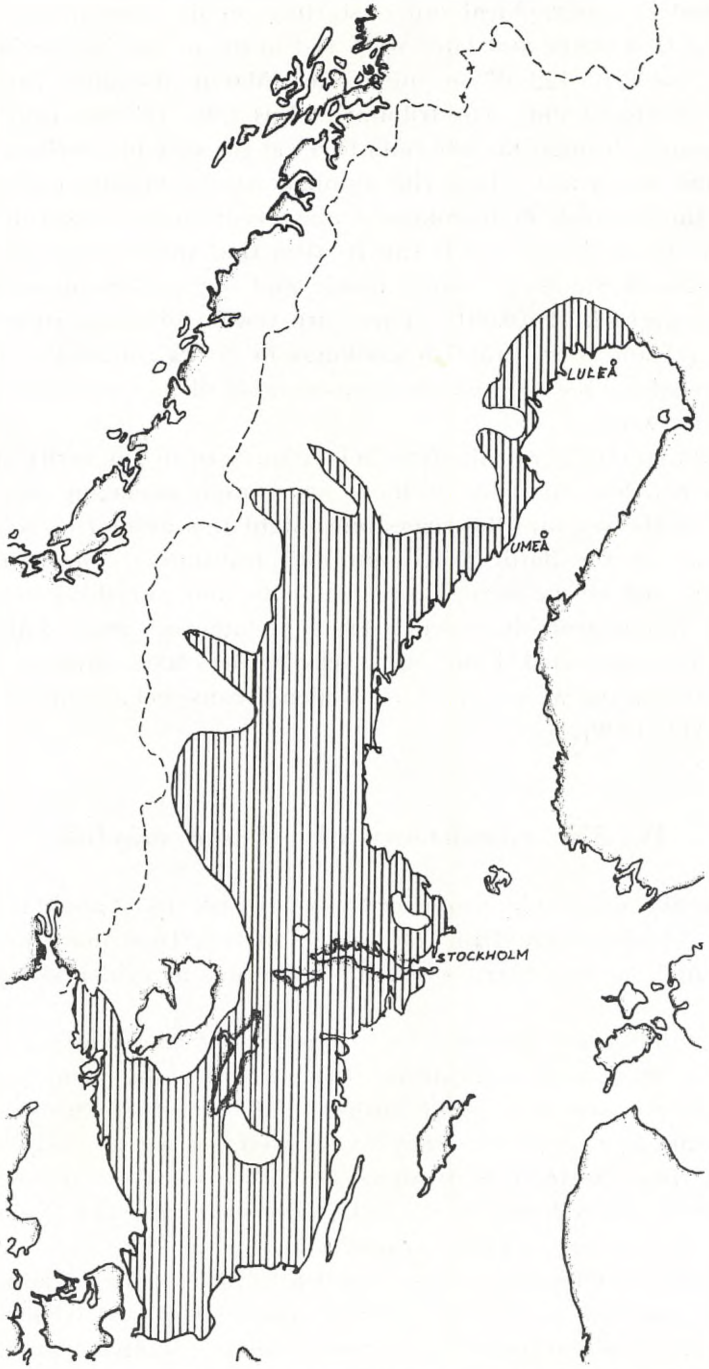


Fig. 1. Distribution of eel in freshwater in Sweden (modified after LUNDBERG 1899). The large Väner basin was blocked for eel at the Trollhättan falls until a canal was built in the year 1800.

are arranged in geographical order, starting on the central eastern Baltic coast, going first south and later west and north to the Norwegian border. The rivers Nos 121—129 all run into Lake Mälaren (its outlet, No. 61, River Norrström at Stockholm). The tributaries Nos 130—143 run into Lake Vänern and empty through No. 108 Göta River at the City of Göteborg (Gothenburg) on the west coast. The serial numbers are given only for the biggest rivers by the Swedish Meteorological and Hydrological Institute (SMHI).

From the totals in Table 2 it can be seen that there are significant differences between the Baltic Sea drainage and the western drainage to the Kattegat/Skagerrack ($P<0.001$). There are fewer eel lakes, more crayfish lakes, less eel and more crayfish stockings in rivers running to the Baltic Sea. This confirms the old and very considerable difference between eastern and western Sweden.

STEFFENBURG (1872) was the first to be impressed by the rarity of crayfish in western Sweden. He said "is there an animal, damaging the crayfish, coming from the sea into the rivers and might this animal thrive better in Kattegat than in the Baltic Sea?" (author's translation). Since he did not know where the elvers were coming from he did not think the eel was responsible but instead discussed NILSSON's statement about Lake Vänern and found it exaggerated. Later on, several writers have stressed that crayfish are sparse in the western part of Sweden because eel abounded (ARWIDSSON 1918, ALM 1929).

IV. The co-existence of eel and crayfish

The general statement by professor SVEN NILSSON (1855) about the capacity of eel to exterminate crayfish indicates allopatry. Tendencies to allopatry were obvious between eastern and western Sweden as evidenced by the last section.

The numerous lakes, where eel and crayfish do live sympatrically have consequently been used as evidence that NILSSON's statement was wrong. Some opponents have gone even further, and interpreted the sympatry of the two species as evidence that they do not even interact seriously (STEFFENBURG 1872, TRYBOM 1893, SCHIEMENZ 1935, MAGNUSSON 1961, K. NILSSON 1971). These writers have overlooked, however, that SVEN NILSSON may have noted the extreme of a general tendency.

Not only the predation by eel on crayfish influences their sympatry. Also the habitat selection of the two species obviously plays its part. Species having the same habitat requirements most often live sympatrically.

Before entering upon the problem whether eel and crayfish actually live sympatrically as often as they should do according to chance, their habitats must be discussed.

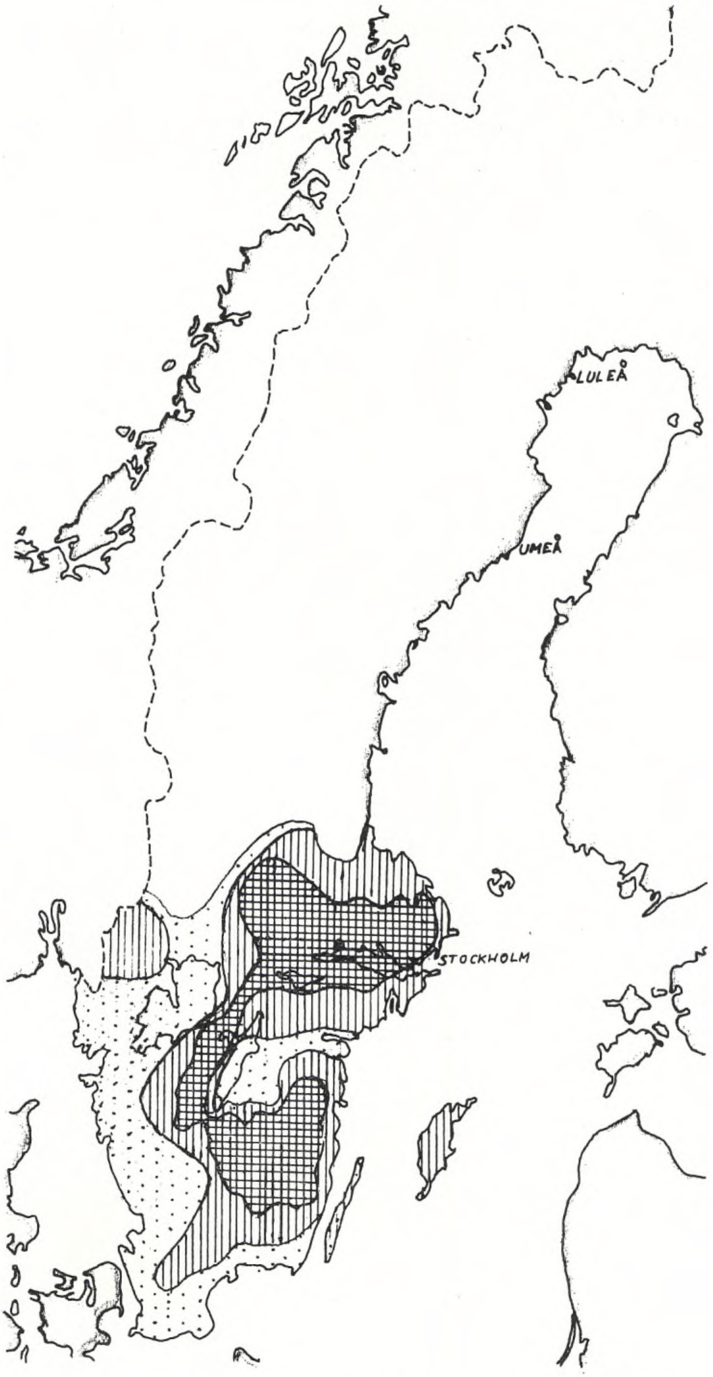


Fig. 2. Distribution of crayfish in Sweden (modified after ALM 1929). Scattered localities along the northern Baltic coast, where crayfish have been introduced lately by man, are omitted. Stippled area: sparse. Vertical bars: common. Crosshatched: abundant.

Table 2. Occurrence of eel and crayfish within different basins.

River system	Lakes				Lakes, stocked	
	Surveyed	With eel	With crayfish	With both	With eels	With crayfish (failures)
43 Gnarpsån	5	5	0	0	—	1 (1)
44 Harmångersån	14	12	0	0	—	—
45 Delångersån	9	6	1	1	—	3 (2)
46 Örängeån	5	4	0	0	—	—
Enångersån	4	4	0	0	—	—
47 Norralaån	15	10	0	0	—	—
48 Ljusnan	106	93	1	1	—	4 (2)
49 Skärjån	1	1	0	0	—	—
50 Hamrångeån	4	4	3	3	—	2
51 Testeboån	15	15	0	0	—	—
52 Gavleån	18	16	4	4	—	4 (1)
54 Tämnarån	5	5	4	4	—	—
58 Broströmmen	1	0	1	0	—	—
59 Norrtäljeån	5	5	5	5	—	—
Penningbyån	2	2	2	2	—	1
Bergshamraån	3	3	3	3	—	—
Östanån	6	5	6	5	—	—
60 Åkerström	2	2	1	1	—	—
61 Mälaren-Norrström	9	6	7	5	1	—
121 Svartån (Hjälmaren)	30	6	15	4	—	1
122 Arbogaån	79	16	44	14	1	8
123 Hedströmmen	15	6	10	6	1	—
124 Köpingsån	7	2	4	0	—	2
125 Kolbäcksån	23	18	20	17	1	2
126 Svartån	15	5	12	5	—	—
127 Sagån	6	2	4	2	—	3
128 Örsundaån	8	3	7	3	—	2
129 Fyrisån	2	0	2	0	—	—
62 Tyresån	9	7	3	2	—	1
Bränningeån	3	3	2	2	—	—
Järnaån	3	3	2	2	—	—
63 Trosaån	10	9	8	7	1	—
65 Nyköpingsån	13	10	9	6	—	—
67 Vättern-Motala ström	89	31	63	24	4	9
Stångån	18	3	14	2	—	—
Svartån	22	8	18	6	—	—
Finspångsån	8	3	8	3	—	—
Småbäckar till Bråviken	2	1	2	1	—	—
68 Söderköpingsån	2	1	1	1	—	—
70 Storån	6	5	5	4	—	—
74 Emån	27	18	17	11	5	5
75 Alsterån	3	2	2	1	—	—
80 Lyckebyån	7	7	1	1	1	—
81 Nättrabyån	3	2	0	0	—	—
82 Ronnebyån	7	5	5	4	2	3
83 Vierydsån	4	2	0	0	—	—
84 Bräkneån	4	4	1	1	—	1
Kolsbroån	3	2	0	0	—	—
Modalaån	4	2	0	0	—	—
85 Mieån	6	6	3	3	—	—
86 Mörrumsån	27	27	15	15	3	—
87 Skräbeån	3	3	2	2	1	—
88 Helgeån	14	14	9	9	4	—
96 Rönneån	4	4	2	2	2	—
98 Lagan	29	26	13	10	8	2
101 Nissan	36	34	5	5	11	1

River system	Lakes				Lakes, stocked	
	Surveyed	With eel	With crayfish	With both	With eels	With crayfish (failures)
103 Ätran	60	59	17	17	12	1 (1)
105 Viskan	61	61	10	10	12	1
106 Rolfsån	21	21	1	1	1	1
107 Kungsbackaån	4	4	0	0	—	—
108 Göta älv, Mölndalsån	7	4	1	1	—	1
Säveån	27	26	6	6	7	3
Lärjeån	2	2	0	0	—	—
Alaforsån	5	5	0	0	—	—
Slumpån	2	1	0	0	—	—
Bastån	2	2	0	0	—	—
Anråsån	8	8	0	0	1	—
Kolbengtseredsbäcken	4	4	0	0	—	—
Resterödsbäcken	2	2	0	0	—	—
130 Dahlbergsån	12	10	8	8	—	—
131 Upperudsälven	107	89	42	40	19	2
Tydjeån	2	2	1	1	—	—
Åmålsälven	7	7	1	1	1	—
132 Byälven	104	94	25	20	31	3
133 Borgviksälven	24	13	15	11	1	—
134 Norsälven	78	59	4	4	14	2 (1)
135 Klarälven	94	66	9	8	16	2
136 Alsterälven	11	11	6	6	4	—
Varnan	3	3	1	1	2	—
137 Visman	2	2	2	2	—	—
138 Gullspångsälven	135	86	59	46	12	3
140 Tidan	24	17	17	14	5	2
141 Sjöråsaån	5	5	5	5	2	—
142 Lidan	19	10	13	9	2	1
143 Nossan	4	3	3	2	—	—
109 Bäveån	8	6	1	1	1	1
110 Örekilsälven	22	22	4	4	—	1
111 Strömsån	11	11	0	0	—	—
Hogdalsån	4	4	0	0	—	—
112 Enningsdalsälven	10	10	0	0	—	—
Baltic Sea drainage	711	434**	346**	192	25	52
Kattegat/Skagerack drainage	960	793	271	235	164	27
All lakes	1,671	1,227	617	427	189	79 (8)

Figures for Baltic Sea drainage marked ** are significantly ($P<0.001$) different from those of Kattegat/Skagerack drainage.

When the lakes included in the surveys are grouped according to their altitude, the following picture emerges:

Per cent lakes with	<50 m	51—100	101—150	151—200	201—250	251—300	>300 m	Average
Eel	92	76	80	71	65	57	49	73
Crayfish	45	45	42	36	34	17	5	37
Neither	4	12	7	14	24	30	47	15

Both species are more often occurring in low altitude lakes. The eel frequency falls from a staggering 92 per cent in the lowland lakes to 49 per cent in the lakes above 300 metres. It is obvious that it must be progressively more difficult for the eel to reach high altitude lakes. The crayfish, however, exhibits a constant occurrence frequency up to an altitude of some 150 metres. After another 100 metres they become more sparse. No crayfish lakes above 300 metres are known, except in the southernmost highlands of Småland.

The lower summer temperature is no doubt the main reason for this situation (ABRAHAMSSON 1972). In Table 2 there are some recorded failures to introduce crayfish in northern lakes. Fishery consultant E. MOLIN has kindly informed about 14 different large scale introductions in Värmland, on altitudes of 135—286 metres, all of which have failed to establish reproducing populations. The adult crayfish, however, live and grow. In the 1940s crayfish survived and grew to big size in a river close to the Kälarne fishery research station in the province of Jämtland (altitude 288 m). No young were produced.

When the same lakes are grouped according to size this result appears:

Per cent lakes with	<25 ha	26—50	51—150	151—300	301—600	601—1000	>1000 ha	Average
Eel	55	64	75	81	87	92	93	72
Crayfish	32	35	39	38	49	50	49	38
Neither	30	21	14	8	5	0	2	16

Again the two species do have the same kind of habitat, both are more often found in large lakes than in small ones. The eels occur in roughly half of the small lakes but they occur in almost all big lakes (more than 1,000 hectares). Usually more water flows through the large lakes which therefore offer better opportunities to climb for the young eels. Very small lakes, on the other hand, have small outlets, which may dry out completely in the summer when eels climb most actively.

The crayfish is less dependent on lake size than is the eel. The tendency is obvious, however, smaller lakes are not favoured habitats. This situation is probably correlated to a higher frequency of soft bottoms in small lakes, whereas the crayfish prefer a firm bottom. The oxygen shortage and/or higher predatory pressure from perch (*Perca fluviatilis*) may add to this.

It is very often remarked in the lake surveys that crayfish, when their density is low, tend to hang on to the in- and outlets of a lake. This is almost certainly caused by lesser predation by perch in those places, but better shelter in the banks and a better oxygen supply may be further reasons. The stream habitat is of course rather different from that of a small stagnant lake and helps to explain why the crayfish are relatively less abundant in such lakes.

Finally, the lakes were grouped according to the maximum depth recorded:

Per cent lakes with	<3 m	3—5	6—9	10—14	15—20	21—30	31—45	>45 m	Average
Eel	72	73	75	72	72	79	79	85	74
Crayfish	26	45	38	39	31	36	38	45	37
Neither	16	15	15	14	17	10	14	8	15

Both species are most often found in deep lakes. The eel seems to be independent of the depth of the lake, as it is common even in very shallow ones. The apparent slight correlation to deeper lakes is rather a correlation to large lakes which offer the species better possibilities to climb as argued above. The eel is thus as a rule not sensitive to the morphometry of the habitat but rather to the accessibility of the lake. The crayfish is rarer in the most shallow lakes, where the risk of oxygen shortage is greater. On the whole the crayfish is a rather tolerant species, capable of living in many types of lakes, but it is not as hardy as the eel. In the handbooks the crayfish is often said to prefer oligotrophic lakes. This is not true. On the contrary, the species has its best habitats in large lowland lakes, which tend to be eutrophic.

The eel and the crayfish do have rather similar habitat preferences.

In Table 3 the lake survey material has been compared to two older lake samples. HOLMGREN (1916) reported about fish and crayfish fauna of 636 lakes in the province of Dalsland, on the western coast of Lake Vänern. The lakes were sampled 1901—04. HOLMGREN was inspired by CEDERSTRÖM (1895) who published an impressive book with data on 2,073 lakes, all in the province of Värmland, on the northern coast of Lake Vänern. Some of the lakes included in the nation-wide survey were also dealt with by HOLMGREN and CEDERSTRÖM. If there was no interaction and we suppose that the eel occurs in 75 per cent of all lakes then the frequency of sympatry should be 75 per cent of the crayfish lakes.

In the 1932—40 lake sample the frequency of sympatry is significantly lower than expected. In the Dalsland sample, and even more in the Värmland sample, there is again a statistically significant deviation in sympatry. In these samples, however, sympatry is more common than it should be according to chance.

These conflicting results indicate that in the 1932—40 sample consisting of generally large lakes, the predation by eel on crayfish does appear as a factor causing fewer cases of sympatry than expected. This refers to the higher altitudes, where crayfish live more close to their ecological temperature limit.

The too high frequency of sympatry in the 2 regional samples is caused by the numerous small, shallow lakes at relatively high altitudes, *i.e.* lakes which are unsuitable for both eel and crayfish.

The general conclusion from this section is that the eel predation actually

Table 3. Occurrence of eel and crayfish in three lake samples. The lakes are grouped according to altitude.

Area	<50 m	51—100	101—150	151—200	201—250	>250 m	Total
Southern Sweden mainly 1932—40							
lakes sampled	125	329	452	367	211	187	1.671
with eel	115	251	363	261	138	99	1,227
with crayfish	56	147	192	131	71	20	617
eel and crayfish	51	110	136**	76**	49	5*	427*
Dalsland 1901—04							
lakes sampled	9	74	334	202	17	—	636
with eel	9	71	177	38	1	—	296
with crayfish	7	39	100	36	1	—	183
eel and crayfish	7	38	61	11	—	—	117**
Värmland before 1895		<100 m					
lakes sampled	—	171	959	408	296	239	2,073
with eel	—	128	264	112	80	40	624
with crayfish	—	41	83	24	14	—	162
eel and crayfish	—	33	63**	14**	11**	—	121**

Significance of deviations from distribution (x^2-test):
0.01>* P<0.001**

results in fewer cases of sympatry of the two species. There is a local tendency of allopatry, just like the difference between eastern and western Sweden, although of less magnitude.

Since the two species do have very similar habitats they will appear sympatrically in many lakes, and statistically most frequent in areas including many small lakes, which are avoided by both species.

V. The yield of lakes

As already mentioned the yield of the surveyed lakes should be given. In most cases this was made only verbally. The yield of eel, in kg, was available for 125 lakes, 54 of which were also inhabited by crayfish (*i.e.* crayfish were at least noted). The yield was extremely variable, no doubt partly due to differences in the gear used. When a trap at the lake's outlet is used the catch tends to be much higher than if long lines are used only. Moreover, the catch of the trap in one lake may actually include silver eels emigrating from other lakes upstream.

Catch of eel, kg per hectare of lake area:

	<0.05	0.06—0.25	026—0.50	0.51—0.75	0.76—1.00	>1.0	Total number of lakes	Average	Median
with crayfish	20	19	4	3	3	5	54	0.31	0.11
no crayfish	9	35	11	6	2	8	71	0.40	0.22

It appears that there is a higher yield of eels in lakes with no crayfish. The distribution of yield classes is different ($\chi^2=41.03$, df 5, $P<0.001$) in the two types of lakes.

The annual yield of crayfish, in scores per hectare, was available for 159 lakes, 82 of which were inhabited also by eel. Again, when eel was noted in the lake, it was classed as an eel lake, irrespective of the number of eels.

Catch of crayfish, scores per hectare of lake area:

	<0.25	0.26—0.50	0.51—1.00	1.01—3.00	3.01—6.00	6.01—10.00	>10.0	Total number of lakes	Average	Median
with eel ..	17	8	14	22	13	7	1	82	2.1	1.1
no eel ...	9	4	8	24	14	8	10	77	5.2	2.3

Apparently the higher yield of crayfish is reported from lakes with no eel. The distribution of yield classes is different between the two categories of lakes ($\chi^2=19.71$, df 6, $P<0.001$).

From the median values it can be estimated that eel populations, yielding 0.22 kg/hectare or 1 kg eel per four or five hectares rarely allow crayfish to live sympatrically. When the density is reduced to 0.11 kg/hectare or 1 kg eel per ten hectares, crayfish may occur in the same lake.

When we consider the crayfish, a median annual catch of 22 crayfish per hectare may develop when the eel is still sympatric. For the highest yields, however, or 46 crayfish (2.3 scores) per hectare, it is a prerequisite that the lake is free from eels.

Summarizing this section is can be said that a lake producing a good crop of eels most often is not producing any crayfish at all. All kinds of moderate production of the two species may occur in the very same lake. The rich crop of crayfish, however, most often occurs when there are no eels whatsoever in the lake.

VI. Reserved population trends. Case histories

River No 53 Dalälven, Lakes Axen (283 metres above sea level, 50 hectares) and Rällsjön (273 m, 350 hectares)

Crayfish were introduced by J. O. Silfverström at Sundborn before 1687 (Steffenburg 1872). They spread over the region around the town of Falun and were for a long time the northernmost crayfish populations of the country.

In 1928 some 80 scores were taken in two nights in the river between the two lakes Axen and Rällsjön. The crayfish population was dense. Around 1930 young eels were planted in a small lake, Holmtjärn, which empties by a small creek into Lake Rällsjön. No fishing for eels was performed but they obviously survived, as they usually do. In 1965 a very big eel damaged the turbines of a small hydroelectrical plant at the outlet of the lake.

The crayfish population of the lakes dwindled in the 30s and only a few large specimens were caught in recent years (pers.comm. Mr. G. WESTGÄRDS, and Fishery Consultant O. FILIPSSON).

River No 58 Broströmmen, Lake Erken (11 m, 2,500 hectares)

The lake was, when in its prime, the second best producer in Sweden. The total yield was estimated at 100,000 scores (SVENSKT FISKELEXIKON 1955). M. KJELL MATTSSON, however, living on the lake and catching himself some 6,000 scores annually in the late 20s, says that the highest yield on record probably was only 40,000 scores. The crayfish plague struck the lake in 1929.

There are two mills on the outlet stream, at least partly obstructing the eels. The upper mill was erected in 1840, rebuilt in 1905. The lower mill, Karlösa, probably completely blocked the eel around 1910. It was reported (EKMAN 1918) that eel had recently decreased and crayfish increased in Lake Erken. MATTSSON (pers.comm.) reports that formerly eel were trapped at Rönsbo, the upper mill, when leaving the lake. Later eels disappeared. In 1916, the crayfish catch was 20,200 scores (ALM 1929). Crayfish yields increased every year 1920—29 (MATTSSON). Some 400 *Pacifastacus* were released by the Institute of Freshwater Research in 1966—69 and the population was expanding in 1972. It is planned that this lake will be the donor for *Pacifastacus* introductions elsewhere.

River No 121 Eskilstunaån, Lake Hjälmaren (22 m, 48,000 hectares)

Lake Hjälmaren had by far the richest crayfish population of the country when struck by the *Aphanomyces* disease in 1908. The annual production was 150,000—200,000 scores and sometimes more than 200,000 scores (ALM 1929). In 1904 the catch was estimated at 5 million crayfish.

CARL UGGLA (1786) writes in a treatise on the lake: "Crayfish are not of old the inhabitants of Lake Hjälmaren but were accidentally planted about 50 years ago, when containers crashed . They have later increased a lot, being detrimental for some fish species. But when they moult or come in deeper waters, the perch takes back its right and gulps them. Those perch having almost red flesh, are very delicious" (author's translation). Also, he notes that eel were rather big and abundant and were hard to catch in seines.

The rarity of crayfish in central Sweden in preindustrial times is dealt with in a later section. Crayfish may have been absent from Lake Hjälmaren since the Litorina period.

Lake Hjälmaren empties through the Eskilstunaån to Lake Mälaren, which has its outlet at the City of Stockholm. There are several series of falls on the Eskilstunaån, giving impetus to industrial work at Torshälla and Eskilstuna from the seventeenth century onwards. It seems reasonable to assume that eels, by industrialism at Stockholm and Eskilstuna, became progressively more sparse in Lake Hjälmaren.

A yard stick of the change of eel frequency is given by the catch of silver eels in big traps on the outlet of the lake. The figures were made available by courtesy of Fishery Consultant GUNNAR SVENSSON, Örebro.

1833	5,277 eels	1856	1,589 eels
1834	6,758	1857	1,610
1835	2,908	1858	892
1836	5,617	1859	877
1837	4,698	1860	2,041
1838	4,598	1861	1,038
1839	4,409	1862	716
1840	2,687	1863	782
1841	3,709	1864	756
1842	3,868	1865	633
average	4,452 eels	average	1,093 eels

This reduction in number of descending eels is corroborated by their weight. In a document, dated May 12th 1865, the average weight of silver eels taken at Rosenholm, on the outlet, was given as 1.8 kg. This impressive weight indicate a sparse population with plenty of food per eel specimen.

A generally decreasing number of eels is also stated by ALM (1917) in his paper on the lake fauna.

Since the beginning of the 18th century, when crayfish were planted or first spontaneously spread from some refugium to the lake, their number increased continously up to 1907—08. At that time the production of the lake constituted about one third of the total Swedish crayfish catch.

This is the lake into which *Pacifastacus* were planted in 1969—70 and eel in 1970—72!

River No 122 Arbogaån, Lakes Sörmogen (100 m, 700 hectares) and Norrmogen (104 m, 600 hectares)

Mr. A. ERIKSSON, owner of fishery rights on part of the lakes and the river between them recalls the good fishery for crayfish in the 1940s. In the river, up to 100 scores could be caught in a single night. In the late 40s and onwards the crayfish dwindled in number and eel began to appear and increase. In 1968 30 eels were taken on 150 hooks in one night. Several had crayfish, even large ones, in their stomachs. Eight crayfish in one eel seems to be the record. In the season 1970 only 8 scores of crayfish could be trapped during the whole open period.

Beginning in 1944 the State Forestry Board planted eels in Lakes Sångaren (1944), Övre Sandsjön (1949—56) and L. Korslången (1955). A total of some 70,000 small and 3,000 larger eels were released in order to improve the fishery in a region, where no crayfish occurred. The eels, however, spread downstream to the lakes Sörmogen and Norrmogen, a distance of some 5—15 km.

River No 125 Kolbäcksån, Lakes Uppsveten (178 m, 120 hectares), V. Sveten (114 m, 300 hectares) and Ö. Sveten (110 m, 300 hectares)

After building an eel-trap on the outlet of Lake Uppsveten, eels were planted in the lake around 1935. Some eels, however, emigrated from the lake and appeared in the crayfish producing lakes V. Sveten and Ö. Sveten. Mr D. PETTERSSON, recalls he once caught 37 eels on a 125 hook long-line and that some eels had 20—30 crayfish in their stomachs. The crayfish crop was ruined. (Pers.comm. Fishery Consultants E. MOLIN and A. TÄGTSTRÖM.)

River No 67 Motalaström

Tributary Huskvarnaån, Lake Lillsjön (280 m, 8 hectares)

Lake Lillsjön belongs to the Lekerydsån River which is a tributary of Huskvarnaån. Fifteen kg of young eels were planted in the lake by a man as a revenge to the land-owner. He was most successful and the crayfish population of the lake was strongly reduced and has not recovered (Fishery Consultant B. AHLMÉR, pers.comm.).

Tributary Stångån, Lake Hemsjön (128 m, 130 hectares)

Around 1935 the outlet of the lakes Jutten and Krön was blocked by a dam at Horn, near Lake Åsunden. The ladder for young eels did not function at all. As a compensation some 75 kg of young eels were taken in 1955 from the coast off Skåne. They were released in the river between the lakes Jutten and Krön. From Jutten some eels must have spread downstream and later climbed some 25 metres up to Lake Hemsjön, situated 10 km northwest of the place of release.

No eel was known from Lake Hemsjön earlier. From now on several were caught on long lines, which were tried because the newspapers reported on the eel planting. Eels continued to be caught and gradually they grew larger, up to 2 kg. One eel was caught in 1970.

The crayfish population of Lake Hemsjön reacted by falling off to only a fraction of the original density. Not until the last few years the trend has changed and the population has begun to increase again (Fishery Consultants U. LUNDIN and W. ZETTERGREN, pers.comm.).

River No 70 Storån

Lake Lermon (55 m, 300 hectares)

Lake Lermon has a small outlet, falling 40 metres in a short distance. A hydroelectric plant blocked the possibility for yellow eels to climb the lake in the 20s. Crayfish appeared in the lake, without planting. In the year 1940 some 250 scores were taken. In the next few years, however, 75 kg of young eels were planted as a late compensation for the damming. The crayfish were virtually exterminated. Up to 25 eels were taken on long lines, their stomachs containing crayfish. After a lapse of 5—8 years crayfish began to be seen again and gradually the population recovered to the earlier density (Fishery Consultant U. LUNDIN, pers.comm.).

Lake Antvarden (126 m, 200 hectares)

After the outlet was blocked, the eels decreased and crayfish began to increase. One land-owner, having no right to fish in Lake Antvarden but in two small lakes upstream the lake, suggested that eels be planted in his lakes, referring to an old eel trap in one of them. The association of fishery right owners of Lake Antvarden would not allow him to introduce eel, but after some years of hesitation, they did so (1945).

The eel trap was repaired in order to make the downstream area inaccessible to eels. They were not blocked from Lake Antvarden, however, but were soon found there and made exactly the damage anticipated by the local people to the crayfish population.

Before raising the eel-project, the owner of the two small lakes had tried to plant crayfish in them but in vain. Obviously the habitat was not suitable for them (Fishery Consultant U. LUNDIN, pers.comm.).

Small lakes near the town of Västervik

Lake Maren (2 m, 30 hectares)

Lake Maren close to the Gamleby Bay of the Baltic Sea had some stray crayfish in the 30s. The hospital St. Gertrud used the lake as a water reservoir and the surface of the water was lowered, drying up the outlet in summertime.

The isolation from the sea during the season of eel climbing caused an expansion of the crayfish population in the lake in the 50s. The town of Västervik used the crayfish as a recreation fishery for its community members (Fishery Consultant U. LUNDIN pers.comm.).

Lake Hjorten (20 m, 500 hectares)

Lake Hjorten empties into the Verkebäck's Bay of the Baltic Sea. The lake was dammed in 1959 and crayfish appeared spontaneously in the 60s. Eel were to be planted as a compensation for the damming but were not obtainable until 1965. This year 4,000 were planted, 1967 an additional 6,500 and 1970 some 200 larger eels. The crayfish were eradicated in the last few years of the 60s (Fishery Consultants U. LUNDIN and H.-K. MOLANDER pers.comm.).

Lakes Kvännaren (10 m, 250 hectares) and Hästhagssjön (1 m, 50 hectares)

Lakes Kvännaren and Hästhagssjön empty in the very town of Västervik. There is a small creek between them. Eel were native to both lakes, as proved by traditional fishing with long lines. The upper lake, Kvännaren, had a sparse crayfish population, the lower lake none.

In the 50s the paper mill of Västervik was allowed to pump water from Hästhagssjön. A dam was built on the outlet to prevent brackish water from running into the lake when the pumping was too effective. Eels were thereby blocked from both lakes and the water court decided that young eels should be planted. This did not happen until 1965—70, when 2,700 young eels were released into Lake Kvännaren.

In the meantime, crayfish had increased considerably in Lake Kvännaren. They were seen also in Hästhagssjön and were common in the creek between the lakes. The town of Västervik leased the fishery for crayfish in Lake Kvännaren.

After the eel planting the trapping of crayfish went down to almost nil in a few years in Lake Hästhagssjön and the creek and was very heavily reduced in Lake Kvännaren (Fishery Consultants U. LUNDIN and H.-K. MOLANDER, Mr. B. SVÄRDSON, pers.comm.). Cold winters, predation by mink and crayfish disease were blamed for the development.

River Botorpsströmmen, Lakes Anen (123 m, 400 hectares) and Yxern (92 m, 1,500 hectares)

Lake Anen empties through a small stream, 10 km long, into Lake Yxern. The latter lake was dammed in 1945. The eel ladder of the dam was not functioning. Crayfish were known in Lake Yxern before the damming but increased rapidly afterwards. They were noticed in 1950 in the sound between the two halves of the lake. On this locality no crayfish were known earlier. The upper lake, Anen, reacted in the same way but stronger. On one particular stretch of shore the annual crayfish catch during the period 1952—69 changed from 25 scores to 300, indicating a tenfold expansion of the population.

It was realized by the fishermen that the absence of eel was responsible for the change in crayfish abundance. Consequently test fishing with long lines was made now and then in Lake Anen to check whether eels had entered the lake (Fishery Consultant U. LUNDIN, pers.comm.).

River No 74 Emån

Lake Nömmen (219 m, 1,500 hectares)

ROGBERG (1770) did not mention crayfish from Lake Nömmen but notes that the lake had an abundance of large eel.

TRYBOM (1899) described the lake, which was in his time a well-known crayfish producer. He collected local information indicating that in 1860—90 there were opposite trends of the crayfish and eel populations of the lake. The crayfish yield of salted tails increased in that period from 150 to 300 litres.

There are no quite equivalent figures on the yield of eels, however, annual catches of 200—300 silver eels in the outlet trap were reported to TRYBOM. The size of eels had then been 0.5—1.0 kg. After repairing a downstream dam (which nevertheless allowed some young eels to climb) eels became less abundant and their size increased. September 6th, 1894 was a good night for the eel trap with a catch of 22 eels. None of the eels weighed less than 2 kg. The record size was 3.8 kg.

In the late 1890s the crayfish catch may have reached its peak with an annual average catch of 35,000 scores, in some years even 40,000 scores (TRYBOM, *op.cit.*). In 1916 the catch was 25,200 scores (ALM 1929). Later the yield was lower, some 15,000 scores were taken in 1951, the year when the *Aphanomyces* disease completely ruined the lake. At that time it was still the best producer of the country (after Hjälmaren and Erken which had been ruined earlier).

In 1969 some 2,000 *Pacifastacus leniusculus* from Lake Tahoe were planted in the lake.

Lakes Bexhedassjön (181 m, 447 hectares), Norra sjön (181 m, 102 hectares) and Näsbysjön (184 m, 186 hectares)

Lake Bexhedasjön is also called Grumlan, Näsbysjön is alternatively named Flögen.

These are the classical lakes of Sweden, apart from Lake Vänern, as far as the predation by eel on crayfish is concerned.

The lakes are situated just above the famous "Seventh Fall" at Vetlanda on the Emån River. These falls were insurmountable to climbing eels (LUNDBERG 1899, TRYBOM 1901).

ROGBERG (1770) was the first to be struck by the "strange richness of the crayfish fishery of this parish" and mentions Lake Grumlan. He says the parish was blessed by this richness. Crayfish were transported on horse-wagons by the local inhabitants for 160—200 km "to be sold in the cities". This traffic continued up to 1868 at least (TRYBOM, *op.cit.*).

TRYBOM made use of the abundant crayfish for ecological studies, *i.e.* sex ratio, size, growth rate and food. No estimate of the total yield was given but one fisherman caught some 2,000 scores in 1892, 500—600 scores in 1896, 125 scores in 1898 and less than 20 scores in 1900. Other fishermen having less area of water had smaller catches but their losses during the 1890s were similar.

This heavy reduction of the crayfish population to a few per cent of the original wealth only, was caused by the planting of a total of 5,000 small eels from Trollhättan in three lakes (Vallsjön, Bjädesjön and a small nameless lake) in 1888 or 1889. The plantings were made 15—20 km upstream of Lake Bexhedasjön, where the losses were recorded. Eels were noted in all lakes of the area and they had crayfish in their stomachs. Their faeces had the brick-coloured appearance noted for crayfish-feeding eels.

River No 80 Lyckebyån, Lake Tjugosjön (156 m, 75 hectares)

The lake received 2,000 young eels in 1931. At that time it had a crayfish population, which, however, was completely gone by 1937. No further details are known (Fishery Consultant G. JOHANSON, lake survey files).

River Silletorpsån, Lake Sillhövdingen (93 m, 150 hectares)

Limborg (1896) noted eel and "some crayfish" in this lake. Later on, several dams were built on the outlet.

Mr. O. HÅKANSSON (*in litt.*), who spent 60 summers on the lake has informed that eel were rare in 1910—20 and crayfish were abundant.

In the late 20s several thousand eels, sized 30—40 cm, were introduced into the lake. Mr. HÅKANSSON recalls catching a number of eels with crayfish in their stomachs. After a few years the formerly abundant crayfish disappeared and catches declined to insignificant levels.

The eels later emigrated and in the 1950s good catches of crayfish were made again. There are probably no eel in the lake at present.

River No 82 Ronnebyån

Lake Rottnen (149 m, 3,400 hectares).

ROGBERG (1770) mentioned eel and crayfish in this lake. The eel trap on the outlet was known in the year 1560 and most probably goes back to the Middle Ages as do other eel fisheries in this area (GRANLUND 1958).

Mr. TOR KRANTZ (*in litt.*) states that his mother, born in 1869, told him that her parents had caught large numbers of crayfish and sold them in the towns of Ronneby and Växjö. This indicates an unusual richness of crayfish. Actually several falls in the river must have been a partial obstruction to eel during pre-industrial times.

In 1908 the access of eels to the lake was completely blocked when the Supreme Court of Sweden confirmed that the lake level should be regulated by a dam on the outlet. The owners of the ancient eel-fishery were compensated by 145 Sw. crowns. per annum, equal to a lost catch of 102 kg. This indicates a rather sparse population of eels.

At present Lake Rottnen yields some 6,000 scores of crayfish annually, which ranks the lake as one of the best producers of the country. There is no general opinion that crayfish have increased, but the number of crayfish traps has mounted (Fishery Consultant E. AHL, pers.comm.).

Lakes Hjorten (96 m, 80 hectares), Linnerydssjön (136 m, 150 hectares) and Rolsmosjön (136 m, 75 hectares)

The River Ronnebyån was blocked by a dam at Djupafors in 1920 and pollution by pulp mills makes it rather safe to assume that eel cannot climb the river. The new possibilities for crayfish production was realized by a man, employed at Djupafors, and he initiated several introductions. Lake Hjorten got its crayfish in 1926 and gave rise to a population, yielding 600 scores in 1941.

The spontaneous crayfish populations of Lakes Linnerydssjön and Rolsmosjön were damaged by a further eel planting in 1931 (JOHANSSON 1942 and in the lake survey files).

A small lake of the area received 250 eels in 1931. The crayfish yield dropped from several scores to one single crayfish (JOHANSSON, *op.cit.).*

River No 86 Mörrumsån, Lake Åsnen (138 m, 15,000 hectares)

ROGBERG (1770) does not mention crayfish from Lake Åsnen. He stresses, however, the abundance of eel and cites a letter from King Gustav I to his son Erik of October 30th, 1558 in which the eel fisheries were described. On the outlet of Lake Åsnen, and on several other sites along River Mörrumsån, the stream was narrowed and simple nets were placed in frames to catch the downstream migrating eels. The velocity of the water was too high to allow the eels to swim out of the trap from the current. These special eel traps were called "werner" or later "värmane" and date from the twelfth and thirteenth century. The net and its frame is called "lana". One "värmane" could have 4—6 "laner". The nets were used by private land owners, the right to fish them was inherited and after some time there were complicated rules for utilizing them and the whole fishery was regulated by local laws. Therefore, they are mentioned in old official documents of the courts, their history can be traced and has been described by GRANLUND (1958).

Until River Mörrumsån was blocked by a dam at Fridafors in 1893 salmon ran into Lake Åsnen. Therefore, the access for young eels must have been good and the abundance of eels in old times is natural. Apparently crayfish have not been noted in the lake until fairly recently. Eels were planted in Lake Åsnen to compensate for the Fridafors blocking but obviously in too small numbers. The eel fishery began to dwindle. Crayfish appeared in some bays and may have culminated in the 30s. From the 40s and onwards, larger number of young eels were released and the eel fishery recovered.

In the years 1947—49 yield data were gathered from the Skatelöv Bay in the northern part of Lake Åsnen. Some 30 fishermen took part.

Year	Pike kg	Perch kg	Eel kg	Crayfish scores
1947	3,712	1,328	156	310
1948	4,404	1,059	368	104
1949	3,209	700	152	65

During the period 1954—58, the average annual catch in the whole Lake Åsnen (based on 683 records) was 24,000 kg pike, 10,400 kg perch and 3,040 kg eel (not including the river catch). Crayfish were at this time very few. There are still some specimens caught in isolated bays (Fishery Consultant E. AHL, pers.comm.).

In this famous eel lake, crayfish are thus rare but have temporarily increased to give some local yield during a period when the eel was less abundant.

River V. Orlundsån, Lake Vitavatten (70 m, 40 hectares)

LIMBORG (1896) notes eel but not crayfish in this lake.

According to Mr. G. SVENSSON (pers.comm. through courtesy of Mr. BRODDE ALMER) who fished the lake, crayfish were present in the 20s. There was an eel trap in the outlet, indicating a regular emigration of eels. Big eels were caught in the 40s (B. ABRAHAMSSON, pers.comm. by courtesy of ALMER).

In 1959 a complete obstacle to eels was created in connection with the building of a starch factory.

Two men, nowadays fishing Lake Vitavatten, have reported their crayfish yields. Mr. B. ABRAHAMSSON, who takes the larger share, crops some 500 scores a year. Mr. OLA BJÖRNSSON caught some 25 scores in 1970—71 but only 1—2 scores in 1960. The increase of the crayfish density is undisputable and the total yield of this small lake is very high indeed.

River No 87 Skräbeån

Lake Ivösjön (6 m, 5,400 hectares)

A pulp mill, Nymölla AB was established on the outlet of the river in 1962. It began to take water from the river in 1963. The mill used on an average 21 per cent of the river flow in June, 32 per cent in July and 33 per cent in August up to 1971. This might have influenced the climbing of elvers or young eels into the river. The decrease of eel in the whole river system, discussed below, may, however, also be explained by intensive fishing in Lake Ivösjön or by both factors.

Lake Ivösjön has been fished by a local organization of land-owners or summer visitors for years. There is some commercial fishery as well. Data have been collected by Fishery Consultant H. ANHEDEN. Fishery Consultant B. ALMER has kindly supplied a great deal of local information. He was born in the area and has fished the lake since his boyhood years.

The interesting trends of the yield of the lake may be introduced by this average catch:

Period	Crayfish, scores	Eel, kg
1944—48 . . .	18	4,100
1949—53 . . .	2	4,100
1956—60 . . .	49	1,700
1961—65 . . .	140	2,100
1966—70 . . .	451	2,500

To these figures should be added the information that the eel catch of the first two periods comprised silver eels, taken in a trap on the outlet and coming from the whole river system. This catch dwindled in later years. The catch of yellow eels, nowadays totally dominant, has not been possible to separate from the total catch of the first two periods.

In more detail the recent development can be given below:

Year	Crayfish			Eels			
	Scores	Traps	Yield/trap	Kg	Fyke nets	Long lines	Kg/effort
1957	43	39	1.1	1,769	210	204	4.3
1958	46	40	1.2	2,165	203	217	5.1
1959	48	51	0.9	1,446	199	209	3.5
1960	58	119	0.5	1,819	225	221	4.1
1961	58	135	0.4	2,087	207	271	4.4
1962	65	131	0.5	2,157	213	305	4.2
1963	117	303	0.4	2,305	184	334	4.4
1964	245	529	0.5	2,255	222	381	3.7
1965	214	118	1.8	1,512	126	218	4.4
1966	242	456	0.5	1,959	115	202	6.2
1967	353	543	0.6	2,056	153	305	4.5
1968	444	718	0.6	3,783	185	275	8.2
1969	574	915	0.6	2,638	191	223	6.4
1970	642	1,236	0.5	2,062	217	254	4.4
1971	870	1,832	0.5	1,987	241	289	3.7

Mr **Brodde Almer** adds to this information, that in 1965 an outbreak of *Diphyllobothtrium latum* caused great concern and many members of the association did not fish at all. This arrested the upward trend for crayfish for two years. The expanding population has prompted the number of crayfish traps to increase. In the 1957—59 period many crayfish were caught by hand. The fyke nets, used for eel, have changed recently. The ones first used were ordinary fyke nets, taking pike and other fish as well. In the last few years, especially after 1965, a new type of "twin fyke nets" has been used, specifically designed for catching eel and being very efficient. The "effort" of the eel catch is simply the total catch divided by the total number of fyke nets and the number of long lines (each carrying 100 hooks).

Mr. **Jean Jönsson**, one of the commercial fishermen on the lake, has supplied the following complementary statistics from his own files.

A large commercial fyke net, operating near the outlet to take silver eels, very clearly demonstrates the falling trend:

1966	615 kg
1967	447
1968	298
1969	134
1970	116
1971	109

Mr. **Jönsson** also fishes for crayfish and among his traps he has used ten individually marked traps, the catch of which has been registrated thus:

Year	Fishing effort	Crayfish	Catch/ effort
1963	130	156	1.2
1964	150	192	1.3
1965	110	166	1.5
1966	120	191	1.6
1967	140	255	1.8
1968	160	269	1.7
1969	130	241	1.9
1970	170	353	2.1
1971	140	277	2.0

There has been heavy fishing for coarse fish in Lake Ivösjön during this period, some 20 tons of bream and roach being removed from the lake annually. Therefore it was supposed (**Svärdson** 1970) that the lessened competitive pressure allowed both eel and crayfish to increase. However, at that time the greatly increased yellow eel fishery with twin fyke nets as well as the effect of the Nymölla pulp mill was not considered.

Lake Ivösjön thus presents a most illuminating case where the trends of the eel and crayfish populations are reversed.

Lake Oppmannasjön (6 m, 1,450 hectares)

The lake is connected by a channel to Lake Ivösjön. There has been a famous eel fishery in this channel at least since 1688 (ALMER 1970). This silver eel trap is at present operated by Mr. FRITZ NILSSON, who informs (through B. ALMER) that his yield has dwindled to some 25 per cent of the weight obtained only ten years ago. He blames the "twin fyke net epidemic" for this. In 1969 alone a further 800 pairs of this gear started to operate in Lake Oppmannasjön. In spite of heavy annual stocking of yellow eels from the coast (1,000 kg in 1970) the silver eel trap is catching less and less. It should be noted that no eels, except very small ones, could pass through the trap down to Lake Ivösjön.

There is no obvious trend so far in the small crayfish population of the lake. At present crayfish are caught at a rate of 1 crayfish per 25 traps.

Lake Immeln (81 m, 2,400 hectares)

This lake is situated upstream of Lake Ivösjön. There are several hydroelectric plants on the connecting river. Up to 1942 some young eels may have reached into Lake Immeln through an alternative outlet (ALMER 1971) but after the construction of the Olofström hydroelectric plant this was impossible. In the years 1946—53 some 8,000 young eels were released in Lake Immeln, in 1966—71 a further 6,500 were planted. In the years 1954—65, however, only 1000 were introduced.

Statistics of the yield of this lake was collected by DAHLÉN (1969):

Period	Number of fishermen	Eel catch, kg	Crayfish catch, scores
1917—21	48	579	20
1943—47	51	275	40
1963—67	69	107	251

Again, an inverse correlation appears. Probably the upward trend of the crayfish catch will be broken by the eel plantings in 1966—71.

River No 88 Helgeån

Lake Hammarsjön (1 m, 2,017 hectares)

The information about this highly eutrophic lake was supplied by the commercial fisherman of the lake, Mr. FRITZ NILSSON (through B. ALMER).

Mr. NILSSON operates a silver eel trap on the outlet. His annual catch around 1950 was some 5,000 kg of small eels, average size some 0.25 kg. After heavy rains larger eels came into the trap, presumably from the upper parts of the river system. These fish very often had their spines broken after passage through the many turbines on the river. In one single night up to 50 silver eels with broken spines were recorded.

The remarkably small size of the local silver eels of that time indicates the presence of male eels.

Nowadays the catch of silver eels has dwindled to some 500 kg. Their size is larger, 0.6—0.7 kg as an average. The reason for this change, in Mr. NILSSON's opinion, is the more than 1,000 pairs of fyke nets introduced in the lake since 1957. The catch during the six weeks in early summer, when the nets are effective, may be very large. Mr. NILSSON himself operated 200 nets in one year and got 12,000 small yellow eels.

The crayfish were rare in 1950 and very large. The catch was then one crayfish per trap and their weight 0.1 kg. Nowadays they are smaller and have spread all over the lake and the catch is roughly 20 per trap.

Lake Tydingesjön (58 m, 400 hectares)

A dam to hold the water of the lake was built in 1950. There were no arrangements made to allow eel to climb to the lake, which they could before. It is generally agreed that eels have become progressively more rare in the lake and much larger.

According to Fishery Consultant H. ANHEDEN and to the chairman of the fishery association of the lake, the crayfish have responded in the usual way, *i.e.* they have become more abundant. However, Mr. TAGE TRUEDSSON (through B. ALMER), who is of the opinion that mink are to blame rather than eel, says crayfish have become more sparse.

River No 98 Lagan, Lake Bestorpasjön (173 m, 50 hectares)

In 1913 no less than 50,000 elvers from River Severn, England, were planted in this small lake. The density of the population became enormous and their growth rate was depressed. Ten years afterwards, in 1923, up to 80 eels, sized 35—45 cm could be caught on 100 hooks of long lines. Eels could be taken also on rod and line.

The outlet of this lake was known for its abundant and large crayfish, before 1913. In 1923 there was not a single crayfish left. (J. LILLIECREUTZ in H. NORDQVIST 1929).

River No 103 Ätran

Lake Lönnern (241 m, 900 hectares)

In about 1920 eels were planted in this lake. Earlier, crayfish were abundant. They were heavily reduced in number but recovered when eels started to emigrate. (Fishery Consultant E. **Skoglund** in the lake survey file, 1933).

Lake Rammsjön (206 m, 30 hectares)

Seventy kg of young eels were planted in this lake in the late 50s. Crayfish were at that time abundant and 30 specimens were often caught in a traditional trap in one single night.

The reduction of crayfish became severe, the catch fell to 2 crayfish per trap and, finally, in 1968, one crayfish per 30 traps. Eels, on the contrary, were common. In 1967 two consecutive catches each gave 9 eels on 100 hooks and their total weight was 8.5 and 8.2 kg respectively. When the eels were gutted, crayfish remains were striking. Claws from legal crayfish (9 cm size) could be identified.

Before the planting there were few eels and they had reached the lake in a natural way. They were known however, to be exceptionally large. One 5 kg specimen is recorded. (Mr R. **Jacobsson** *in litt.*)

River No 108 Göta älv, Lake Vänern (44 m, 555,000 hectares)

The mighty outlet of Lake Vänern, with an average flow of 575 m^3/sec., forms several consecutive falls at Trollhättan. The total height of the falls was 32 metres. Eels could not pass this obstacle and therefore had no access to Lake Vänern and its tributaries until August 14th, 1800, when the first ship sailed through the canal (built 1794—1800).

The discovery of this valuable new fish, of course appealed to the fishermen of Lake Vänern. One unexpected consequence, however, was the disappearance of crayfish not only from Lake Vänern itself but also from numerous other lakes in the tributaries. This fact was widely known and commented upon (**Lloyd** 1854, **Nilsson** 1855, **Steffenburg** 1872, **Cederström** 1896, **Trybom** 1897, **Lundberg** 1899).

Fishermen and landowners were convinced of this predation by eel on the crayfish, but **Steffenburg** (*op.cit.*) challenged this opinion and pointed out the sympatric occurrence of the two species in many lakes which indicated that eel could not exterminate crayfish.

Lake Vänern offered a most favourable growth habitat to eels and **Lloyd** (1854) talks about specimens of 10—11 pounds, *i.e.* 4.25—4.68 kg. The father of one of his informants had caught one eel, weighing 14 pounds, *i.e.* 5.95 kg. The Scandinavian record may have been an eel, according to **Lloyd** caught in a lake in Dalsland and marketed in the town of Vänersborg. It was reported to weigh 18 pounds, *i.e.* 7.65 kg (**Lloyd**, *op.cit.* p. 147). **Holmgren** (1916) tells about the tradition that an eel weighing 8 kg was caught long ago in Lake Knarrebysjön (altitude 104 m) in the Ånimmen water system in the province of Dalsland. This most probably is the very same specimen that LLOYD was referring to. These heavy eels have no counterparts in recent times and corroborate that the eel was a new species to the lake in the year 1800.

It was later discovered (CEDERSTRÖM 1896) that the climbing small eels did not reach Lake Vänern only by means of the sluices but also through a small creek, that spilled water from the upper canal beside the falls. "Millions" of young eels are said to have climbed this creek up to the 1890s when it was closed.

Mr N. J. HOLST of Trollhättan based his private enterprise on these eels, selling them for 15 Sw. crowns per 1,000 specimens. He transported them in large match-boxes, filled with *Potamogeton* (TRYBOM 1893). TRYBOM encouraged Mr HOLST's activity and TRYBOM's book on fishery management of 1893 may have given Mr HOLST many new customers. This became disastrous for numerous crayfish populations to judge from reports in the lake survey files from nearby rivers flowing to Lake Vänern.

River No 130 Dahlbergsån

Lake Teåkerssjön. "Long ago a rich population of crayfish. Disappeared and fishing was closed already in 1912" (Lake Survey 1939).

Lake Bäckforssjön. "At the turn of the century crayfish were significant economically, nowadays they are gone" (1938).

River No 131 Upperudsälven

Lake Fyllingen. "Fifty years ago very abundant, nowadays none" (1938).

Lake Knarrebysjön. "Crayfish disappeared 30 years ago" (1939).

Lake Vångsjön. "Occurred abundantly around 1900 but disappeared, it is said after plantings of eel" (1932).

Lake Furusjön. "Occurred long ago, now completely lost" (1938).

River Tydjeån

Lake Käppesjön. "Are said to have occurred long ago. None now." (1935).

River Åmålsälven

Lake Kälven. "Present according to old records, now lacking." (1934).

It is a most astonishing fact that after two waves of crayfish destruction by the eel, the first during the early decades of the 19th century and the second at the turn of the last century, the practise of planting eel in crayfish localities has continued in the great Göta River drainage up to this very day. This can be seen from the following documentation, all dealing with tributaries of the Göta River, running into Lake Vänern.

River No 132 Byälven

Lake Emneskogssjön (136 m, 117 hectares)

In the years 1929—32 45 kg of young eels were planted. In the lake survey form the local Fishery Consultant (A. BJÖRNEMARK) writes in 1936: "after eel plantings in the Lillälven River (tributary of Byälven) the crayfish catch has decreased in all lakes above Lake Emneskogssjön".

Lake Lilla Björsjön (171 m, 94 hectares)

Ten kg of young eels were planted in 1920. Mr. BJÖRNEMARK notes in his lake survey form in 1936 "earlier yield very high, but considerably lower after eel plantings. It is said that the farmers of the village Ö. Boda released the eels on purpose to get rid of the crayfish".

River Varnan, Lake St. Vilången (126 m, 260 hectares)

Eel were planted in 1910 and in the lake survey form it was noted that crayfish, earlier rather common, disappeared (1936).

River No 140 Tidan

Lake Jogen (250 m, 400 hectares)

Eel were planted in the lake in 1906 and again in 1912 and crayfish almost disappeared. It was reported in the lake survey form of 1934 that crayfish again showed up, especially in the inlet stream. At present (1971) Lake Jogen is known as a very good crayfish producer.

Lake Ymsen (71 m, 1,300 hectares)

A biological study of this lake was made by VALLIN (1929). He notes that eel always had been rare in the lake but had become progressively more so in later years. The catch was 150 kg in 1918 and 10—20 kg in 1927. The eels had become larger, a further indication of dwindling numbers.

The trend of crayfish was reversed. The yield was 42 scores in 1915, more than 200 in 1926 and 400 in 1927.

River No 141 Sjöråsaån

Lake Vristulven (111 m, 407 hectares)

Eels were stocked in 1911—19, many were caught in the 20s. Fishery Consultant FABIAN OLOFSSON (1936) wrote about the effect on crayfish and commented on the development in the lake survey form (1940). The crayfish yield was more than 400 scores before the eel plantings and the lowest annual crop recorded afterwards was 40 scores.

Lake Flarken (108 m, 17 hectares)

This lake is situated close to Lake Vristulven and got eels from that lake. A few eels were planted also in Lake Flarken. Crayfish were almost completely gone in 1926—28 (lake survey from 1940). The nearby Lake Fursjön, altitude 129 metres, probably also got some eels at the same time. Its crayfish population dropped almost to nil.

River No 142 Lidan, Lake Skärvlången (128 m, 173 hectares)

Some 30,000 small eels were planted by A. G. WÄRNQVIST around 1912. A new batch of eels was planted 1920. Major JOHN LINDGREN (*in litt.*) informs that when he first get to know the lake, in 1932, there were very few crayfish left but many eels were taken on long lines. Major LINDGREN may have taken the last eel of the lake, in 1941. It weighed 1.6 kg, gutted and without head. Its stomach had the characteristic brick-coloured contents known from crayfish-feeding eels.

During the 40s and 50s crayfish recovered even more. After 1960, however, their abundance seems to have been reduced through intensive fishing.

Two adjacent lakes, Lake Vagnsjön (127 m, 23 hectares) and Lake Bysjön (126 m., 27 hectares) both had their crayfish populations heavily reduced by the eel plantings in Lake Skärvlången.

Summary of the section on case histories

It is a monotonous list of documented cases known from Sweden where crayfish populations have been interfered with by the eel. The list covers lakes from the whole area of crayfish distribution within the country. Effects are known from the very largest lake (Vänern) down to small tarns. Eutrophic as well as oligotrophic lakes are included in the list. It is a rather striking feature that several of the best crayfish producing lakes have an earlier history of less crayfish and more eels.

Human activities on the rivers explain the varying frequency of eels in the lakes. When annual releases of young eels were prescribed by the water court this often could not be performed due to the short supply of young eels. Then, in one single year, the accumulated material of several years was released. An artificial wave of eels thus rushed through the river system. Obviously the eels spread much more efficiently than hitherto had been realized. The recently discovered territoriality of the eels when feeding

(NYMAN 1972) may help explain the centrifugal spreading. It is documented that eels may spread, first downstream and then upstream a tributary to a crayfish lake.

The evidence from Sweden would seem sufficient to prove the case. In the local discussion that has taken place in recent years, however, various arguments have been used to minimize the impact of eel on crayfish. Eutrophic lakes in the southernmost province of Skåne are said to be populated by large numbers of both eels and crayfish. Apart from the evidence from Lakes Ivösjön and Hammarsjön (p. 171—173) which is proof of the contrary, a final citation from the book by KNUD LARSEN (1947) on crayfish in Denmark may be added. The rich eutrophic lakes of this country normally have only scattered crayfish because of eel and shortage of oxygen. "Only in some clear-water lakes in Jutland where eels are rare or non-existing there are crayfish populations dense enough to give yields of economic significance" (Larsen, p. 24, transl. by the present author).

VII. The pre-industrial distribution of crayfish

SAMUEL ROGBERG, a county dean within the Växjö diocese, lived from 1698 to 1760 and in 1725 started his work on the history of the province of Småland. His work was finished by his relative ISRAEL ROGBERG and ERIC RUDA and was published in 1770. To some extent, his work can be used as a fish fauna record, as he mentioned the items of economy of all 209 parishes.

His book is an overlooked reference as far as the spontaneous distribution of fish and crayfish is concerned. From his notes on eel and crayfish distribution a rough map covering the middle of the 18th century may be drawn (Fig. 3).

Some of his notes have been cited earlier in the case histories. From the map it can be learnt that the eel was common all over the province of Småland while the crayfish was much more restricted. Five out of the ten parishes, which are recorded as having crayfish, are situated above well-known, insurmountable falls and consequently in areas without eel. Two other cases comprise lakes in high altitudes which probably had no eels, although eel-blocking waterfalls are not known. Only three cases out of the ten are real sympatric occurrences where crayfish are mentioned together with eel. In two of these lakes, eels may have been fairly numerous since eel traps were built on their outlets (Lake Rottnen in the River Ronnebyån (*cf.* p. 168) and Lake Helgasjön in the River Mörrumsån.)

The only cases where ROGBERG actually mentioned crayfish as common are those above the falls. The blessing of the Bexheda parish where Lake Grumlan is pointed out was referred to above (p. 167). The traditional traffic

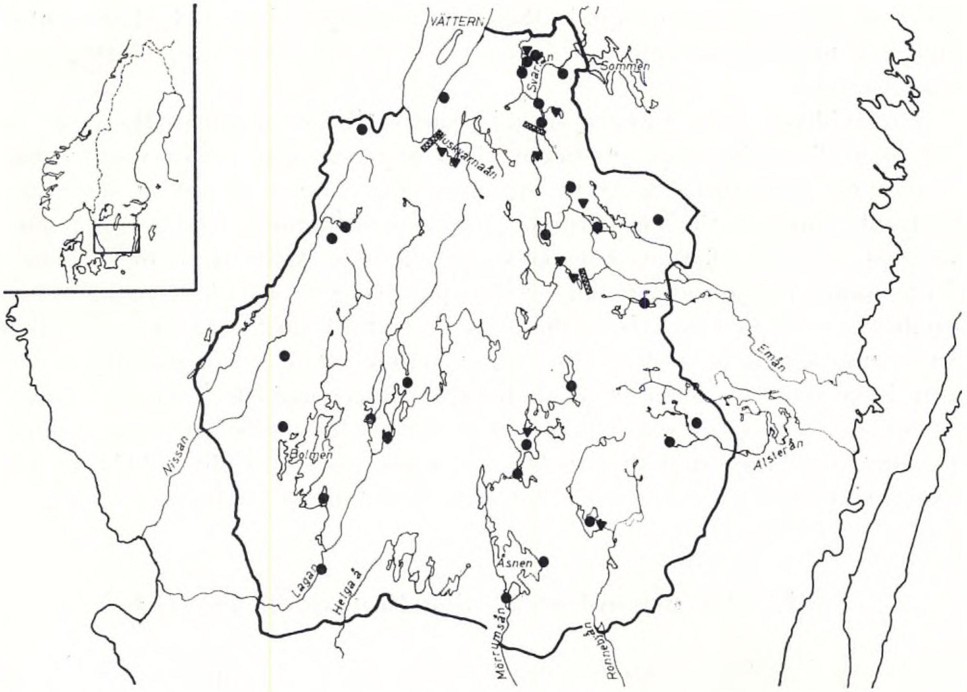


Fig. 3. Distribution of eel (circles) and crayfish (triangles) in about 1750 in the province of Småland, according to ROGBERG (1770). Crayfish were known mostly from the upper parts of the Rivers Emån, Huskvarnaån and Svartån, all of which had waterfalls (bars on the map) known to be impossible to climb for young eels.

of horse-wagons loaded with salted crayfish tails to the consumers in towns up to 200 kilometres away definitely indicate that crayfish were rare outside certain lakes.

There are a number of known letters and orders coming from the Wasa kings Erik XIV (1533—77), Johan III (1537—92) and Karl IX (1550—1611) indicating the royal interest in crayfish. The crustaceans were highly esteemed by these gourmets and some of the letters request crayfish to the royal table, others order local bailiffs to plant them or to guard plantings already made (STEFFENBURG 1872, ARWIDSSON 1918, BERG 1962, ABRAHAMSSON 1969). The surroundings of the castles were selected for stocking, *i.e.* Uppsala and Strängnäs, probably Kalmar as well. LINNEAUS was aware of this and pointed out that crayfish had become more abundant at Uppsala since the days of Johan III (LÖNNBERG 1913).

This introduction of crayfish into new lakes or streams continued later on. Queen Kristina (1626—89) is credited for plantings on localities not mentioned and the royal habit spread. The wealthy mining engineer J. O. SILFVERSTRÖM introduced them on his estate at Sundborn near Falun (be-

Fig. 4. The early maximum of the Litorina Sea, roughly 6,500 years B.P. (Before Present). Redrawn from FROMM (1953). This period was probably a record low as far as the distribution of crayfish is concerned. The Litorina Sea was warmer and more saline than the present Baltic Sea. The eel could probably penetrate far inland from the coast.

fore 1687, when he died) and Reverend P. WIDMARK planted crayfish in streams on the island of Gotland in 1840.

STEFFENBURG (1872), in his monograph on the crayfish, was so impressed by the documented non-existence of crayfish in many lakes in older time that he questioned if the crayfish was a spontaneous invader in postglacial time. Subsequent authors have acknowledged his scepticism but tended to think crayfish were spontaneous after all (ARWIDSSON 1918, EKMAN 1922, ABRAHAMSSON 1969).

We know that plantings were made in the 16th century near the place of the potential consumer, which is quite natural. If crayfish were artificially brought to Sweden (from areas in Germany or Poland which are mentioned in letters by Johan III) this should have happened in the WASA period, *i.e.* the middle of the 16th century.

In those days, however, the stretches of the Rivers Huskvarnaån, Svartån and Emån where eel were blocked by water falls, were inhabited by a sparse and poor human population, which was often fighting partisan wars or involved in skirmishes with the bailiffs and troops of the kings. It is highly improbable that any crayfish plantings should have been performed in those remote districts and yet, two hundred years later, those areas comprise the very stronghold of the crayfish, and induce trading with far away places. ROGBERG's book must consequently be judged as convincing evidence that crayfish really are spontaneous on the Scandinavian peninsula.

In ROGBERG's time numerous water wheels were used to run mills or other early industrial enterprises. Evidently the eel was not blocked by this human activity, since it penetrated to the uppermost lakes of most rivers in substantial frequencies, unless high water falls blocked the passage. This gives us a clue why crayfish were rare at the same time.

One additional factor may add to the earlier rarity of crayfish, especially in the lowland part of the lake district of Sweden. The Litorina Sea, being warmer and more saline than the present Baltic Sea drained this area some 50 metres above the present sea level (Fig. 4). When entire present river systems emerged from the Litorina Sea, there was no natural pathway for crayfish to invade such a stream. The pike-perch (*Lucioperca lucioperca* L.) was also absent from lots of suitable habitats in rather recent time for the same reason. Eel might have been abundant in the Litorina period and certainly exterminated crayfish in the lowest regions above that sea. Actually this period must have been a record low as far as the distribution of crayfish is concerned. Only remnants of the older populations may have survived in refugia of highland streams.

Going back to the previous stage, the Ancylus period, one finds much better conditions for the crayfish. The huge Ancylus Lake was filled with fresh water and had its early outlet at Trollhättan, where the falls were just showing up (Fig. 5). Crayfish thus could easily spread from their eastern

Fig. 5. The maximum of the Ancylus Lake, roughly 8,500 years B.P. (Before Present). Redrawn from FROMM (1953). This huge lake enabled the crayfish to spread from the east to the Scandinavian peninsula. For some hundred years, eels were probably non-existent in this lake. This occurred after the appearance of the Trollhättan falls at the outlet of the Ancylus Lake and before the second outlet was opened in the Danish straits. Owing to land upwarping in the north the Ancylus Lake tilted south.

principal area of distribution by means of freshwater *with no eels for some hundred years.* The latter part of this period, just before the Ancylus Lake was tilted south and found a new outlet within present Denmark, must have been the real Golden Age for the crayfish within the Baltic basin. The climate was mild, as evidenced by the invasion of catfish (*Silurus glanis* L.) and eels were non-existing. Crayfish probably were capable of living up to the northernmost end of the Bothnian Bay at that time, as the contemporary invador, the pike-perch, has continued to do. Eels rather than climate probably have exterminated the crayfish in those northern areas later on.

The impact of eel on the crayfish thus may explain the puzzling features of the crayfish distribution not only in the present but also in the past.

VIII. General ecological aspects. Discussion

The interaction between fish and crustaceans has been recently studied in some detail. Some of the results seem to have far reaching aspects for more theoretical considerations on predation, for the ecology and distribution of plankton as well as the relation between stock and recruitment in fisheries biology.

HUTCHINSON (1967) summarized that "there can be little doubt that being on the whole large and rather slow-moving organisms, few members of the three groups (*Anostraca, Notostraca* and *Conchostraca*) can live perennially in association with fishes". This is evident from the fact that these crustaceans inhabit small temporary waters or those of extreme salinity, where fish normally do not occur.

NILSSON (1972) gives a convincing example. An anostracan fairy shrimp, *Polyartemia forcipata,* lived in the large lake Pieskejaure, altitude 578 m, in Swedish Lapland. In this 60 km^2 lake a cottid, *Cottus gobio* was the only fish present (presumably introduced by man earlier) and some introduced non-spawning brown trout also lived there. But when *Salvelinus alpinus* was introduced in 1961 and rapidly expanded, *Polyartemia* became exterminated already in 1968 but remained in small adjacent waters.

The only exception within the groups mentioned by HUTCHINSON is *Lepidurus arcticus* which is known to occur together with brown trout in mountain lakes in Scandinavia. AASS (1969) discussed *Lepidurus*' distribution and the increase of the species in lake reservoirs where the conditions became more arctic and the fish population reacted by thinning. *Lepidurus* seem to be an exception only because its deep-water habitat allows some predatory pressure from trout. Therefore, in sparse trout populations it can build up in number sufficiently to be of significance to the growth of the trout.

DAHL (1915) was an early pioneer in fisheries biology and he also noted the inverse relation in abundance between brown trout and *Gammarus* in Norwegian mountain lakes. Where there were no trout whatsoever *Gammarus* abounded and were even pelagic and they gnawed at boats! When trout were introduced, *Gammarus* dwindled in a few years.

FISK (1970) found no *Gammarus* in Lake Grinntjärn, 65 hectares, altitude 658 m, where a stunted population of *Salvelinus alpinus* with white flesh was heavily thinned by rotenone treatment in September 1964. When the predatory pressure lessened *Gammarus* appeared, however, and were seen along the shore. The density was found to be some 20 specimens/m^2 in April 1967 at a depth of 3 m. The growth of the char was more rapid after the treatment and the red colour of the flesh indicated that they fed on the *Gammarus*.

BERGLUND (1968) studied the heavy predation by brown trout on the isopod *Asellus* in a pond. It was found that the biomass of *Asellus* culminated in late winter, just before the grazing by trout began. The trout attained its maximum growth very early in the spring but lost weight in summer and autumn.

Recently fish predation on the larger species within the plankton community has been found to have great effect on the appearance of smaller species of plankton. The more clever plankton feeders in a fish community also tend to reduce other fish species, not equally adapted to the plankton diet. The literature on the subject is already large and a recent summary is found in STENSON (1972). NILSSON and PEJLER (unpubl.) found the distribution of various plankters in Swedish Lapland to depend on the occurrence of certain fish species. The wellknown elimination of char by whitefish and the supreme competitive power of *Coregonus albula* over *Osmerus eperlanus* (SVÄRDSON 1966) are supposed to be ecologically related to the ousting of several fish species in the Laurentian Great Lakes by the planktophagous alewife (*Alosa pseudoharengus*) (SMITH 1972).

One of the most interesting aspects of the impact of fish on plankton seem to be cases where different age fractions of the very same fish species compete for size fractions of the same plankters, as in *Coregonus albula* (AIRAKSINEN 1967). If young and adult fish compete for plankton a cyclical fish population abundance may develop. This situation is found in *Coregonus albula* (SVÄRDSON 1956 and unpubl., AASS 1972).

The predatory impact by eel on the populations of crayfish fit into the framework of known and important relations between fish and crustaceans. Principally the effect of the eel is not different from fish predation on *Gammarus, Lepidurus,* and *Asellus.* If the predatory pressure of the eel rises, *Astacus* becomes more and more sparse, survives only in running water and finally disappears completely from the water system. Such a situation, however, rarely develops.

There is one new aspect, however. Since the *Astacus* shares its most favourable habitat with the eel, the smell of *Astacus* could, if reacted on by the eel, guide the climbing yellow eels to excellent habitats where the *eel population is sparse.* From the case histories we have learned that sparse eel populations grow large eels. It may well be assumed that these eels produce more (and possibly larger) eggs. The capacity of the eel to locate far away populations of *Astacus* thus should have a strong survival value. The case histories give the general impression that eel really do locate crayfish, like when introduced young eels first spread downstream, then turned and climbed a tributary to destroy a crayfish population, tens of kilometres from the site of release.

Finally, it should be pointed out that perch (*Perca fluviatilis*), burbot (*Lota lota*) and other fish species of course prey on the crayfish. Their predation is more difficult to study, however, since their populations are more stable than the number of eels. The consequences for management, too, are less significant.

IX. The management of eel and crayfish lakes

Eel as well as crayfish nowadays are considered delicacies. On the market eel can be sold the whole year for a very good price (US $ 2—3 per kg to the fishermen). Crayfish are sold during a very short season of 2—4 weeks only in August, and the price soars to roughly US $ 4—5 per kg first hand. Both species are imported to meet the demand which is higher than the domestic catch. The annual crayfish import (mostly from Turkey) is bigger than the whole catch before 1907 — the year when the *Aphanomyces* disease started to spread.

The association of freshwater fishermen officially states that eel is more important to the fishermen than crayfish. These fishermen mostly rent fishery rights or fish "free" waters. Most fishery right owners, on the other hand, prefer crayfish. Moreover, the actual catch of crayfish may have great recreational values and is regarded as a kind of angling.

The Swedish association of commercial fishermen on the Baltic claims that more eels should be stocked in freshwater, in order to give opportunities to catch migrating silver eels in the significant eel fishery on the southeastern coast.

Traditionally, the blocking of fish ways in running water by building dams is regarded as a blow to the fishery. There are special laws and water courts to deal with these problems. Local fishery administrators tend to suggest to the water court that compensatory eel plantings should be made. Finally the eel has a firm place in the traditions of the fishery in the southwestern part of the country where crayfish always have been rare or are nonexistent. In the eastern part of the country, where crayfish traditions are overwhelming, the emigrating eels on the other hand do have the chance of adding to the profit of the most important Baltic fishery.

In some river systems in the provinces of Värmland, Västmanland and Dalarna crayfish can live only in the lowest regions where the lakes are sufficiently warm. In higher altitudes, however, eel plantings in the lakes yield the best profit.

It is obvious that there are many problems to solve for the manager and the administrator. These problems have been largely ignored for the last decades, when crayfish grew of less importance for every year, a situation correlated to the spread of the *Aphanomyces* disease. Recently, however, when *Pacifastacus* has become the new hope for many lakeowners, the conflict is rather virulent. It is possibly true that the *Pacifastacus* may stand the predatory pressure from the eel better than *Astacus*. The scanty information obtained so far, however, does not indicate any fundamental difference. In Lake Långträsk in the vicinity of Stockholm the *Pacifastacus* has failed to hold its own. Four young stray individuals have been caught after heavy introductions. In the last three seasons not a single crayfish was trapped in spite of great efforts. No doubt predation is to blame for this. Huge perch (*Perca fluviatilis*) and some rather big eel, are supposed to be responsible. PIEPLOW (1938) said the American crayfish *Orconectes affinis*, introduced on the European continent, may flourish sympatrically with eels, but a more thorough study appears necessary. His arguments are the same as those of STEFFENBURG (1872), which are discussed above (p. 154).

The present management of eel versus crayfish in Sweden cannot be judged as satisfactory. Even though introductions of eels are recommended not to take place where crayfish populations may be damaged, the decision is normally up to the local fishery consultant. Also, the whole range, within which eel may influence crayfish, is still largely left open to personal opinion. No case seems to be known where the damage on crayfish has been paid for by those interested in the eel plantings.

It is a personal legitimate interest that one's property is taken care of. There is also a general interest of the society that the production capacity of a river or lake is canalized to produce the best profit feasible. Thus, there is a need for a new instrument or principle in the management.

The model could be fetched from a nearby situation. There is a special legislation for the *Aphanomyces* disease. An official list is published annually where all those waters are included, where fishing for crayfish is prohibited in order not to spread the disease.

In a similar way an annual list could be published for "crayfish rivers" or preferably the "non-eel-rivers" of the country. In such a river system plantings of eel should be criminalized according to a special legislation. The adoption into this category of non-eel-rivers should be formalized and be executed by the state fishery board, the governor of the province or the government. A suggestion to include a certain river or defined part of a river into this category should be made by the local fishery officers.

Prerequisites to reserve a river as a non-eel-river might be:

1. A safe barrier in the lower part of a river or tributary, blocking the natural climbing of young eels. Since barriers mostly are artificial, any river may suddenly be brought into this category by industrial activities.
2. Most of the river should run within a climate region where crayfish can reproduce. If *Pacifastacus* should turn out to be more tolerant to low temperature than *Astacus* — which has been suggested — a number of northern rivers should be included as potential candidates.
3. The majority of fishery right owners must be in favour of the change. A legally fixed procedure should be followed in order to find out the opinion of those concerned.

It may seem too cumbersome to initiate this new management. The present one has largely failed, however, and it might be assumed that already the establishment of the proposed system would focus the general interest on the dilemma and thus discourage those hitherto most interested in eel production of inpropriate waters.

X. Summary

The Trollhätte Canal was completed in 1800 and ships could sail from Gothenburg into Lake Vänern. Eels (*Anguilla anguilla* L.) were allowed to penetrate into the lake where they ousted crayfish (*Astacus astacus* L.) from the lake and some of its tributaries. The knowledge of the gain and loss for the fishery was once widely known but has later, gradually, faded away.

There is a general allopatric occurrence of the two species, eel dominating the western part, crayfish the eastern part of southern Sweden.

Surveys from some 1,600 lakes indicate that the species do have rather similar habitats; large eutrophic lakes being favoured by both. The eel is the tougher of the two species and may live in all kinds of lakes to which it can climb. Crayfish cannot reproduce in summer-cold lakes, although older crayfish may survive and grow in them.

When favourable lakes are sampled, the sympatric occurrence of the two species is less frequent than it should be according to chance. The yield tends to be reversed, high eel catches occur in crayfish-free lakes and vice versa. The median annual catch of crayfish is 46 specimens per hectare in lakes with no eels and 22 crayfish when eels are present but sparse. Moderate yields of both species thus may be obtained in cases of sympatry but really good yields are obtained when the species are allopatric only.

A number of case histories are presented where eel and crayfish have fluctuated in reversed direction. Several of the best crayfish producing lakes have had an early history of fewer crayfish and more eels.

Crayfish were found to be spontaneous and not introduced in Scandinavia by man. They were much more rare, however, in the sixteenth century. An hitherto overlooked reference from 1760 indicates sparse crayfish in the province of Småland except where steep waterfalls blocked the climbing of eels. It is suggested that crayfish invaded Scandinavia from the east in the Ancylus period, some 8,500 years ago, when the Baltic basin was filled with fresh water. Eels probably did not exist in the Ancylus Lake for some hundred years, when the lake had its outlet at Trollhättan, where waterfalls blocked them.

The impact of eel on the crayfish is compared to a number of similar cases where fish interact with crustaceans. This has far reaching consequences for several problems in fisheries biology. From a more theoretical point of view the eel's predation on the crayfish may be interesting since it gives a survival value to those eel having the best capacity to locate crayfish lakes from a distance. These eel are thereby led to excellent habitats sparsely populated by eel. They can grow large and probably produce more eggs.

The practical consequences of the eel's impact on crayfish are important. The crayfish is a much sought-after delicacy and gives much higher yield per hectare from an economical point of view and thus should be favoured in most cases. The recent introduction of the *Aphanomyces*-resistant American crayfish *Pacifastacus leniusculus* (DANA) in Swedish lakes has stressed the importance of a new management. Some details on how such a management should be outlined are suggested.

XI. References

AASS, P. 1969. Crustacea, especially *Lepidurus arcticus* PALLAS, as brown trout food in Norwegian mountain reservoirs. *Rep. Inst. Freshw. Res. Drottningholm* 49: 183—201.

— 1972. Age determination and year-class fluctuations of cisco, *Coregonus albula* L., in the Mjøsa hydroelectric reservoir, Norway. *Rep. Inst. Freshw. Res. Drottningholm* 52: 5—22.

ABRAHAMSSON, S. 1969. Historik, allmän översikt och reformförslag beträffande fångst och handel med flodkräfta. *Fauna och flora* 64(3): 97—104. (In Swedish.)

— 1972. Fecundity and growth of some populations of *Astacus astacus* LINNÉ in Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 52: 23—37.

AIRAKSINEN, K. J. 1967. The vendace (*Coregonus albula* L.) of Varmavirta in northern part of Lake Saima (SE-Finland). *Suom. Kalatal.* (Finlands Fiskerier) 30: 1—32. (In Finnish, with Swedish and English Summary.)

ALM, G. 1917. Undersökningar rörande Hjälmarens naturförhållanden och fiske. *Medd. K. Landtbr. Styr.* 3(204): 1—111. (In Swedish.)

— 1929. Der Krebs und die Krebspest in Schweden. *Z. Fisch.* 27(2): 123—138.

ALMER, B. 1970. Bäckaskogsfisket. *Fisksumpen* 17: 29—31. (In Swedish.)

— 1971. Åter dags för Näsumlax? *Fisksumpen* 18: 24—30. (In Swedish.)

ARWIDSSON, I. 1918. Om kräftor och kräftfiske. *Almanack för alla.* Stockholm. p. 174—178. (In Swedish.)

— 1920. Kräftpesten i Sverige. *Medd. K. Lantbr. Styr.* 10(229): 1—126. (In Swedish.)

BERG, G. 1962 Kräftorna i svensk matkultur. *Fataburen* 63—84. (In Swedish.)

BERGLUND, T. 1968. The influence of predation by brown trout on *Asellus* in a pond. *Rep. Inst. Freshw. Res. Drottningholm* 48: 77—101.

CEDERSTRÖM, C. 1895—96. Wermlands läns fiskevatten. I—III. Wermlands-Tidningens Tryckeri. Karlstad. 590 p. (In Swedish.)

— 1896. Fisket i Vermland. *Sv. Fisk. Tidskr.* 5: 83—88. (In Swedish.)

DAHL, K. 1915. En studie over grundaatens eller matfloens biologi og utbredelse i Norge. *Norsk Jaeger & Fisker Foren. Tidskr.* 44(5): 1—32. (In Norwegian.)

DAHLÉN, T. 1969. P. M. angående inverkan på fisket av sjön Immelns reglering. 24 p. (Mimeographed in Swedish.)

EKMAN, TH. 1918. Kräftor och ål. *Svensk Fisk. Tidskr.* 27(4): 154—155. (In Swedish.)

— 1922. Djurvärldens utbredningshistoria på den skandinaviska halvön. Bonniers Stockholm. 612 p. (In Swedish.)

FISK, E. 1970. Fiskevård med rotenon i svältrödingsbestånd. *Inform. Inst. Freshw. Res. Drottningholm* (14). 10 p. (Mimeographed in Swedish.)

FROMM, E. 1953. Nedisning och landhöjning under kvartärtiden. Atlas över Sverige 19—20. Generalstab. Lit. Anst. Förl. Stockholm. (In Swedish.)

GRANLUND, J. 1958. Ålfiskena i Mörrumsån. Kronobergsboken 1957. Växjö. 143 p. (In Swedish.)

GYLLENBORG, J. G. 1770. Afhandling om Insjö-Fisket i Swea Riket. Wennberg & Nordström. Stockholm. 70 p. (In Swedish.)

HOLMGREN, E. 1916. Undersökningar af fiskevatten å Dalsland. Carlsson efterträdares boktryckeri, Vänersborg. 239 p. (In Swedish.)

HUTCHINSON, G. E. 1967. A treatise on limnology. II. John Wiley & Sons Inc. N.Y. 1,115 p.

JOHANSSON, G. 1942. Några lyckade inplanteringar av kräftor i vattendrag och insjöar i Blekinge. *Svensk Fisk. Tidskr.* 51(3): 60—61. (In Swedish.)

LARSEN, K. 1947. Krebsebogen. Clausens forlag. Copenhagen. 69 p. (In Danish.)

LIMBORG, H. 1896. Beskrifning å insjöarne i Blekinge. *Hushåll. sällsk. Blekinge Tidskr.* 1895/96: 38—64. (In Swedish.)

LLOYD; L. 1854. Scandinavian adventures. I. Richard Bentley Publ. London. 512 p.

LUNDBERG, R. 1899. Om svenska insjöfiskarnes utbredning. *Medd. K. Landtbr. Styr.* 10(58): 1—87. (In Swedish.)

LÖNNBERG, E. 1913. LINNÉS föreläsningar öfver djurriket. Akad. Bokhandeln. Uppsala. 607 p. (In Swedish.)

MAGNUSSON, M. 1961. Ålen i Hasselforssjöarna. *Svensk Fisk. Tidskr.* 70(11): 153—155. (In Swedish.)

NILSSON, K. 1971. Ålen och kräftorna. *Insjöfisket* (2/3): 15—18. (In Swedish.)

NILSSON, N.-A. 1972. Effects of introductions of Salmonids into barren lakes. *J. Fish. Res. Bd. Can.* 29(6): 693—697.

NILSSON, S. 1855. Skandinavisk Fauna. IV. Fiskarna. Gleerups, Lund. 768 p. (In Swedish.)

— 1860. Aufenhalt, Lebensweise, Nahrung und Fortpflanzung des Süsswasser-Aales. (*Muraena anguilla* LINN.). *Z. ges. Naturwissenschaften* 16: 15—31.

NORDQVIST, H. 1929. Försök rörande import och inplantering i svenska sjöar av engelsk glasål. *Skr. S. Sveriges Fisk. Fören.* 1928; (2): 60—86. (In Swedish.)

NYMAN, L. 1972. Some effects of temperature on eel (*Anguilla anguilla* L.) behaviour. *Rep. Inst. Freshw. Res. Drottningholm* 52: 90—102.

OLOFSSON, F. 1936. Ålen och kräftorna. *Svensk Fisk. Tidskr.* 45(10): 279—280. (In Swedish.)

PIEPLOW, U. 1938. Fischereiwissenschaftliche Monographie von *Cambarus affinis*. *Z. Fisch.* 36(3).

ROGBERG, S. 1770. Historisk Beskrifning om Småland. Kungl. Amiralitets Boktryckeriet. Karlskrona. 1,035 p. (In Swedish.)

SCHIEMENZ, P. 1935. Untersuchungen und Beobachtungen über den Aal. *Z. Fisch.* 33: 615—680.

SMITH, S. H. 1972. Factors of ecological succession in oligotrophic fish communities of the Laurentian Great Lakes. *J. Fish. Res. Bd. Can.* 29(6): 717—730.

STEFFENBURG, A. 1872. Bidrag till kännedomen om flodkräftans naturhistoria. Holms boktryckeri, Falun. 72 p. (In Swedish.)

STENSON, J. A. E. 1972. Fish predation effects on the species composition of the zooplankton community in eight small forest lakes. *Rep. Inst. Freshw. Res. Drottningholm.* 52: 132—148.

SVENSKT FISKELEXIKON. 1955. Editors: N. ROSÉN, A. LINDROTH and G. S. O. SVENSSON. Esselte AB. Stockholm. 704 p. (In Swedish.)

SVÄRDSON, G. 1949. Eels (*Anguilla anguilla*) found in Sweden in partial nuptial dress. *Rep. Inst. Freshw. Res. Drottningholm* 29: 129—134.

— 1956. Lambarfjärdens siklöja. *Svensk Fisk. Tidskr.* 65(5): 73—80. (In Swedish.)

— 1959 a. Om nordamerikanska kräftor. Redogörelse byggd på en studieresa till USA och Canada 1958. *Insjöfisket* (8—9): 6—10. (In Swedish.)

— 1959 b. Nordamerikanska kräftor tänkbara för introduktion i Sverige. *Svensk. Fisk. Tidskr.* 68(10): 121—123. (In Swedish.)

— 1964. Signalkräftan. p. 175—183. *In* Svärdson, G. and N.-A. Nilsson (Eds.) Fiskebiologi. Halmstad. (In Swedish.)

— 1965. The American crayfish *Pacifastacus leniusculus* (DANA) introduced into Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 46: 90—94.

— 1966. Siklöjans tillväxt och utbredningsgränser. *Inform. Inst. Freshw. Res. Drottningholm* (4). 57 p. (Mimeographed in Swedish.)

— 1967. Vad kostar ålen i kräftor? *Inform. Inst. Freshw. Res. Drottningholm* (10). 19 p. (Mimeographed in Swedish.)

— 1968. Ålen som kräftpredator. *Zool. Revy* 29(2): 61—72. (In Swedish.)

— 1970. Effekter av hårt fiske. *Inform. Inst. Freshw. Res. Drottningholm* (6). 13 p. (Mimeographed in Swedish.)

TRYBOM, F. 1881. Om s.k. ålvinner vid Elfkarleby och plantering af ålyngel. *K. Lantbr. Akad. Handl. Tidskr.* XXXIV(3): 1—4. (In Swedish.)

— 1893. Fiskevård och fiskodling. Bonniers Förlag. 199 p. (In Swedish.)

— 1897. Huru bör kräftan lämpligast skyddas i våra fiskeristadgor?. *Svensk. Fisk. Tidskr.* 6(2/3): 52—76. (In Swedish.)

— 1899. Sjön Nömmen i Jönköpings län. *Medd. K. Landtbr. Styr.* 2(50): 1—51. (In Swedish.)

— 1901. Bexhedasjön, Norrasjön och Näsbysjön i Jönköpings län. *Medd. K. Landtbr. Styr.* 9(76): 1—67. (In Swedish.)

UGGLA HILLERBRANDSSON, C. 1786. Inträdes-Tal om sjön Hjelmaren hållet för Kongl. Vetenskaps Academien den 9 augusti 1786. Johan Georg Lange. Stockholm. 1786. 32 p. (In Swedish.)

UNESTAM, T. 1969. Resistance to the crayfish plague in some American, Japanese and European crayfish. *Rep. Inst. Freshw. Res. Drottningholm* 49: 202—209.

— 1972. On the host range and origin of the crayfish plague fungus. *Rep. Inst. Freshw. Res. Drottningholm* 52: 192—198.

VALLIN, S. 1929. Sjön Ymsen. *Medd. K. Lantbr. Styr.* 6(277): 1—43. (In Swedish.)

On the host range and origin of the crayfish plague fungus

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Abstract

Evidence is accumulating that resistance to the crayfish plague fungus, *Aphanomyces astaci,* is high in groups of Crustacea other than Decapoda and is basically low in the latter group. Hitherto, it is only in North America that a situation has been found where the fungus could exist as a naturally-behaving parasite on crayfish. In that continent a parallel resistance may have developed in several crayfish groups.

The presence of the fungus in *Pacifastacus leniusculus* from Lake Tahoe represents the first record of *Aphanomyces astaci* outside Europe. Only a very low percentage of these animals were visibly attacked, however.

I. Introduction

In previous investigations the host range of the crayfish plague has been investigated both in several taxonomic groups of crayfish (Unestam 1969a, Schikora 1916) and in some plankton crustaceans (Unestam 1969a) and also in a crab (Benisch 1940). Thus, *Pacifastacus leniusculus,* a species from the west coast of North America which is closely related to the European species, has been shown to have a resistance as high as that of taxonomically distant groups on the North American continent, while a Japanese species, related neither to the European nor to any American crayfish group, appeared to be quite as susceptible as any of the European species. Furthermore, it has not been found possible to infect any of a number of freshwater plankton crustaceans under laboratory conditions. Both because the crayfish plague fungus, *Aphanomyces astaci,* seems to be ecologically associated with freshwater arthropods (Unestam 1969b) and because it is far too aggressive in Europe to be a natural (original) parasite here, it has been postulated that the natural hosts are crayfish of non-European origin (Unestam 1969a).

This article concerns an investigation into the resistance of some additional crustaceans and observations on the possibility that American crayfish carrying the plague fungus are the natural hosts.

II. Materials and Methods

The crayfish used were *Euastacus kershawi* SMITH from Victoria, Australia, *Astacus astacus* L. from Lake Ullvettern, Värmland, Sweden, and *Pacifastacus leniusculus* DANA from Lake Tahoe, California, USA. *Mysis relicta* LOV. was collected in Lake Mälaren, inland from Stockholm, Sweden.

Strain D_1 of *Aphanomyces astaci* SCHIKORA was used in the infection experiments. The methods for culturing the fungus and for the production of zoospores, as well as the basic methods for the infection experiments, have been described by UNESTAM and WEISS (1970). Ten thousand spores per ml were added to the aquarium water (6—7 litres per aquarium).

For the crayfish redistilled water was used in the aquaria, and for the plankton crustaceans water from the lake where these were collected was used. The temperature was 12°C. Each aquarium contained 2—6 crayfish or about 20 plankton animals. Ten-litre plastic aquaria were used.

The crayfish were fed weekly with carrot slices (UNESTAM and WEISS 1970) and the plankton crustaceans with commercial fish food, and the first meal was given about six days after the addition of fungal spores.

III. Results

In an earlier paper (UNESTAM 1969a) attempts to infect some plankton crustaceans with *Aphanomyces astaci* were described. None of the 8 species was visibly infected in a short-term experiment (6 days) whereas the very much bigger crayfish *Astacus astacus* showed its first attacks within 2 days.

In this investigation *Mysis relicta,* a plankton crustacean belonging to Thoracostraca, Malacostraca, was also challenged with the same fungus. In repeated experiments the death rate was the same as in control aquaria without added fungal spores. The last animals died after about 6 weeks and no signs of infection were seen in either the dying or the dead animals. Control animals of *Astacus astacus* died from *Aphanomyces* infection within 3 weeks.

Three specimens of the Australian crayfish *Euastacus kershawi* were also challenged in the same way. They all died from *Aphanomyces* attacks within 11 days after spore addition. Five specimens of *Pacifastacus leniusculus* survived the challenge without any signs of infection. *P. leniusculus* had earlier been shown to be very resistant to the plague fungus (UNESTAM and WEISS 1970).

In a basin used for storing about 50 specimens of *Pacifastacus leniusculus,* most individuals showed clear plague attacks. These crayfish had never had any contact with Swedish crayfish. Moreover, the tap water passing through this basin first flowed through an aquarium containing *Astacus astacus,*

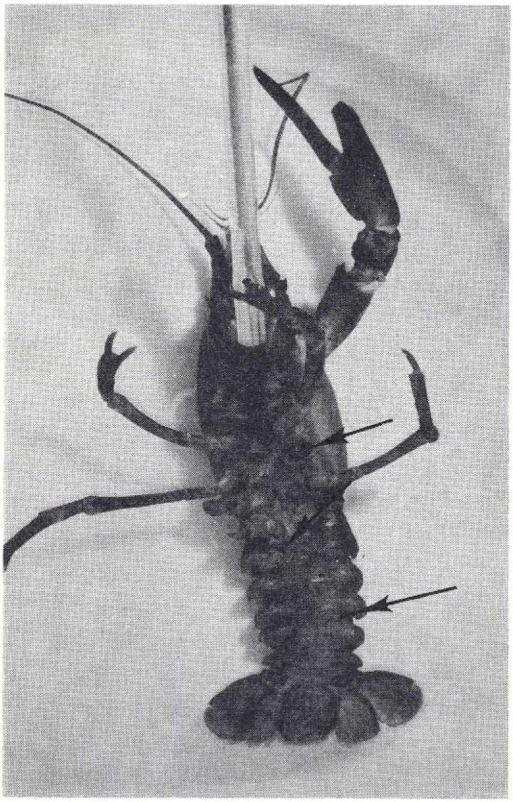

Fig. 1. *Pacifastacus leniusculus* attacked by *Aphanomyces astaci.* The animal has lost several legs as a result of the attacks and several pleopods are deteriorating. The attacked spots are always dark brown or black owing to melanin (arrows). About 0.7 X.

which remained healthy. This excludes the water as a source of infection. The disease appeared after a few weeks and killed a number of healthy *A. astacus* kept in the same basin. The fungus was also isolated in pure culture (for method, see UNESTAM 1965) whose zoospores could also infect *A. astacus*. This is the first case of spontaneous (no spores added) infection in *P. leniusculus*. Earlier only aquaria with stationary water and high spore densities had been used (UNESTAM and WEISS 1970) when *P. leniusculus* was attacked.

After a few months many individuals lost the attacked legs or chelae owing either to autotomy or deterioration of the cuticle (Fig. 1). Apparently, the attack was not normally directly lethal to *P. leniusculus,* since after one year some animals had lost all ten legs but still survived for months in the basin.

It was mainly the soft cuticle in the joints of the legs that was attacked but also affected were the tips of the pleopods, which deteriorated slowly from the tip inwards. The ventral, intersegmental membranes of the abdomen were seldom attacked. In the European crayfish, *Astacus astacus,*

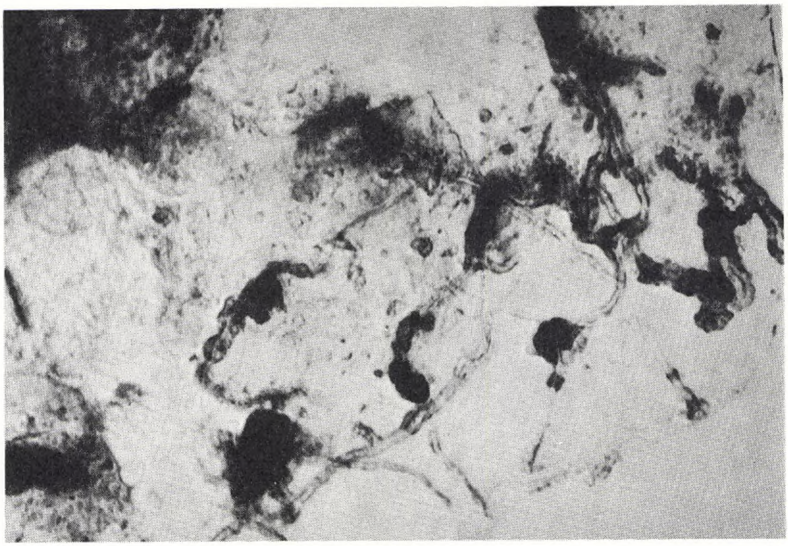

Fig. 2. A few hyphae, all melanized, in the soft cuticle of *Pacifastacus leniusculus* 150 X.

these membranes are the main sites of infection. The hyphae grew extremely slowly compared to the hyphae in *Astacus*. They were also surrounded by melanin (Fig. 2) to a much greater extent than in the latter crayfish. Therefore the whole depth of the tegument of the attacked spots was always dark brown or black. The spots had no specific shape. No hyphae were found in the body inside the tegument. The inner surface of the attacked portion of the tegument was covered by a soft "tissue", probably formed by haemocytes; this was not studied in detail.

Among 2,300 crayfish of *Pacifastacus leniusculus* collected from Lake Tahoe in August, 1970, four animals were selected since they had symptoms similar to those of infected aquarium animals of the same species. In some of the brown spots in these specimens a few melanized hyphae of *Aphanomyces* type (Fig. 2) were found growing in the soft cuticle. The frequency of apparent infection in a natural population is therefore probably very low.

These observations in North America represent the first record of *Aphanomyces astaci* outside Europe.

IV. Discussion

Apparently, the crayfish plague fungus, *Aphanomyces astaci,* strain D_1, is not as aggressive towards plankton crustaceans (UNESTAM 1969a and this study) as it is towards some crayfish species. No attack was found even on *Mysis relicta,* which belongs to the Mysidacea, a group in Thoracostraca,

Table 1. Host range of *Aphanomyces astaci*. (Based upon this paper and that of Unestam, 1969.)

CRUSTACEA	Number of species tested	From	Susceptible or resistant
Malacostraca: Thoracostraca			
Decapoda			
CRAB: *Eriocheir*	1	China	S
CRAYFISH			
Astacidae			
Cambaroides	1	Japan	S
Procambarus	2	USA	R
Cambarus	5	USA	R (incompletely)
Faxonella	1	USA	R
Orconectes	4	USA	R (incompletely)
Pacifastacus	1	USA	R (incompletely)
Astacus	2	Europe	S
Austropotamobius	2	Ireland and Central Europe	S
Parastacidae			
Euastacus	1	Australia	S
Mysidacae			
Mysis	1	Sweden	R
Plankton crustaceans outside Malacostraca	8	Sweden	R

close to the Decapoda, to which crayfish and crabs belong. A high resistance to the plague fungus might therefore exist outside the Decapoda.

In the Decapoda, the crab, *Eriocheir sinensis,* was moderately susceptible to the plague (Benisch 1940), the European crayfishes were highly (or, in one experiment with *Astacus leptodactylus,* moderately) susceptible, and the only endemic Japanese crayfish, *Cambaroides japonicus,* was highly susceptible (Schikora 1916, Unestam 1969a). Although, owing to difficulties in air transportation, only three Australian specimens could be tested, the fact that all of these were attacked very easily strongly indicates that *Euastacus kershawi* has very little resistance to the plague fungus existing in Europe. This fungus probably does not exist in Australia, at least not on *E. kershawi,* for if it did and if it had the same degree of virulence as against *Astacus astacus* it would have been observed there, since extensive studies have been made on the crayfish on this continent (Riek 1969). The Australian crayfishes belong to a group, Parastacidae, found also in South America, New Guinea, New Zealand and Madagascar. There is no reason why this (or any other) group of crayfish should have developed specific resistance without the presence of the parasite. Similar arguments are valid also for the Japanese species. There have been no reports of a plague like crayfish mycosis occurring outside Europe. Thus, in the Decapoda as a whole resistance is probably weak and has developed only in the presence of the parasite.

It is thus likely that the plague fungus exists widely in America. American species show a high but incomplete resistance, thereby being much more suitable hosts for the fungus than is the European *Astacus astacus,* which is eradicated wherever it is attacked by the fungus.

The spontaneous attacks on individuals of the American *Pacifastacus leniusculus* in the basin and the paucity of the fungus in a natural population (Lake Tahoe) support the suggestion that *P. leniusculus* is a natural host. On several occasions other than those reported by UNESTAM (1969a) it has been observed that *Astacus astacus* contracted the disease and vanished soon after the introduction to the same water of *P. leniusculus* directly imported from the USA. The rare, weak and non-lethal attacks accord with the suggestion that the fungus is a more "natural" parasite in *P. leniusculus* than in European animals.

This is the first time the fungus has ever been found outside Europe. The mysterious appearance of the plague in Italy in 1860 (SELIGO 1895) can now, after a century of speculation, be explained. The disease was probably introduced with American crayfish.

Since the fungus apparently occurs in North America, resistance to this pathogen must have evolved independently and in a parallel fashion in the different groups of crayfish species. Of these groups only the west-coast genus, *Pacifastacus,* is closely related to the very susceptible European species.

The following working hypothesis is suggested. The fungus is a parasite basically limited to crayfish, or Decapoda, as a taxonomic group (see Table 1). It occurs widely in North America but is found neither in Australia nor in Japan.

It is planned to isolate the fungus from different American crayfish species and also to test the resistance of the crayfish from other areas not yet investigated.

V. Acknowledgments

The author gratefully acknowledges the assistance of Mrs Anita Grandin, the gift of *Mysis relicta* from Dr Magnus Fürst, the gift of *Euastacus kershawi* from Dr A. Neboiss, and the help given in many different ways by Dr Sture Abrahamsson and Mr Hans Olsson. The research was supported by grants from the Swedish Natural Science Research Council and the Fishery Board of Sweden.

VI. References

BENISCH, J. 1940. Künstlich hervorgerufener *Aphanomyces*-Befall bei Wollhandskrabben. *Z. Fisch.* 38: 71—80.

RIEK, E. F. 1969. The Australian freshwater crayfish (Crustacea: Decapoda: Parastacidae), with descriptions of new species. *Aust. J. Zool.* 17: 855—918.

SCHIKORA, F. 1916. Die Wiederbevölkerung der deutschen Gewässer mit Krebsen. Neudamm. 195 p.

SELIGO, A. 1895. Bemerkungen über Krebspest, Wasserpest, Lebensverhältnisse des Krebses. *Z. Fisch.* 3(6): 247—261.

UNESTAM, T. 1965. Studies on the crayfish plague fungus *Aphanomyces astaci.* I. Some factors affecting growth *in vitro. Physiol. Plant.* 18: 483—505.

— 1969a. Resistance to the crayfish plague in some American, Japanese, and European crayfishes. *Rep. Inst. Freshw. Res. Drottningholm* 49: 202—209.

— 1969b. On the adaptation of *Aphanomyces astaci* as a parasite. *Physiol. Plant.* 22: 221—235.

— and D. W. Weiss. 1970. The host — parasite relationship between freshwater crayfish and the crayfish disease fungus *Aphanomyces astaci:* Responses to infection by a susceptible and a resistant species. *J. gen. Microbiol.* 60: 77—90.

An electrical barrier for preventing migration of freshwater crayfish in running water. A method to stop the spread of the crayfish plague

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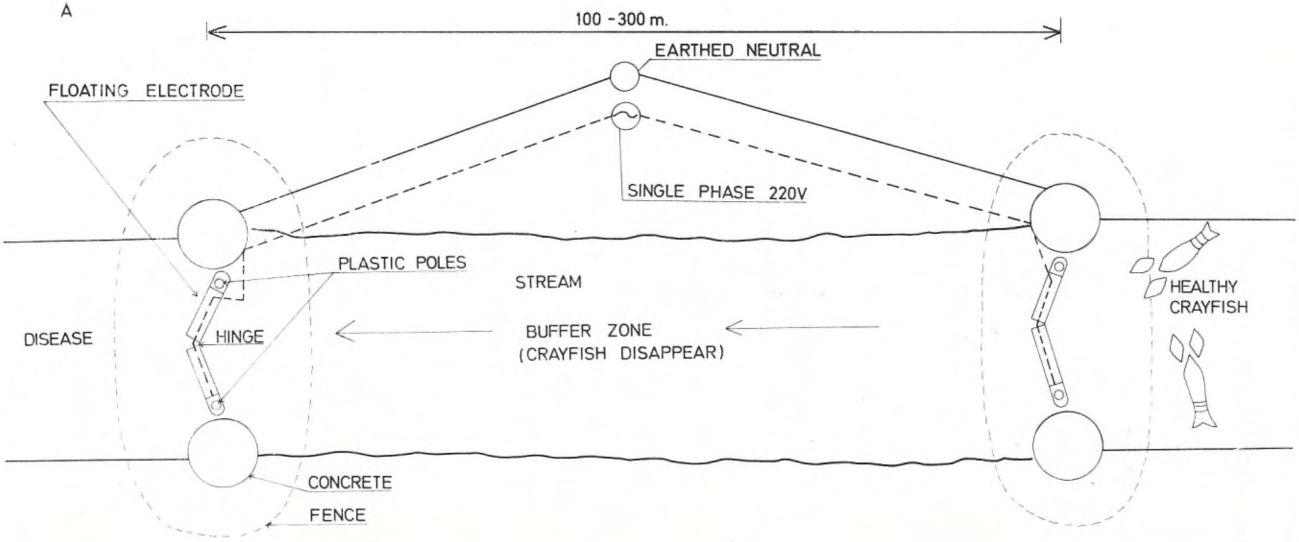
The crayfish plague was first discovered in Italy in 1860 (Seligo 1895). The disease has later exterminated the crayfish, *Astacus astacus,* in great parts of central Europe.

The continuous spread of the crayfish plague in Scandinavia has been considered inevitable during the last few decades, despite strict laws to prevent the spread due to man's imprudence. The reason for this is the complete lack of resistant individuals in *Astacus astacus* (Schikora, 1916, Nybelin 1936, Unestam 1969a). Attempts were made to kill the animals locally using calcium hydroxide (freshly prepared from calcium oxide) in water courses where the disease spread upstream (Vallin 1936). The drastic increase in the pH in the stream killed crayfish (among other animals) and thus a zone free of crayfish was formed. Unfortunately such treatment does not often last long enough to ensure 100 per cent mortality of crayfish in the treated area of the stream and the disease may spread through it with remaining infected crayfish. But, the very fact that it was sometimes successful showed that the basic idea was correct. We were therefore interested in designing a method (using the same principle) where upstream as well as downstream migration of diseased and healthy animals could be locally completely prevented.

Since, when electrofishing in freshwater an electrical current is very effective in influencing fish over a relatively long distance (Meyer-Waarden, Halsband and Halsband 1965) we decided to use electricity for our purpose. Electrical barriers have also been useful in preventing the mitten crab, *Eriocheir sinensis,* from migrating up rivers (*op.cit.*) and for catching crayfish in density investigations (Abrahamsson 1966).

Preliminary experiments were conducted with a voltage of 220 V A.C. (since this is the standard low voltage in Sweden) in a eutrophic pond ($\varkappa$, 3.4×10^{-4}, water temperature about 20°C) using crayfish (*A. astacus,* 8—11 cm) and trout (about 20 cm) as test animals. From these tests it was found that a naked wire (stainless steel, 5 mm in diameter) along the surface,



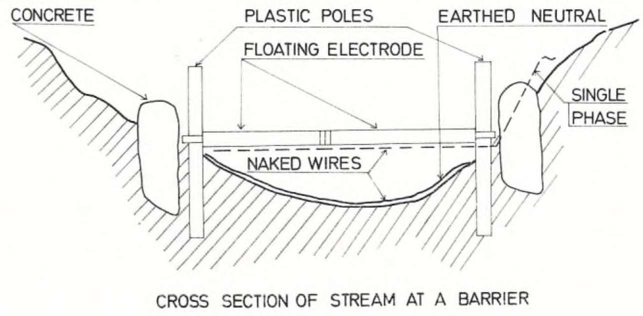
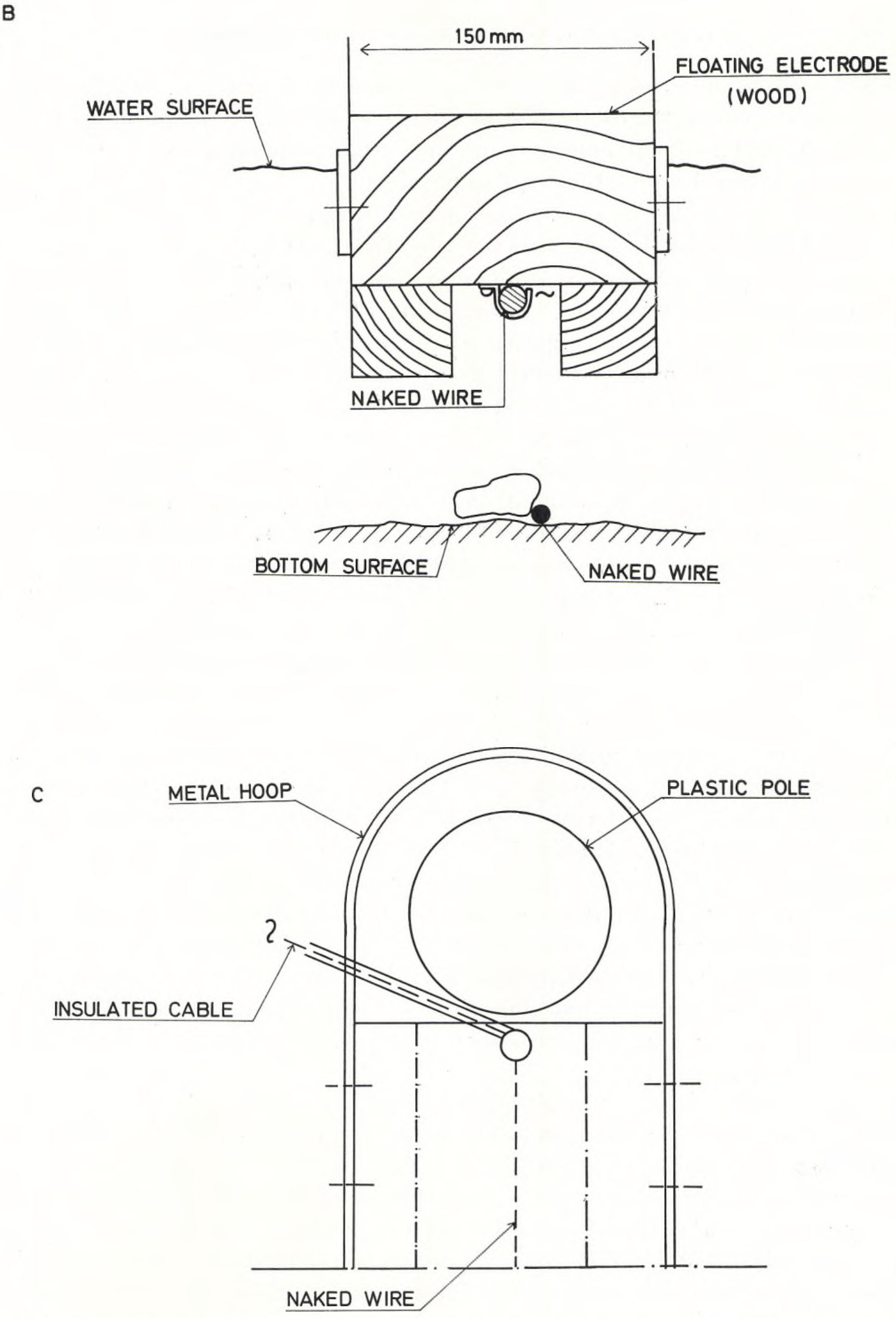


Fig. 1. Electrical migration barriers in a stream. A. Two barriers in a stream, 100—300 m apart, which will soon form between them a zone empty of crayfish. This buffer zone prevents the spread upstream of the crayfish plague by keeping diseased and healthy crayfish apart and prevents fish (and other animals) from transferring the disease.



B. A section of the flotaing electrode with its naked wire (connected to 220 V A.C.) attached underneath the wooden board and the wire (connected to the O-line) fixed on the bottom surface. Between these two wires and even on both sides of the bottom wire the electrical field paralyses crayfish. Even as far as 1—2 m from the bottom wire crayfish feel and react to (swim) the current. C. One end of the floating electrode seen from underneath. The metal hoop anchors the board loosely to the plastic pole to allow for changes in the water level.

connected to the active side (∼) and another, parallel, wire along the bottom and connected to the neutral side (0) would serve our purpose. However, the water depth should not be more than approximately 1 m. if the trout are to be killed and the crayfish paralysed.

Fig. 1 shows the final construction and combination of two electrical barriers later used in a stream of the River Tidan system, province of Västergötland, Sweden, during the autumn of 1970. They were placed 200 m apart in the same stream in September ($\varkappa$, 7.5×10^{-5}). After connecting the electrical current, several crayfish placed on the bottom of the stream as far as 1 m away from the neutral wire were completely paralysed and thus unable to move. After the current was switched off the animals usually recovered unless kept in the current for more than 15—30 min. Small fish of different kind passing through the electrical field (between the wires) all died immediately. In the autumn, 1971, in an attempt to prevent the plague from reaching into Norway, a double barrier of the same construction was placed in the River Vrangselven in southern Norway, close to the Norwegian-Swedish border. The attempt has so far been a complete success and the details will soon be published by HÅSTEIN and GLADHAUG (1973).

The double barrier was used permanently for about one year in River Tidan and is still (Jan. 1973) in use in River Vrangselven. Since the ice covers of both rivers were rather thin in the winter they did not cause any trouble. It was found in both cases that after a few months all crayfish (several hundred) had disappeared from the zone between the barriers although normal densities were maintained on both sides outside the zone. The most probable explanation is, that due to normal migration in the zone the animals finally reached the upper or lower electrical barrier. At the upper barrier they became paralyzed and either died or were brought back to safety by the water current and survived. Reaching the lower barrier they either succumbed or drifted paralyzed to the area downstream of the zone. It is of course possible that the electrical current in the water slightly affected crayfish over long distances, thus probably increasing their tendency to migrate.

The "frontier" of the crayfish plague spreading upstream is usually rather sharp and its position can be determined by observing the dead or dying crayfish and taking into consideration that, at summer temperatures, the animals die one to three weeks after infection. Thus, the barriers should be placed at a safe distance from this frontier, perhaps 1—2 kilometres away.

Apparently this kind of double barrier can effectively prevent migration of crayfish (and other water-living animals) from the infected area below the lower barrier up to the "healthy" water above. If the disease is intentionally introduced by means of infected crayfish to the water immediately below the lower barrier, the plague will spread rapidly downstream and very soon (in the summer normally in a few weeks) no live crayfish will exist below the barrier zone (this was done in River Vrangselven). Since the plague fungus will not survive very long, probably only a few weeks after the last crayfish has succumbed to the disease (UNESTAM 1969b), the necessary time for maintaining the barriers will be shortened by such a procedure. However, this time has to be determined by using healthy test crayfish in cages placed on the bottom on several places in the river, from the barriers and downstream. It is also important to examine any ditch or small stream merging downstream the barriers. If live crayfish are present there it will be necessary to infect such tributaries at the same time.

The empty barrier zone will also function as a buffer preventing terrestrial animals, such as minks and birds, from carrying diseased crayfish up to the uninfected water.

The method of forming a buffer zone by means of electrical barriers is in principle very similar to the calcium hydroxide method described by VALLIN (1936). But the present method is much more effective and possible to use under controlled conditions. Together with proper control of the movement of the disease frontier and intentional infection of the crayfish downstream the barriers this method may prove to be an important tool in halting the spread of the crayfish plague in European river systems.

The method might also be useful for controlling the migration of crayfish (or other water-living animals) for other reasons.

Acknowledgments

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References

ABRAHAMSSON, S. 1966. Dynamics of an isolated population of the crayfish *Astacus astacus* LINNÉ. Oikos 17(1): 96—107.

HÅSTEIN, T. and O. GLADHAUG. 1973. The occurrence of the crayfish plague in Norway and attempts to prevent further spread of the dissease. p. 181—184. *In* Abrahamsson, S. (Ed.) Papers from the First International Symposium on Freshwater Crayfish. Austria 1972.

MEYER-WAARDEN, P. F., I. HALSBAND and E. HALSBAND. 1965. Einführung in die Elektrofischerei. Heenemann, Berlin. 292 p.

NYBELIN, O. 1936. Untersuchungen über die Ursache der in Schweden gegenwärtig vorkommenden Krebspest. *Rep. Inst. Freshw. Res., Drottningholm* 9. 29 p.

SCHIKORA, F. 1916. Die Wiederbevölkerung der deutschen Gewässer mit Krebsen. J. Neumann, Neudamm. 195 p.

SELIGO, A. 1895. Bemerkungen über Krebspest, Wasserpest, Lebensverhältnisse des Krebses. *Z. Fisch.* 3(6): 247—261.

UNESTAM, T. 1969a. Resistance to the crayfish plague in some American, Japanese and European crayfishes. *Rep. Inst. Freshw. Res. Drottningholm* 49: 202—209.

— 1969b. On the adaptation of *Aphanomyces astaci* as a parasite. *Physiol. Plantar.* 22: 221—235.

VALLIN, S. 1936. Åtgärder mot kräftpestens härjningar. *Svensk. Fisk. Tidskr.* 45(9): 236—240. (In Swedish.)

Blood glucose in hatchery-reared Atlantic salmon (*Salmo salar* L.) following exercise

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I. Introduction

There have been many studies concerning the changes in carbohydrate metabolism in fish due to muscular activity (von BUDDENBROCK 1938, KIERMIER 1939, SECONDAT and DIAZ 1942, SECONDAT 1950, BLACK 1957a, b, c, NAKATANI 1957, PARKER and BLACK 1959, PARKER *et al* 1959, MILLER *et al* 1959, 1962, BLACK *et al* 1961, 1962, HEATH and PRITCHARD 1962, CAILLOET Jr 1964, 1967, DEAN and GOODNIGHT 1964, WENDT 1964a, b, 1965, 1967. HAMMOND and HICKMAN Jr 1966, STEVENS and BLACK 1966, BURROWS 1969). Muscle glycogen is rapidly mobilized by severe exercise in most investigated species. In salmonoids the activity always causes an accumulation of lactate both in the muscle and in the blood. At high water temperatures in the summer the rise in blood lactate in exercised Atlantic salmon is more pronounced than at low water temperatures in the winter (WENDT 1965).

The influence of exercise on blood sugar or blood glucose is contradictory. KIERMIER (1939) found that there was no significant increase in blood sugar with exercise. BLACK (1957a, b) did not find any increase immediately after exercise. In lake trout (*Salvelinus namaycush*) the blood-glucose level rose during recovery after exercise (BLACK 1957b). In rainbow trout there seemed to be a significant change only during the later part of recovery (BLACK 1957a, BLACK *et al.* 1961). However, SECONDAT (1950) found an increase in blood sugar in carp (*Cyprinus carpio*), as did DEAN and GOODNIGHT (1964) in *Ictalurus melas, Micropterus salmoides,* and *Pomoxis annularis* at 5°C and 20°C, but in *Lepomis macrochirus* only at 20°C and not at 5°C. HAMMOND and HICKMAN (1966) did not find any significant change during exercise in rainbow trout but a slight rise during recovery. Chinook salmon fingerlings (*Onchorhynchus tshawytscha*) subjected to fatigue test responded by an increase in plasma glucose (BURROWS 1969). Further information is to be found in the comprehensive study of CHAVIN and YOUNG (1970).

The aim of the present investigation was to get information about the

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blood glucose in hatchery-reared Atlantic salmon after exercise. Together with earlier findings concerning blood lactate, muscle and liver glycogen (WENDT 1965, 1967), these results could serve as a tool in studying the influences of handling, transportation and release on hatchery-reared Atlantic salmon.

II. Materials and Methods

The experiments were carried out at the Salmon Research Laboratory, Älvkarleö, Sweden, during 1966, 1967, 1968 and 1969. Depending on the time of the year, the fish used were 1-year-old to 2-year-old hatchery-reared Atlantic salmon (*Salmo salar* L). from the River Lule älv. All the fish were held in 11.5 m^2 troughs, and they were fed on a raw diet[1] with the exception of one group used in September 1969 as a comparison, which was fed on pellets.[2] The food consumption changed with the water temperature, but the food was always presented in surplus.

Before testing, the fish were transferred to covered dark basins of flowing water in which they were kept without feeding for 18—22 hours. One at a time the fish were chased by hand in a hatchery trough (0.9 m^2), and left there to recover without feeding. Ordinary hatchery water mostly saturated with oxygen was supplied to the troughs and basins.

Individual fish were sampled before exercise, immediately after 15 minutes of exercise, and at different times during recovery. The method of sampling blood was the same as that described by WENDT (1965), but for deproteinization perchloric acid (PCA) was used instead of trichloracetic acid (TCA). 0.1 ml of blood was ejected into 2 ml of PCA buffered with glycine to pH 2.7, and centrifugated at 2000 r.p.m. for 10 minutes. The protein-free fluid was then analysed for glucose, using the reagent GLOX (*glucose oxidase*) manufactured by KABI.[3]

III. Results

Methodology

In order to ensure an unexercised condition before exercise, it was necessary to keep the fish undisturbed for 18—22 hours in dark basins. Without this treatment, higher blood-lactate values were recorded (WENDT 1965, unpubl.). The influence of confinement did not significantly change the

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[1] 20 % liver, 30 % spleen, 20 % prawns, 24 % small cod, 5 % yeast, 1 % salt.

[2] 48 % protein, 20 % cereals.

[3] KABI AB, Box 317, S-104 25 Stockholm, Sweden.

Table I. Blood glucose in hatchery-reared *Salmo salar* L. sampled by heart puncture and by severing the tail.

		Blood glucose mg %	
Exercise (min)	Recovery (hours)	Heart	Tail
0	0	42.6 ± 3.3	49.5 ± 13.0
15	0	48.4 ± 12.9	65.2 ± 18.1
15	2	80.6 ± 26.7	73.6 ± 19.4
15	15	55.1 ± 28.3	93.0 ± 41.1

blood-glucose levels. The mean value of a group sampled after confinement in a basin was 37.4 ± 9.6 mg per cent. Another group sampled immediately after having been taken out of the hatchery trough had a mean value of 28.3 ± 6.8 mg per cent. There was a tendency, however, for lower levels to occur in the absence of the above-mentioned treatment.

In this way it was also possible to avoid increasing blood-glucose values due to feeding. On the other hand, starvation might cause slowly declining values. However, fasting for 20 hours did not significantly change the level, this being 44.9 ± 7.9 mg per cent before starvation compared with 42.9 ± 7.1 mg per cent after. In another experiment, starvation for 40 hours caused a slight decrease from 52.7 ± 6.5 mg per cent to 44.1 ± 6.2 mg per cent, but again the difference was not significant.

Heart puncture was used as sampling technique to avoid interference with tissue fluid. A comparison between samples obtained by heart puncture and by severing the tail, collecting the free-flowing blood in graduated micro-pipettes, showed differences in recorded glucose values (Table 1). With very few exceptions, sampling was completed within 1 minute.

As the experiments were performed during different times of the year it was necessary to get information about seasonal changes in the normal blood-glucose levels. As shown in Fig. 1, there was a variation in normal blood-glucose levels between different times of the year. The values were lowest during October and November, and thereafter they increased again until March. Values from April, through July are excluded in this report as the picture in April, especially, seemed to be very complicated, exhibiting a great variation between different groups and between individual fish within the same group.

Behaviour during exercise

All the fish were considered to be in an unexercised condition before exercise. After 2—5 minutes of exercise the first sign of fatigue was seen.

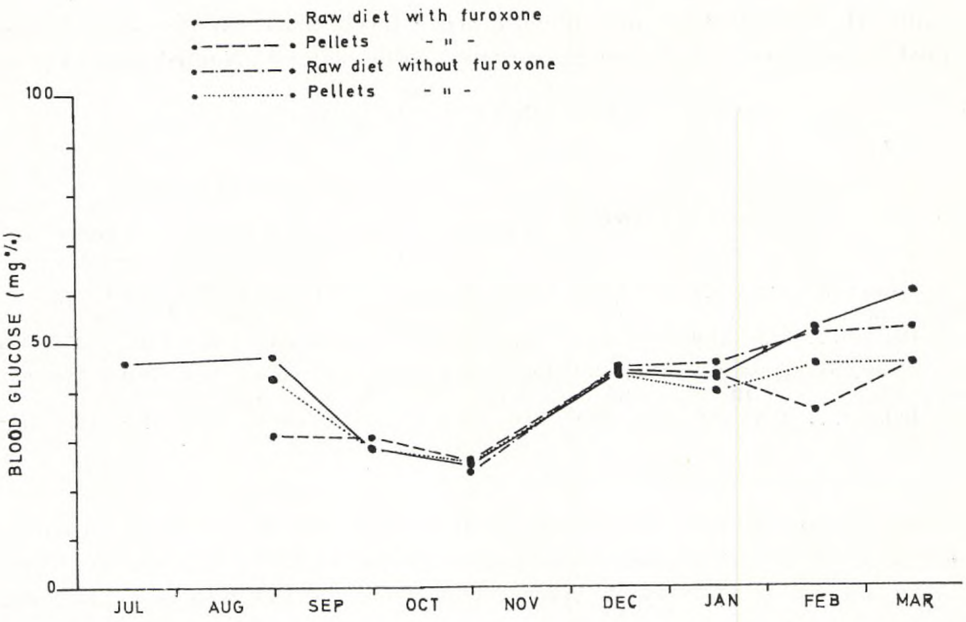

Fig. 1. Blood-glucose levels in hatchery-reared *Salmo salar* L. during their second summer, autumn, and winter.

The stimulated fish seemed to disregard the stimulation. If left alone they would stop swimming and rest on the bottom. At the end of the exercise the fish were, almost without exception, exhausted, and they remained motionless in the trough until sampled. In this investigation, however, no sign of mortality appeared as reported by WENDT (1967) who found 22 out of 73 fish from different groups to be moribund when sampled during recovery.

Unexercised, exercised and recovery states

Temp. 15°C. August 1967

The unexercised average level was 41.9 ± 7.0 mg per cent. This increased to 58.4 ± 13.4 mg per cent at the cessation of exercise. After 2 hours of recovery the blood glucose had reached an average level of 105.3 ± 32.3 mg per cent, but thereafter it decreased. Fifteen hours after exercise the average value was 79.0 ± 33.9 mg per cent and after 20 hours of recovery it was 65.7 ± 32.3 mg per cent (Table II; Fig. 2).

Temp. 15°C. September 1969

The group used this year were fed on pellets instead of a raw diet (Table III). The unexercised average level was about the same as that for the

Table II. Body weights and blood-glucose levels after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1967. Temp. 15°C. $(\mathrm{SD} = \pm \frac{S(x - \bar{x})^2}{n - 1})$

		Unexercised	Exercised 15 min	Recovery from exercise				
				2 hours	4 hours	6 hours	15 hours	20 hours
Body Weight (g)	Mean ± SD	47.2 ± 14.4	52.4 ± 21.9	52.0 ± 10.9	51.3 ± 20.6	52.5 ± 17.9	54.9 ± 20.7	53.5 ± 14.9
	(n)	(10)	(10)	(9)	(10)	(10)	(8)	(7)
	Range ...	33.0—81.0	35.0—99.5	34.5—70.5	33.5—88.5	33.5—85.0	34.5—87.5	35.0—75.0
Blood Glucose (mg %)	Mean ± SD	41.9 ± 7.0	58.4 ± 13.4	105.3 ± 32.3	88.8 ± 21.2	86.0 ± 18.0	79.0 ± 33.9	65.7 ± 32.3
	(n)	(10)	(10)	(9)	(10)	(10)	(8)	(7)
	Range ...	34.9—48.9	45.0—71.8	73.0—137.6	67.6—110.0	68.0—104.0	45.2—113.0	33.4—98.0

former group or 42.5 ± 3.0 mg per cent. Fifteen minutes of hard muscular exercise raised the average blood-glucose value to 48.4 ± 12.9 mg per cent. After 1 hour of recovery the average level had increased to 71.5 ± 13.2 mg per cent, and after 2 hours of recovery it had reached 80.6 ± 26.7 mg per cent. Fifteen hours after exercise the average value had decreased to 55.1 ± 28.3 mg per cent, but the level was still above that recorded before exercise.

Temp. 6.5°C. October 1966

As shown in Table IV and Fig. 2, the average for unexercised fish was 35.5 ± 8.7 mg per cent, which increased to 40.0 ± 5.2 mg per cent after 15 minutes of exercise. After 2 hours of recovery the average value was 72.0 ± 8.8 mg per cent. Thereafter the values decreased, but after 15 hours of recovery the average level 62.8 ± 14.7 mg per cent was still above that of the unexercised fish.

Temp. 0.2°C. March 1967; February—March 1968

In March 1967 hard muscular work for 15 minutes raised the blood glucose from an average level of 61.3 ± 6.3 mg per cent before exercise to an average level of 69.4 ± 12.6 mg per cent after exercise. In February—March 1968 the values were 52.7 ± 6.5 mg per cent and 61.9 ± 16.2 mg per cent respectively. The average level still increased during the recovery. In 1967 the average level 15 hours after exercise was 91.2 ± 16.1 mg per cent and 20 hours after exercise 123.1 ± 13.1 mg per cent. In 1968 the average level after 15 hours of recovery was 86.5 ± 34.2 mg per cent (Tables V and VI; Fig. 2). In contrast to the findings in August, September and October, there appeared in March no decrease in blood glucose within the recovery time investigated.

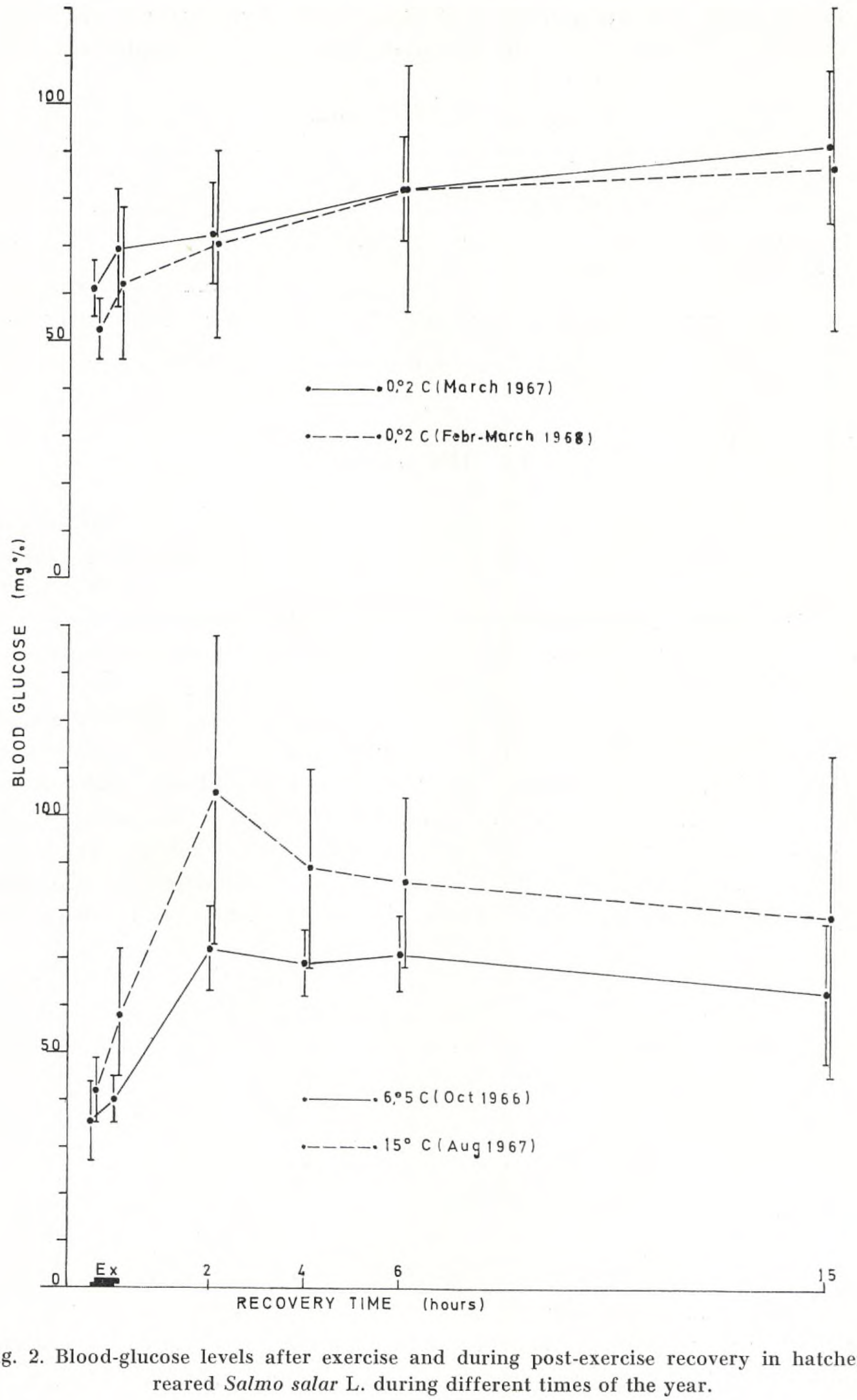

Fig. 2. Blood-glucose levels after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. during different times of the year.

Table III. Body weights and blood-glucose levels after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. September 1969. Temp. 15°C. $(\mathrm{SD} = \pm \frac{S(x-\bar{x})^2}{n-1})$

				Recovery from exercise		
		Unexercised	Exercised	1 hour	2 hours	15 hours
Body Weight (g)	Mean ± SD ..	14.1 ± 0.9	14.5 ± 1.1	16.6 ± 2.7	14.7 ± 0.9	14.5 ± 0.6
	(n)	(5)	(5)	(7)	(8)	(6)
	Range	13.2—15.2	13.6—15.7	13.1—15.3	13.2—15.9	13.5—15.2
Blood Glucose (mg %)	Mean ± SD ..	42.5 ± 3.0	48.4 ± 12.9	71.5 ± 13.2	80.6 ± 26.7	55.1 ± 28.3
	(n)	(5)	(5)	(7)	(8)	(6)
	Range	39.6—46.6	30.6—67.0	50.0—87.4	44.8—113.4	20.4—119.5

IV. Discussion

Blood-sugar levels of teleosts show great variations not only between species but also within a certain species (CHAVIN 1964). There are relations between the habits of the species and the blood-sugar levels; low levels occur in sluggish forms and high levels in active forms (GRAY and HALL 1930, FUKUDA 1958). Certain environmental factors have long been known to affect the blood-sugar values. MCCORMICK and MACLEOD (1925), KIERMIER (1939) in her comprehensive study of carps, DEAN and GOODNIGHT (1964), AMLACHER (1957), NACY *et al.* (1964) and UMMINGER (1969) found an influence from temperature. MCCORMICK and MACLEOD (1925), SHELL (1961) and NACY *et al* (1964) discussed the influence of the season of the year. Feeding and starvation are well known to affect blood-sugar values (FALKMER 1961, PHILLIPS 1961, AMLACHER 1957, PICKFORD *et al.* 1969). Acclimatization to aquaria influences the blood sugar (MCCORMICK and

Table IV. Body weights and blood-glucose levels after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. October 1966. Temp. 6.5°C. $(\mathrm{SD} = \pm \frac{S(x-\bar{x})^2}{n-1})$

				Recovery from exercise			
		Unexercised	Exercised 15 min	2 hours	4 hours	6 hours	15 hours
Body Weight (g)	Mean ± SD ..	29.6 ± 5.2	28.8 ± 3.5	31.3 ± 7.2	32.9 ± 2.7	29.3 ± 4.3	27.7 ± 2.9
	(n)	(10)	(10)	(10)	(6)	(6)	(8)
	Range	21.0—40.5	23.5—33.5	24.5—47.0	30.0—37.0	25.0—35.5	26.5—31.0
Blood Glucose (mg %)	Mean ± SD ..	35.5 ± 8.7	40.0 ± 5.2	72.0 ± 8.8	69.3 ± 6.7	71.1 ± 7.9	62.8 ± 14.7
	(n)	(10)	(10)	(10)	(6)	(6)	(8)
	Range	26.8—44.3	37.7—45.2	80.9—63.2	62.6—76.0	63.3—79.0	48.1—77.5

Table V. Body weights and blood-glucose levels after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. March 1967. Temp. 0.2°C. (SD $= \pm \frac{S(x-\bar{x})^2}{n-1}$)

				Recovery from exercise			
		Unexer-cised	Exercised 15 min	2 hours	6 hours	15 hours	20 hours
Body Weight (g)	Mean ± SD	30.4 ± 5.4	31.6 ± 3.4	35.1 ± 4.9	34.5 ± 4.7	35.4 ± 4.5	32.9 ± 5.9
	(n)	(10)	(10)	(10)	(10)	(10)	(6)
	Range ...	25.0—42.0	27.0—37.5	25.0—40.0	28.0—42.0	30.0— 43.5	26.0— 42.5
Blood Glucose (mg %)	Mean ± SD	61.3 ± 6.3	69.4 ± 12.6	72.6 ± 10.8	82.0 ± 11.3	91.2 ± 16.1	123.1 ± 13.1
	(n)	(10)	(10)	(10)	(10)	(10)	(6)
	Range ...	55.0—67.6	56.8—82.0	61.8—83.4	70.7—93.3	75.1—107.3	110.0—136.2

MacLeod 1925). Another important factor is asphyxiation hyperglycaemia (Scott 1921, Amlacher 1957). The influence of exercise is contradictory (*cf.* p. 1). Chavin (1964) emphasized the effects of stress. Differences between analytical procedures such as glucose oxidase technique or reducing methods are well known (Falkmer 1961, Nacy *et al.* 1964). With this background it is difficult to establish a normal blood-sugar level in any species. I agree with the opinion of Chavin (1964, p. 63) that "the various published data dealing with fishes is of utility only as a guide to the introductory evaluation of a given problem, and should not be considered valid until confirmed by a series of precisely controlled and repeatable experiments under standardized conditions in a given laboratory".

The present investigation was performed under standardized hatchery conditions common to the fish since their hatching. Care was taken to avoid effects of stress before the experiments started. No hyperglycaemic effect

Table VI. Body weights and blood-glucose levels after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. February—March. 1968. Temp. 0.2°C. (SD $= \pm \frac{S(x-\bar{x})^2}{n-1}$)

				Recovery from exercise		
		Unexercised	Exercised 15 min	2 hours	6 hours	15 hours
Body Weight (g)	Mean ± SD ..	43.5 ± 9.5	52.5 ± 11.3	46.5 ± 7.0	48.0 ± 7.5	47.0 ± 6.0
	(n)	(10)	(10)	(10)	(10)	(10)
	Range	31.5—58.5	36.5—70.0	36.5— 59.5	36.5— 57.0	39.0— 58.5
Blood Glucose (mg %)	Mean ± SD ..	52.7 ± 6.5	61.9 ± 16.2	70.4 ± 19.8	82.1 ± 26.1	86.5 ± 34.2
	(n)	(10)	(10)	(10)	(10)	(10)
	Range	46.0—59.2	46.8—89.0	44.4—109.0	51.8—130.0	36.0—156.0

was found from keeping the fish in dark basins before experimentation started. The experiments were also performed at about the same time every day during the investigation period.

The normal blood-glucose levels of hatchery fish investigated during July—March showed a seasonal variation. The lowest values with a small variation between different groups appeared in the autumn during October—November, and the highest values appeared during March, but then with a greater variation between different groups. PAVLOW (1939) reported a rise in the blood-sugar level with the maturation of the sexual products. NACY *et al.* (1964) presumed that temperature and reproductive changes together were responsible for the decrease found by them in *Opsanus tau*. PICKFORD *et al.* (1969) found no correlation between high blood sugar and sexual maturity in *Fundulus heteroclitus*. As all the salmon used in our experiments were only 1 1/2 years old and were juvenile ones, all the precocious males were excluded, the low levels obtained in October—November could hardly be associated with the reproductive cycle, although salmon normally spawn at that time of the year. The increase in blood glucose during the winter, ending up in a very complex picture in April, may be correlated to an increased osmoconcentration due to the low water temperature. SCHOLANDER *et al.* (1957) reported such an increase in osmotic concentration in arctic fish. UMMINGER (1969) found a striking increase in serum glucose in supercooled *Fundulus heteroclitus*. At the same time there was a depletion of liver glycogen. In salmon, however, the situation is far more complicated. In nature the smoltification of young salmon usually takes place during the second spring. This transformation is associated with marked changes in morphology, chemical composition, physiological and biochemical function and behaviour (HOAR 1953, FONTAINE 1954), and may well be responsible for an increase in blood glucose apart from the effect of low water temperature.

This theory is supported by experiments performed in May 1970 at the Fisheries Research Board of Canada, St. Andrews, New Brunswick, Canada. Two comparable groups (B and C) of unexercised Atlantic salmon smolt showed increasing blood glucose levels from May 4 to May 19. The mean value changed from 63.6 ± 21.9 (B) and 66.1 ± 17.5 (C) mg per cent to 112.0 ± 30.3 and 96.7 ± 25.4 mg per cent, respectively. At the same time the temperature was rising from 11.0°C to 14.2°C. When on May 19 group C was transferred to full sea water, there seemed to be a sudden drop in the blood-glucose level. On May 21 the value was 45.5 ± 15.7 mg per cent. Group B, still in freshwater during the same time, further increased its blood-glucose value to 122.4 ± 48.7 mg per cent (WENDT and SAUNDERS, 1972). On May 27 and 28, 1970, the mean level recorded in natural smolt migrating downstream in the Miramichi River at a water temperature of 14.0°C was 60.6 ± 13.8 mg per cent. The hatchery-reared smolt were 2.5 cm bigger than the natural smolt (WENDT and SAUNDERS, 1972). The difference in blood glucose in hatchery-reared and natural smolt might be an effect of a wrong timing of the smoltification in the hatchery fish in relation to smoltification in the natural fish.

In this investigation, exercise for 15 minutes always caused a rise in blood glucose (*cf.* p. 1). The increase was slighter in October, March, and February than in August and September. During the first two hours of recovery the average levels still increased. The highest levels were obtained in August. The same was shown also for blood lactate (WENDT, 1965). Evidently water temperature plays an important part. In August and October the levels decreased but after 15 hours of recovery the mean values were still about double those recorded before the exercise. In February and March, however, there was no decrease at all. On the contrary, the blood glucose increased all the time during 15 hours of recovery. Again, a wrong timing of the smoltification could be the reason for the observed difference.

V. Summary

Unexercised hatchery-reared Atlantic salmon sampled during their second summer, autumn and winter showed seasonal changes in blood glucose. The lowest levels appeared in October—November, the highest in February—March.

Exercise for 15 minutes at seasonally-differing water temperatures always caused a rise in blood glucose. After a further increase during the first two hours of the recovery period, a decline was observed in August, September and October. In February and March the blood-glucose level increased all the time during 15 hours of recovery.

The suggestion is made that a wrong timing of the smoltification may be the cause of the changed blood-glucose picture after exercise in February and March as compared with that in August, September and October.

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VII. References

AMLACHER, E. 1957. Der Blutzucker normaler an infektioser Bauchwassersucht erkrankten Karpfen (K_2). *Arch. Fish. Wiss.* 8(1/2): 12—31.

BLACK, E. C. 1957a. Alternations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. I. Kamloops trout, *Salmo gairdneri. J. Fish. Res. Bd. Can.* 14(2): 117—134.

— 1957b. Alternations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. II. Lake trout, *Salvelinus namaycush. J. Fish. Res. Bd. Can.* 14(4): 645—649.

— 1957c. Alternations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. III. Sockeye salmon, *Oncorhyncus nerka. J. Fish. Res. Bd. Can.* 15(6): 807—814.

— A. C. ROBERTSON, and R. R. PARKER. 1961. Some aspects of carbohydrate metabolism in fish. p. 89—124. *In* Martin, A. W. (Ed.) Comparative physiology of carbohydrate metabolism in heterothermic animals. Univ. Wash. Press.

— A. ROBERTSON CONNOR, K.-C. LAM, and W.-G. CHIU. 1962. Changes in glycogen, pyruvate, and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. *J. Fish. Res. Bd. Can.* 19(3): 409—436.

VON BUDDENBROCK, W. 1938. Beobachtungen über das Sterben gefangener Seefische und über den Milchsäuregehalt des Fishblutes. *Rapp. Cons. Explor. Mer.* 101 (IV, 2): 1—7.

BURROWS, R. 1969. The influence of fingerling quality on adult salmon survivals. *Trans. Amer. Fish. Soc.* 98(4): 777—784.

CAILLOUET, Jr., C. W. 1964. Blood lactic acid concentration of unexercised and exercised mature carp in winter and summer. *Iowa St. J. Sci.* 38: 309—322.

— 1967. Hyperactivity, blood lactic acid and mortality in channel catfish. *Res. Bull. Iowa St. Univ. Sci. Tech.* 551: 899—915.

CHAVIN, W. 1964. Sensitivity of fish to environmental alterations. *Proc. 7th Conf. Great Lakes Res. Publ.* 11: 54—67.

CHAVIN, W. and J. E. YOUNG. 1970. Factors in the determination of normal serum glucose levels of goldfish, *Carassius auratus* L. *Comp. Bioch. Physiol.* 33: 629—653.

DEAN, J. M. and C. J. GOODNIGHT. 1964. A comparative study of carbohydrate metabolism in fish as affected by temperature and exercise. *Physiol. Zool.* 37: 280—299.

FALKMER, S. 1961. Experimental diabetes research in fish. *Acta endocr.* 37, *Suppl.* Copenh. 59.

FONTAINE, M. 1954. Du déterminisme physiologique des migrations. *Biol. Rev.* 29: 390—418.

FUKUDA, H. 1958. On the blood sugar of freshwater fishes *Bull. Jap. Soc. sci. Fish.* 23(12): 782—784.

GRAY, I. E. and F. G. HALL. 1930. Blood sugar and activity in fishes with notes on the action of insulin. *Biol. Bull.* 58: 217—223.

HAMMOND, B. R. and C. P. HICKMAN, Jr. 1966. The effect of physical conditioning on the metabolism of lactate, phosphate, and glucose in rainbow trout *Salmo gairdneri. J. Fish. Res. Bd. Can.* 23(1): 65—83.

HEATH, A. G. and A. W. PRITCHARD. 1962. Changes in metabolic rate and blood lactic acid of bluegill sunfish, *Lepomis macrochirus,* RAF. following severe muscular activity. *Physiol. Zool.* 35: 323—329.

HOAR, W. S. 1953. Control and timing of fish migration. *Biol. Rev.* 28: 437—452.

KIERMIER, A. 1939. Über den Blutzucker des Süsswasserfishe. *Z. vergl. Physiol.* 27: 460—491.

McCormick, N. A. and J. J. R. MacLeod. 1925. The effect on the blood sugar of fish of various conditions, including removal of the principal islets (isletectomy). *Proc. Roy. Soc.* (*B.*) 98: 1—29.

Miller, R. B., A. C. Sinclair, and P. W. Hochachka. 1959. Diet, glycogen reserves and resistance to fatigue in hatchery rainbow trout. *J. Fish. Res. Bd. Can.* 16(3): 321—328.

— and F. Miller. 1962. Diet, glycogen reserves and resistance to fatigue in hatchery rainbow trout. Part II. *J. Fish. Res. Bd. Can.* 19(3): 365—375.

Nacy, P. F., M. L. Moule, and J. E. Schuh. 1964. The normal blood sugar of the toadfish. *Canad. J. Biochem. Physiol.* 42: 225—232.

Nakatani, R. 1957. Changes in inorganic phosphate and lactate levels in blood plasma and muscle tissue of adult steelhead trout after strenuous swimming. *Tech. Rep. School of Fish., Univ. Wash.* 30.

Parker, R. R. and E. C. Black. 1959. Muscular fatigue and mortality in troll-caught chinook salmon (*Onchorhyncus tshawytscha*). *J. Fish. Res. Bd. Can.* 16(1): 95—106.

— E. C. Black and P. A. Larkin. 1959. Fatigue and mortality in troll-caught Pacific salmon (*Oncorhyncus*). *J. Fish. Res. Bd. Can.* 16(4): 429—448.

Pavlow, V. A. 1939. Hemoglobin and sugar content in the blood of some fresh water fishes (a comparative study). *Bull. Inst. Freshw. Fish.* 21: 120—142. (In Russian with English summary.

Phillips, A. M. 1961. Effect of water temperature and diet on the blood glucose of brook trout. *Progr. Fish-Cult.* 23(2): 66—69.

Pickford, G. E., F. B. Grant and B. L. Umminger 1969. Studies on the blood serum of the euryhaline cyprinodont fish, *Fundulus heteroclitus,* adapted to fresh and salt water. *Trans. Conn. Acad. Arts Sci.* 43: 25—70.

Scholander, P. F., L. van Dam, J. W. Kanwisher, H. T. Hammel and M. S. Gordon. 1957. Supercooling and osmoregulation in arctic fish. *J. cell. comp. Physiol.* 49: 5—24.

Scott, E. L. 1921. Sugar in the blood of the dog-fish and of the sand shark. *Amer. J. Physiol.* 55: 349—354.

Secondat, M. and D. Diaz. 1942. Recherches sur la lactacidémie chez le poisson d'eau douce. *C. R. Acad. Sci. Paris,* 215: 71—73.

— 1950. Influence de l'exercice musculaire sur la valeur de la glycémie de la carpe (*Cyprinus carpio* L.). *C. R. Acad. Sci. Paris,* 231: 796—797.

Shell, E. W. 1961. Chemical composition of blood of smallmouth bass. *Res. Rep. U.S. Fish. Serv.* 57. 36 p.

Stevens, E. D. and E. C. Black. 1966. The effect of intermittent exercise on carbohydrate metabolism in rainbow trout, *Salmo gairdneri. J. Fish. Res. Bd. Can.* 23(4): 471—485.

Umminger, B. L. 1969. Physiological studies on supercooled Killifish (*Fundulus heteroclitus*) II. Serum organic constituents and the problem of supercooling. *J. exp. Zool.* 172: 409—423.

Wendt, C. 1964a. Blodlaktat, muskel- och leverglykogen hos 2-somrig till 2-årig lax (*Salmo salar* L.) före och efter ansträngning. *Medd. Laxforskningsinstitutet* (*Swedish Salmon Res. Institute*) (1), *bil.* 10. 6 pp. (In Swedish with English summary.)

— 1964b. Influence of low temperature on the blood lactate level in *Salvelinus fontinlais* after exercise. *Rep. Inst. Freshw. Res., Drottningholm,* 45: 206—210.

— 1965. Liver and muscle glycogen and blood lactate in hatchery-reared *Salmo salar* L. following exercise in winter and summer. *Rep. Inst. Freshw. Res., Drottningholm,* 46: 167—184.

— 1967. Mortality in hatchery-reared *Salmo salar* L. after exercise. *Rep. Inst. Freshw. Res., Drottningholm,* 47: 98—112.

— and R. L. Saunders. 1972. Manuscript prepared for the International Atlantic Salmon Symposium. September 20—22, 1972. St Andrews, N. B. Canada.

Reports from the Institute of Freshwater Research, Drottningholm

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