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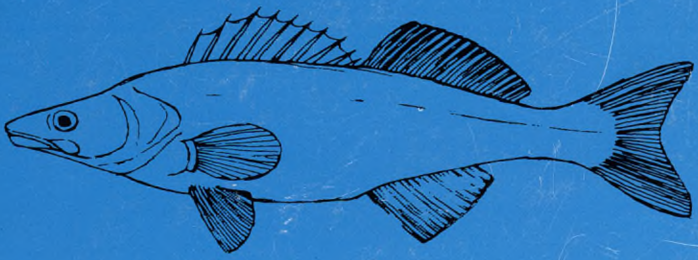

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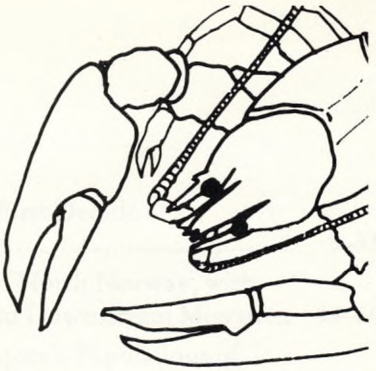

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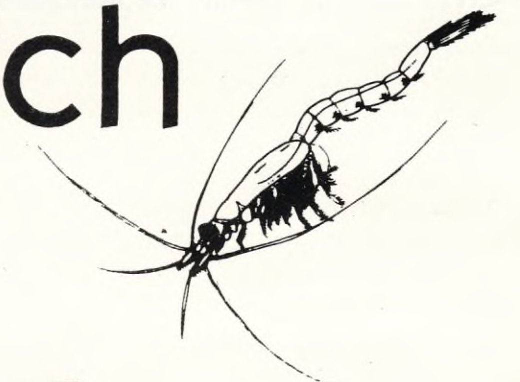

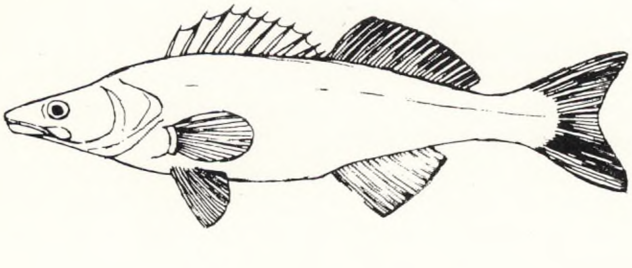

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Contents

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Crustacean Plankton and Fish during the First Decade of a Subalpine, Man-made Reservoir

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Abstract

The Nesjø reservoir, 729 m a.s.l. in central Norway, was made in 1970 by impounding 38.7 km^2. It was studied in 1970–83, with parallel sampling in the adjacent Essand reservoir, regulated since 1940. The reservoirs are oligotrophic and polymictic with maximum temperatures of 11–13°C. In Nesjø the biomass of crustacean plankton was at its maximum in 1970. Chironomids predominated the macrobenthos and were eaten in largest quantities by fish in 1972–74. Brown trout, burbot and Arctic char predominated in succession net catches in the littoral zone. Until 1976, the biomass caught per net was 4–6 times higher than normal in similar Norwegian lakes. Growth rates close to the maximum known for any salmonid were recorded in 1972. Chironomids and cladocerans were the most important prey for the fish. Compared to Essand, the Nesjø cladocerans were larger, carried more eggs and represented a larger biomass. The Nesjø fish took more food, were larger and fatter, grew better and gave higher catches in weight per unit effort. These differences became less distinct, but were still noticeable by the end of the decade. The study gives additional results on the sex ratios, maturing, migrations, diet, size of food rations, seasonal growth cycles, population number, biomass and food conversion efficiencies of the fish, and on the interactions between planktonic crustaceans and Arctic char.

Introduction

Hydroelectric reservoirs have become common in Scandinavia. In Norway they represent 39 % of the total area of fresh waters (Statistisk Sentralbyrå 1984). The biology of Scandinavian reservoirs has been studied for more than 50 years. Some of the many papers which could be mentioned are those of Axelson (1961 a, 1961 b), Lötmarker (1964) and Jensen (1982) on crustacean plankton, Grimås (1961, 1962) and Jensen (1982) on benthic fauna, and Dahl (1932), Nilsson (1961, 1964) and Aass (1969, 1970, 1984) on fish. A review of the effects of water regulations on freshwater invertebrates was recently presented by Nøst et al. (1986).

Since 1970 several reservoirs have been made in Norway by impounding valleys where no lake existed. Research has been carried out on fish in some of these (Bergan 1985, Koksvik 1985), but no long-term studies have been performed on any Scandinavian reservoir of this sort. This study deals with the crustacean plankton and fishes in the completely man-made Nesjø reservoir throughout the first 13 years of its existence. Major scopes were the successions of the present species of fish, their abundance, growth and food. Important aspects were the quality and lasting yield of salmonids in such a reservoir compared with impounded lakes, where the experiences in Scandinavia have been mainly discouraging (Aass and Borgstrøm 1987). Crustacean plankton successions have never been studied in Scandinavian reservoirs. The cladocerans were expected to become important prey for the present Arctic char, *Salvelinus alpinus* (L.). The situation made it possible to study their interactions with varying quantities and sizes of char. The experiences from the Nesjø reservoir are hoped to contribute to the future mangement of boreal man-made lakes.

The benthic fauna of Nesjø have only been sampled twice, but can in part be evaluated from the diet of the fish. Some results from studies of

Fig. 1. The Essand-Nesjø reservoirs, their location and the pre-impoundment system. Depth contours in 7 m intervals, permanent stations for sampling hydrographic data and plankton (stars), transects along which additional plankton sampling took place in 1979, primary stretches for fishing with bottom nets (hatched) and places where tagged char were released (arrows).

fish have been published (Jensen 1971, Haabesland 1973, Koksvik 1974). Since then, all age determinations of fish have been redone and all data recalculated. The efficiency of the gillnets used in the Nesjø study for Arctic char and burbot, *Lota lota* (L.), has been analyzed (J. W. Jensen 1984, 1986). Data on the seasonal growth cycles and the food of the salmonids in 1972 have been published separately (Jensen 1985 a). These data made it possible to predict new limits for the growth of brown trout (*Salmo trutta* L.) and Arctic char (Jensen 1985 b).

The Essand-Nesjø reservoirs

The reservoirs are located in Tydalen in the county of Sør-Trøndelag in central Norway, at 63°N and 12°E, close to the border of Sweden and just below the tree line (Fig. 1). Their catchment area of 696 km^2 is mainly composed of strongly altered Cambro-Silurian–sedimentary rocks and granite (Holtedahl 1960).

The original Essand lake covered an area of 18 km^2 and had a maximum depth of 23 m. About 1/3 of the lake was no deeper than 3 m.

During 1940–47 the water level was gradually increased from 722.4 to 729 m a.s.l. and the surface area to 27.3 km^2 (Fig. 1). The reservoir was more or less full in summer and most often drained to its original level during the winter. The land that was flooded around Essand was similar in quality to that subsequently inundated by Nesjø. Its bottom sediments are a mixture of fine-grained sand and peat transported from the impounded zone. This zone is composed of sandbanks, stretches of stones and peat deposits.

In 1970 a dam was built 14 km downstream across the river Nea, forming the Nesjø reservoir with a volume of 470 millions m^3 (Fig. 1). The area flooded consisted of: bog 22.9, birch forest 8.5, grazing land 1.9, other vegetation 1.6, rivers 2.8 and tarns 1.0 km^2. Birch trees and scrub were cut and burned. At highest water level the 38.7 km^2 Nesjø reservoir consists of a 10 km long, narrow basin increasing in depth to 30 m at the dam, a wide main basin 15–20 m in depth and a shallower channel connecting it to Essand. The corresponding depth at the sill between Essand and Nesjø, again represented by the original outlet of 15–20 m width, is 6.6 m.

Together, the two reservoirs cover 66 km^2, representing the 13th largest area of fresh water in Norway. The mean depth in both reservoirs is 12 m. The often strong westerly winds cause heavy erosion along the shores. Sand and peat are transported to deeper water. Submersed macrophytes do not live in the reservoirs. A patchy cover of various terrestrial plants exists above 726 m.

Three species of fish, brown trout, Arctic char and burbot, were present in the original Essand lake. The salmonids were caught in large numbers. Their usual individual weight was 400–500 g (Sivertsen 1943). Both species fed mainly on bottom animals, *Gammarus lacustris* L., Lymnaeidae, *Pisidium*, and larvae of Trichoptera and Ephemeroptera. In late September and October the trout ate some *Bythotrephes longimanus* Leydig and the char some *Daphnia galeata* Sars. In 1950 *G. lacustris* and Lymnaeidae had completely disappeared from the diet of the fish. The char, which then represented more than 90 % of the catches, in late summer ate mainly *D. galeata*, some Trichoptera larvae, a few *Pisidium* and Planorbidae (Sivertsen 1950).

The same species of fish also lived in tarns pre-existing Nesjø. The impounded rivers included excellent brown trout habitats. In 1947 and the following two years large numbers of char left the Essand reservoir during draining periods (Sivertsen 1950). In 1970 char were only occasionally found below the Essand dam. Minnow (*Phoxinus phoxinus* L.), probably accidentally introduced, was recorded in the Nea tributary in 1974 (Koksvik and Langeland 1975). They have spread to other tributaries, but we have never observed them in the reservoir nor found them in the stomachs of other fish.

Methods and material

The study took place from 1970 to 1983. Crustacean plankton and fish were sampled in the ice-free period 4–6 times a year in 1972–74 and in 1979, twice in 1970–71 and 1977, and once in the remaining years, except for 1978 and 1980. In a few cases parallel data from Essand or plankton samples from Nesjø are lacking owing to bad weather.

Physical and chemical measurements

Water samples were taken at a permanent station in each reservoir (Fig. 1) using a Ruttner sampler with a built-in thermometer. Oxygen concentration was determined by the unmodified Winkler method. pH was measured in the field using a "Hellige" comparator. Specific conductivity as mSm^{-1} at 25°C was measured in field. Total and calcium hardness were determined by Edta-titration (Standard Methods 1965). Secchi depth was read on a 20 cm diameter disc, and colour was observed with the disc at half this depth. Temperature and water quality records are supported by data presented by Heggstad (1974, 1980).

Crustacean plankton

Planktonic crustaceans were sampled by vertical net hauls from bottom to surface. A Wagler normal net with a mouth diameter of 56.6 cm (Schwoerbel 1966) was used in 1970–72. Later a smaller net with a mouth diameter of 29.0 cm was used. Both nets were 100 cm in length, and made of nylon cloth with a mesh size of 90 μm. To make them more representative, the numbers caught by the Wagler normal net and the smaller net were multiplied by 3.2 and 2.0, respectively. The efficiency of the nets was tested on 10 September 1975. Using a 25 l Schindler trap (Schindler 1969) fitted with a sieve of mesh size 45 μm, five units were taken at each metre down to a depth of 17 m. Ten replicate vertical hauls were taken with both nets from a depth of 17 m. A net factor of 2.0, with confidence limits of 1.8 and 2.3 ($P<0.05$), was found for sum Crustacea collected with the smaller net. The net factor for the different species fell within the same range. Precision increased significantly with increasing numbers and decreased with increasing clumping. For the Wagler normal net the factor for sum Crustacea was 3.2. In tests done previously in fresh waters the variance of the plankton has not been separated from the variance of the method. All variance has been related to the net method, which is a main reason for the varying net factors obtained. The only reliable figures given by such tests are the overall mean net factors. For nets comparable to my small one, the following means have been found: 1.7 (Patalas 1954), 1.8 (Prepas and Rigler 1978), 1.9 (Jensen 1982), and above certain density limits 2.0 (Kankaala 1984).

On each occasion in 1979 ten hauls spread at equal distances along a transect of 10 km were taken in each reservoir (Fig. 1). On all other occasions two or three replicate hauls were taken at the permanent stations.

Mean number and confidence limits ($P<0.05$) of the 1979 samples were calculated by lg $(x+1)$ transformation (Cassie 1971, Elliott 1971). The arithmetical mean was used on other occasions.

Clumping factor (c) was calculated as

$$c=(s^2-\bar{x})\,(\bar{x}^2-\frac{s}{n}{}^{2})^{-1} \qquad (1)$$

Table 1. Frequency (%) of different ranges of confidence ($P<0.05$) for the mean number ($\bar{x}$) of crustacean plankton species from 10 stations, and frequency (%) of the fraction $x_p\,\bar{x}^{-1}$, where x_p is the number at the permanent sampling station. Data based on 5 samples from each of the Essand and Nesjø reservoirs in 1979.

Confidence Range	Frequency	Fraction $x_p\,\bar{x}^{-1}$ Range	Frequency
0.6–1.5	43	0.8–1.2	47
0.5–2.0	69	0.6–1.5	67
0.4–2.5	83	0.6–2.0	82
0.2–3.3	100	0.6–4.3	100

where $\bar{x}$ is sample mean, s^2 sample variance and n number of sampling units.

Contagious horizontal distributions implied wide ranges of confidence. In 69 % of the 1979 cases they were between 0.5 and 2.0 of the mean ($P<0.05$), and could be as high as 0.2 to 3.3 (Table 1). The numbers taken in a single haul at the permanent stations in 1979 were in 47 % of the cases within 0.8 to 1.2 of the mean for all 10 stations (Table 1). They fell well within the general ranges of confidence. The mean numbers of the two or three hauls taken at the permanent stations in the other years should be more representative.

In each sample, measurements were made of the body length of the first 50 randomly occurring *D. galeata* (helmet excluded) and *Bosmina longispina* Leydig, and the postabdomen length from the base of the claw to the base of the natatorial setae of *Holopedium gibberum* Zaddach (Larsson 1978). The body length of *H. gibberum* in mm (L_b) was related to the postabdomen length in mm (L) by the regression:

$$L_b=0.21+2.96\,L\ (r=0.97,\ P<0.001) \qquad (2)$$

based on data from 30 well-preserved individuals covering the relevant length interval. At least 15 egg-carrying individuals of each species were measured. The confidence limits ($P<0.05$) of mean lengths were always better than ±5 %. The mean length of different stages of copepods was found by measuring 50 individuals of each stage, to confidence limits better than ±2 %. The dry weight in μg (W) of the various species was calculated from their length (postabdomen length of *H. gibberum*) in mm (L) thus:

Holopedium gibberum $\ln W = 5.395 + 2.055 \ln L$ (Larsson 1978)

Bosmina longispina $\ln W = 3.093 + 2.595 \ln L$ (Langeland 1982)

Daphnia galeata $\ln W = 1.60 + 2.84 \ln L$ (Bottrell et al. 1976)

Cyclops scutifer $\ln W = 1.2286 + 2.6398 \ln L$ (Bottrell et al. 1976)

Heterocope saliens $\ln W = 1.8551 + 1.9756 \ln L$ (Bottrell et al. 1976)

Bythotrephes longimanus $W = 100\ \mu g$.

The weight of *H. gibberum* does not include the gelatinous mantle. The equation for *Heterocope saliens* (Lillj.) was also used for the diaptomids, giving weights more in accordance with those recorded for *Arctodiaptomus laticeps* (Sars) by Rey and Capblancq (1975) than any regression presented for other diaptomids. The calculated copepod weights agree with those given for *Cyclops scutifer* Sars by McLaren (1964), Larsson (1978) and Langeland (1982), and for *H. saliens* by Larsson (1978). With reference to the above works on copepods, the nauplia weight of *C. scutifer* and the calanoids was set to 0.1 and 0.4 μg, respectively.

The summer net production (P) as mg m^{-3} d.w. of copepods in 1979 was calculated as:

$$P = \sum_{1}^{n} 0.5\,(N_i + N_{i-1})\,(\bar{W}_i - \bar{W}_{i-1}) \qquad (3)$$

where N_i is mean density number and $\bar{W}_i$ mean individual weight at the i-th sampling. Production of cladocerans was estimated from selected $P/\bar{B}$ ratios, where $\bar{B}$ is mean seasonal biomass (mg m^{-3} d.w.).

The length measurements are precise, and the confidence of biomass figures is almost entirely dependent on the confidence of the numbers. These ranges are so wide that it is impossible to present them in the illustrations. The contagious horizontal distributions are shown by the following example. Based on 10 vertical net hauls the mean number of Nesjø *D. galeata* on 20 September 1979 was 1,649 m^{-3} with confidence limits of 846 and 3,204 ($P < 0.05$), a situation better than the average. The variance of the transformed figures was 0.1615. If an upper confidence limit of 25 % was desired, i.e. 1,649 + 412 = 2,061, and assuming that the mean and variance did not change, 89 vertical net hauls would be needed. To bring the confidence to such a level would require a sampling effort beyond the bounds of possibility. However, in the example given the arithmetical sample mean progressed very satisfactorily (Table 2), the maximum deviation from the final mean being 19 % after the fourth haul.

Bottom fauna

A few samples were taken in Nesjø, mainly to show the quality of its macrobenthos. In May 1978, 5 localities were sampled through the ice. In June 1980, 3 localities were sampled at different depths. The sample unit was two probes taken with a van Veen sampler covering 0.02 m^2. The material was pooled and sieved through 0.5 mm meshes.

Fish

Fish were caught using series of nylon twine gillnets of mesh sizes 19.5, 22.5, 26.0, 29.0, 31.5, 35.0, 39.0 and 45.0 mm between adjacent knots. The basic material was taken with nets 25 m in length and 1.5 m high, set on the bottom in the littoral zone. The nets were set one by one from the shore with intervals of about 100 m. They were usually catching from 21 to 08 hours local time. Since the nets would become covered with

Table 2. The progression of the arithmetical sample mean of *Daphnia galeata* (No. m^{-3}) in 10 subsequent vertical net hauls on 20 September 1979 in Nesjø reservoir.

Haul no.	2	3	4	5	6	7	8	9	10
Mean	118	123	109	125	126	128	129	132	134

Table 3. The daily catch with two series of nets set in the littoral zone on subsequent days in July 1971.

Date	Locality	Brown trout	Arctic char	Burbot
2 July	Essand	0	85	0
3 July	Essand	1	74	0
4 July	Essand	0	87	0
5 July	Nesjø	82	3	0
6 July	Nesjø	92	22	0
7 July	Nesjø	74	3	0

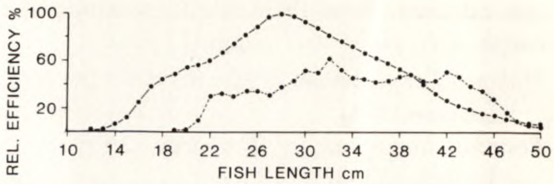

Fig. 2. The pooled relative efficiency of the series of nets used (mesh sizes 19.5–45 mm) for salmonids (solid line) and burbot (broken line), when 100% represents maximum efficiency for salmonids.

twigs and other plant debris if they were exposed to wind, fishing could not take place at fixed or random positions, but only along sheltered stretches. Those most used are shown in Fig. 1. On 11 occasions this effort was supplemented by floating the same series of nylon monofilament nets, 6 m long and 4 m high, in the limnetic zone. In winter 1973, 64 char were angled through holes in the ice.

At least two series of nets were set in each reservoir, but except for 1979 this was most often repeated once or twice. A comparable catch per effort was usually obtained from day to day and on different sections of the littoral zone within the same reservoir, as shown by the example in Table 3. The total catch of 7,693 fish was composed of 1,734 brown trout, 5,043 Arctic char and 916 burbot. The results on catch per unit effort and growth were supported by the data of 19 trout and 325 char from Essand caught in 1967–69 and 117 trout and 9 char from the river Nea caught in 1968. They were caught by the basic net method described above.

The author has analyzed the efficiency of the gillnets for Arctic char (J. W. Jensen 1984), burbot and salmonids in general (Jensen 1986). Based on these results the pooled relative efficiency for salmonids and burbot of different lengths was calculated for the nets used in this study (Fig. 2). Corrected numbers (N_c) per series of nets, representing the number of salmonids >15 cm and burbot >18 cm caught if efficiency equalled 100 % of that for salmonids over all length classes, were calculated.

The catch per effort of salmonids >130–140 g was also evaluated as mean round weight for mesh sizes 26, 29, 31.5 and 35 mm. Larger mesh sizes were taken into account if this led to a higher weight. This method gave comparable results over several years in lakes with stable populations, and has documented species successions in impounded reservoirs (J. W. Jensen 1979).

Relative density of salmonids was described by N_c and related to real density by the following procedure. Number of Arctic char per ha and number of brown trout per km of shoreline in Målsjøen, a lake (surface area 27 ha, maximum depth 13 m) situated at altitude 165 m in the same river system as Essand-Nesjø, have been related to N_c (Fig. 3). These relationships were transferred to the Essand-Nesjø data. For char this could only be done if a positive relationship

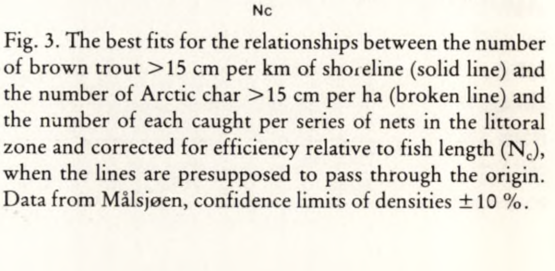

Fig. 3. The best fits for the relationships between the number of brown trout >15 cm per km of shoreline (solid line) and the number of Arctic char >15 cm per ha (broken line) and the number of each caught per series of nets in the littoral zone and corrected for efficiency relative to fish length (N_c), when the lines are presupposed to pass through the origin. Data from Målsjøen, confidence limits of densities ±10 %.

exist between the numbers in the littoral zone and in open water. The number of Arctic char caught in June–August in the littoral zone (N_l) and in an identical series of nets simultaneously floated in open water (N_f) was compared. The nets used in the littoral zone were 25 m long and 1.5 m high, and the catches from open water were calculated for net areas of the same size. For 29 cases from Essand-Nesjø and 16 other lakes (Arnekleiv 1983, Koksvik and Arnekleiv 1982, Langeland 1975, 1977, 1978 a, 1979, 1980, Langeland et al. 1986) where $N_l > N_f$, the usual situation both in Målsjøen and Essand-Nesjø, the following highly significant relationship existed:

$$N_f = 0.94 + 0.30\, n_l \; (r = 0.81,\; P < 0.001) \qquad (4)$$

Population size was calculated from density number and the actual surface area and length of shoreline in each case. Population biomass was calculated from population size and the mean weight of N_c.

Length of salmonids was measured to the fork and that of burbot to the end of the tail. Round wet weight was recorded. Age of trout was read and growth in length back-calculated from scale impressions, as described by Bagenal and Tesch (1978). The increase in length was calculated proportionally to differences between annuli in the scales. The length of 1 year-old trout was probably underestimated by about 1 cm, as shown by Langeland (1982) for trout caught 40 km downstream. The age of char was read from otoliths, as described by Nordeng (1961). The Essand growth was impossible to read from scales, but the Nesjø growth was quite clear. The age of burbot was found by breaking their otoliths, heating them until a light brown colour appeared, and analyzing the fracture surface of the otolith when soaked in ethanol.

The intention was to study the growth of salmonids staying in Essand or Nesjø throughout the growth season. Individuals moving between the reservoirs had to be excluded. The standard deviation (s) of the mean length in cm (L) of trout increased linearly and significantly with L, and reached a maximum at the length above which growth declined. This s to L relationship was established for Nesjø trout caught in 1971 and proved by scale readings to have stayed in Nesjø also in 1970. Its maximum s was 3.2. For growth analysis, the largest Nesjø trout and char from each age class were selected downwards until a value of s corresponding to that relationship or a maximum s of 3.2 was obtained. Maximum s for Essand char caught before June 1972 was 1.7 for age class 4. The smallest Essand char from each age class were selected upwards until $s = 1.7$. This procedure led to exclusion of less than 10 % of the total number of Nesjø salmonids and 11 % of Essand char. In 1972–74 as much as 40 % of certain age classes of char were excluded.

Condition factor (K) was calculated from fish length in cm (L) and wet weight in g (W):

$$K = 100\, W\, L^{-3} \qquad (5)$$

Mean weight for different length classes was calculated from mean length and mean K.

Mean specific growth rate in weight as % day^{-1} (G) was calculated from

$$G = 100\, (\ln W_2 - \ln W_1)\, t^{-1} \qquad (6)$$

where W^1 was the initial and W_2 the final weight over a period of t days. Based on scale readings, the salmonids did not grow in length at temperatures below 7°C (Jensen 1985 a), thus limiting the normal growth season from 15 June to 30 September.

Another expression of G is

$$\ln G = \ln a + b \ln W \qquad (7)$$

(Brett 1974, Elliott 1975 a), splitting the growth rate into a size-independent factor and a size-dependent factor. The first one is equivalent to the growth rate of a fish of unit weight (G_u) (Jobling 1983 a), which was calculated from:

$$\ln G_u = \ln G + 0.325 \ln W \qquad (8)$$

A value of –0.325 for exponent b has been found for both brown trout (Elliott 1975 a) and Arctic char (Jobling 1983 b). Jensen (1985 b) proved it to be valid for Nesjø trout and char up to initial lengths of 29 and 26 cm, respectively.

Over growth intervals the geometric mean of W was used:

$$\ln W = 0.5\, (\ln W_1 + \ln W_2) \qquad (9)$$

Maximum G_u in relation to temperature in °C (T) was taken from Jensen (1985 b):

Brown trout: $G_u = 13.8\,(-0.3471 + 0.1053\,T)$ (10)
Arctic char: $G_u = 12.6\,(-0.0815 + 0.0917\,T)$ (11)

423 spawning char caught in or near the Nøsteråa tributary (Fig. 1) were tagged (Carlin tags) in 1973 and 105 caught in the Nea tributary in 1974.

When possible, the stomach contents of at least 25 individuals of each species of fish were collected from each reservoir and field period. The proportions of the different prey-organisms were estimated as per cent volume for individual stomachs, and mean per cent volume (V) was calculated. In these reservoirs with a limited spectrum of prey-organisms, this procedure was found to characterize the diet better than methods which allow the fullest stomachs to influence the results more (Jensen 1985 a). For each sample the stomach contents containing crustacean plankton were pooled. A subsample was counted, and the length of 30 randomly occurring individuals of each species was measured. From these data the biomass in the sample and the number per stomach of each species were calculated. Stomach contents of char <25 cm were pooled separately.

The fullness of every fish stomach was estimated in a 5-step scale from empty (0.0) to full (1.0). Food rations in g w.w. (Q) for salmonids of round weight in g (W) were calculated from mean fullness (F) thus:

$$Q = 0.101\,F\,W^{0.69} \qquad (12)$$

The basis for this and for the calculation of mean fullness will be given in equation 22 f.

The food rations were back-calculated to the quantity at the time of netting (Q_0) by an equation of Elliott (1972), formulated for brown trout and prey of similar quality:

$$\ln Q_0 = \ln Q + h\,0.053\,e^{0.112T} \qquad (13)$$

where h is the time elapsed in hours and T temperature in °C. h was set to 7 hours, as the efficiency of a net declines with the number of fish entangled and digestion continues also in dead fish.

The number of meals per day (M) was calculated by an equation formulated for brown trout by Elliott (1975 b)

$$M = 1.171\,e^{0.038T} \qquad (14)$$

valid for the temperature interval 6.8–13.6°C. Fish may feed continuously in June–early July and take about twice the mean ration per day (Elliott 1973, Swenson and Smith 1973). Then the salmonids were assumed to have consumed twice the quantities back-calculated to the time of netting.

The electivity index of Ivlev (1961)

$$E = (r-p)\,(r+p)^{-1} \qquad (15)$$

where p represents the relative abundance of a species in the plankton and r that in the stomachs of char, was calculated for the predominant cladocerans.

A plankton consumption index, P_i, expresses the mean number of a species in the stomachs per g round weight of a sample of fish.

Dry weight was set to 25% of wet weight for fish (Lien 1978, A. J. Jensen 1979), 18 % for hatching chironomids (Jonasson 1972), 20 % in general for other aquatic insects (Elliott 1972), and 11 % for planktonic crustaceans (Bottrell et al. 1976), snails and mussels.

Fluctuations of water level

The water level fluctuated in a pattern typical for hydroelectric reservoirs located in northern areas. Water was stored from May to November. The water level fell during winter when demand for electricity was at a maximum and water flow at a minimum. Storing in Nesjø started 25 May 1970, and the water level reached 715.5 m in August (Fig. 4). The following winter the reservoir was almost emptied and had a surface area of only 0.9 km^2 for nearly four months, due to construction work on the dam. The water reached the Essand sill for the first time on 28 July 1971, and culminated at 727.2 m on 16 November. Throughout 1971–76 the reservoir was below 722.4 m only for three short periods. The 1977–80 period was characterized by less

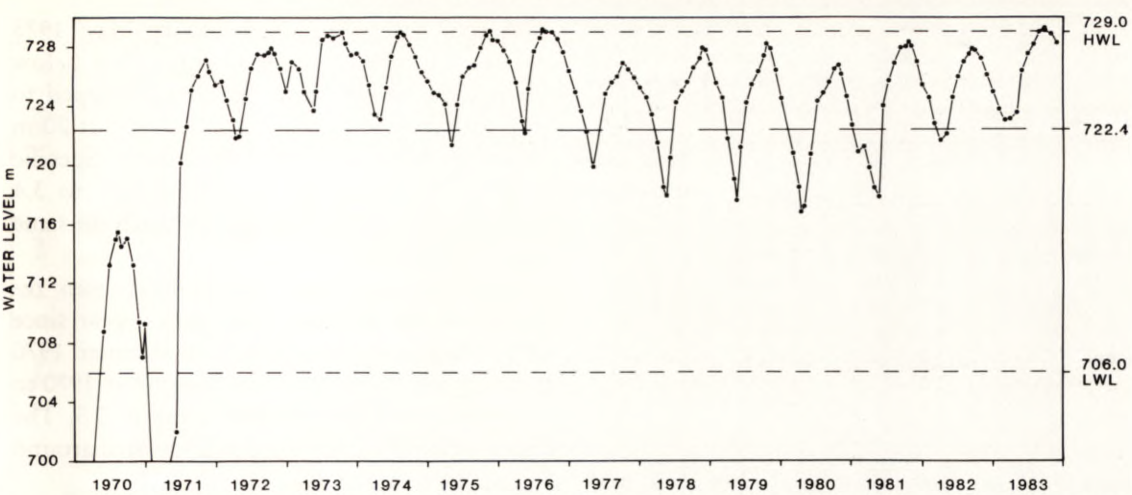

Fig. 4. Water level fluctuations in the Essand-Nesjø reservoirs in 1970–83. The highest (HWL) and lowest (LWL) permitted levels, and the level of the sill between the reservoirs (722.4 m) are shown. The solid sections of this last line represent the normal periods of ice cover.

water. At ice-out there was no or only shallow water on the sill. The situation in 1981–83 was like that in 1971–76.

Results

Physical and chemical measurements

The thermal stratification of the reservoirs was negligible during the ice-free period. The maximum vertical deviation was 3.3°C in Nesjø on 17 August 1976. It was more than 1.6°C on four other occassions, but most often less than 1°C. Complete circulation must have taken place almost continuously. Consequently the surface temperatures describe the temperature regime.

The ice broke up about 15 June. The late June or early July temperature in Nesjø was 10–13.4°C in 1970–72 and 1979 (Fig. 5). In 1973–75 and 1977 it was only 7–8°C. The seasonal maximums usually occurred in August. The temperature was especially low in 1974 and 1977. According to meteorological observations the early summer of 1975 was even colder. The water began to cool down in late August and this process went on evenly, and with small variations from year to year, until ice formed in early November.

The winter temperatures in Nesjø were low.

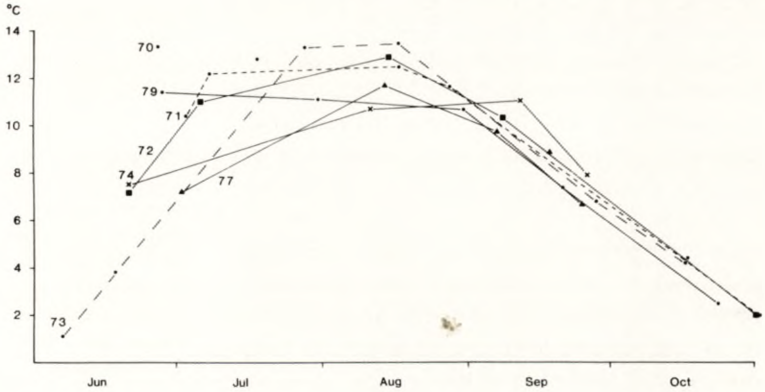

Fig. 5. Temperatures in the ice-free season at a depth of 1 m in the Nesjø reservoir in 1970–79.

Table 4. Ranges of abiotic factors at a depth of 1 m in the Nesjø and Essand reservoirs, and the maximum deviation between the reservoirs for records from the same field period. Data from the ice-free periods in 1970–83.

	Nesjø	Essand	Maximum deviation
Oxygen %	86–108	85–108	2
°dH	0.35–0.60	0.40–0.50	0.15
CaO m/l	2.5–4.0	2.5–4.0	0.10
pH	6.3–7.0	6.4–6.9	0.4
mSm^{-1}	1.8–3.1	2.0–2.9	0.6
Secchi depth m	2.7–6.0	3.2–4.8	1.2

Maximum at any depth was 2.1°C in 1972, and otherwise in the period 1971–78 only 0.7–1.4°C.

The temperature regime of Essand was almost identical to that of Nesjø. Measured on the same day, the maximum deviation at corresponding depths was 0.2°C. During 1–4 day intervals it was 1.7°C.

The continuous circulation in the ice-free period and the minor differences between the two reservoirs are confirmed by the other parameters. Maximum vertical deviation in conductivity was 0.4 mSm^{-1} and in pH 0.3. Mostly no differences existed. Seasonal variations and differences between the reservoirs were also small (Table 4). Oxygen content was always close to saturation. Water hardness and specific conductivity were generally about 10 % higher in Nesjø. Calcium represented about 60 % of total hardness. pH was 6.8–6.9 in Essand, except for June–July 1972 and June 1973, when it was 6.4–6.5. The Nesjø water was more acid throughout 1970–73, with pH 6.3–6.7. From October 1973 pH was 6.8–7.0 in Nesjø, too. On 17 July 1970 the Secchi depth was 5.0 m in Nesjø. Generally it was 4.0–5.0 m in both reservoirs and 0.2–0.4 m less in Nesjø than in Essand. The Secchi colour was always a variant of yellow, most often more or less brownish yellow.

Soluble PO_4 and NO_3 in Nesjø water was found to be 9 and 30 $\mu g\ l^{-1}$ on 1 July 1977, and 1 and 10 $\mu g\ l^{-1}$ on 6 September 1977. Mass occurrence of the diatom *Asterionella formosa* Hass. in late September 1972 and October 1973 indicated higher levels of nutrients.

Monthly sampling in February–May 1973 showed a different winter situation. Just below the ice, the oxygen level in Nesjø dropped to 45 % of saturation and pH to 6.0, and at 20 m depth to 22 % and 5.8, respectively. Specific conductivity increased correspondingly to 3.4 and 5.7 mSm^{-1}. The situation was much the same in both reservoirs.

Turbidity and water colour have been recorded in Nesjø about four times a year since 1970 (Heggstad 1974, 1980). In summer 1970 turbidity was 1–2 ITU, from September 1970 to 1975 about 1, and since then close to 0.5. The colour of unfiltered water has fluctuated around 20 mg Pt l^{-1}.

Crustacean plankton

The initial fauna

In 1969 three species of cladocerans and three of copepods were present in the Essand reservoir. *H. gibberum*, *B. longispina* and *C. scutifer* were most numerous, *D. galeata*, *A. laticeps*, and *H. saliens* occurring in lower numbers. *B. longimanus*, *Mixodiaptomus laciniatus* (Lillj.) and *Acanthodiaptomus denticornis* (Wierz.) lived in two tarns pre-existing Nesjø (Table 5). Most species occurred in the smallest tarn, Honktjern (23 ha). Other standing waters in the catchment area are minor, except for the Sylsjö reservoir drained by the river Nea (Fig. 1). The length of the river between Sylsjö and Nesjø is 5 km, and

Table 5. The planktonic Crustacea (No. m^{-3}) in the two largest tarns, now part of the Nesjø reservoir, on 9 August 1969.

	N. Broksjø	Honktjern
Holopedium gibberum		640
Daphnia galeata	8600	600
Bosmina longispina	180	1520
Bythotrephes longimanus	4	2
Arctodiaptomus laticeps	2	15
Mixodiaptomus		6
Acanthodiaptomus denticornis		130
Heterocope saliens	2	70
Cyclops scutifer	40	360

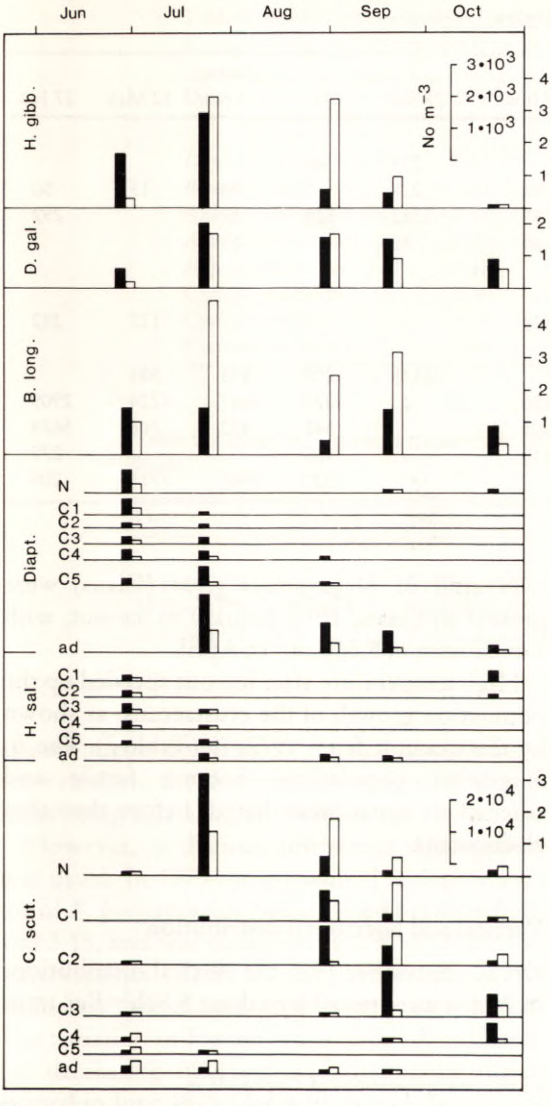

Fig. 6. Densities (No. m^{-3}) of the dominant species of planktonic crustaceans in the Nesjø (black columns) and Essand (open columns) reservoirs in 1979. The scale of *Cyclops scutifer* is different from the others.

drifting crustaceans would according to Hynes (1970) and A. J. Jensen (1984) be unlikely to reach the latter.

The annual cycles

The data from 1979 exemplify the situation in summer (Fig. 6), and some samples from 1972–73 that in winter (Table 6). *H. gibberum* reached its maximum in July–August and was present in low numbers until January. *D. galeata* was most abundant in July–September and occurred in low numbers throughout the winter. Ephippial females were found from mid-August, and comprised 80–90 % of the egg-carrying females in late September and October. Egg-carrying parthenogenetic females were, however, recorded all winter. *B. longispina* was diacmic in both reservoirs, normally with one maximum in July and a smaller one in September. In late September and October it almost exclusively produced resting eggs. A few parthenogenetic females were found until April. *H. gibberum* and *B. longispina* were most numerous in Essand and *D. galeata* in Nesjø in 1979, but these relationships varied through the research period.

The diaptomid cycle is mainly based on *A. laticeps*, which represented 88 % of the Nesjø adults in 1979. Only small differences existed between the three species present, all of which were univoltine. The first nauplii were found in April. Their number increased to a maximum in June. One month later most had reached the adult stage, and the first egg-carrying females of *A. laticeps* appeared. They were found in declining numbers until the end of October, with a maximum in August. Egg-carrying females of *M. laciniatus* have been present from mid-August to the end of September, and of *A. denticornis* in September and mainly October. The two last-mentioned species disappeared during the autumn, whereas both male and female *A. laticeps* survived all winter. A few nauplii were present in September and October, but died in that stage.

The cycle of *H. saliens* was similar to the diaptomid one, but the adults always died during September. The metamorphosis from eggs to copepodites must have been rapid, as nauplii were rarely found.

C. scutifer was the most numerous species. It was univoltine, and the two generations present in summer were clearly distinguishable. In Nesjø egg hatching started in June. The nauplii maximum was in July. Nauplii were present until the end of October, when most of that

Table 6. Densities (No. m^{-3}) of planktonic Crustacea in winter 1972–73.

		Nesjø					Essand				
Date		30 Oct.	7 Jan.	1 Apr.	12 May	17 Jun.	28 Sep.	7 Jan.	1 Apr.	12 May	17 Jun.
H. gibberum		4					274	48			
D. galeata		61		30	82	12	228	20	90	13	30
B. longispina		21	30			35	3382	528	17		292
A. laticeps ad.		130	120	41	56	68	89	96	13		
M. laciniatus ad.		13									
A. denticornis ad.		30									
Diaptomidae	N			45	162	338				122	212
C. scutifer	N										
	C 3						16545	1200	845	384	
	C 4	6528	3239	1036	288	105		4320	4647	4224	2909
	C 5	507	3309	720	202	2505		840	422	768	5674
	ad.	5			28	1919		120			279
M. gigas	N							4320	8563	7718	209

generation had reached Cop. 3 or 4. In January 1973 half of them had reached Cop. 5. From then on no growth seemed to take place until mid-May, and their number decreased by 92 %, to increase again suddenly in June. The metamorphosis to adults started at ice-out. Egg-carrying adults reached their maximum in late June, but were present until the end of September, when the last representatives of that generation died. In contrast, all stages of the Essand population were one month delayed in the ice-free season. It overwintered in larger numbers, mainly as Cop. 4, but also this population increased from May to June.

Nauplii of *Megacyclops gigas* (Claus) were present in Essand from January to ice-out, with a maximum of 8,500 m^{-3} in April.

High temperature after ice-out speeded up the population growth of the crustaceans, as shown by the example from 1977–79 (Table 7). The *B. longispina* populations became fertile and reached its usual mean length before the other cladocerans.

Vertical and horizontal distribution

On 10 September 1975 the vertical distributions in Nesjø were tested by taking 5 Schindler traps

Table 7. The mean numbers of Cladocera and of the new generations of Copepoda in Nesjø reservoir after icke-out in 1977 (7.2°C) and 1979 (11.4°C), mean length of Cladocera in mm (L) and the percentage of fertile ones (F).

	1 July 1977 No. m^{-3}	F	L	26 June 1979 No. m^{-3}	F	L
Holopedium gibberum	769	0	0.64	1736	26	0.99
Daphnia galeata	57	0	—	623	32	1.49
Bosmina longispina	329	22	0.68	1450	38	0.67
Diaptomidae N	912			700		
Diaptomidae C1–C3	187			565		
Diaptomidae C4–C5	0			503		
Heterocope saliens C1–C2	82			383		
Heterocope saliens C3–C5	0			660		
Cyclops scutifer N	969			1159		
Cyclops scutifer C1–C2	18			159		

Table 8. Horizontal clumping (c) in the Nesjø reservoir in 1979, based on 10 vertical net hauls along a 10 km transect for each date and number m^{-3}.

Date	28 Jun.	24 Jul.	30 Aug.	20 Sep.	23 Oct.
Daphnia galeata	0.43	0.22	0.17	0.20	0.49
Bosmina longispina	1.01	0.49	2.15	0.89	1.12
Holopedium gibberum	0.58	0.27	1.12	0.38	0.72
Arctodiaptomus laticeps	0.35	0.30	0.28	0.99	0.55
Heterocope saliens	0.17	0.93	0.63	1.33	—
Cyclops scutifer N	0.36	0.13	0.17	0.99	0.60
Cyclops scutifer C	0.74	0.37	0.09	0.04	0.14
Cyclops scutifer ad.	0.14	0.14	0.17	0.63	—

Table 9. Linear regressions of number m^{-3} (No.) related to depth in m (d), based on 10 vertical hauls.

Date	Locality	Species	Regression	r	P
28 June 1979	Nesjø	*Cyclops scutifer*	$\text{No.} = -82d + 1044$	−0.64	<0.05
27 June 1979	Essand	*Cyclops scutifer*	$\text{No.} = -15d + 317$	−0.74	<0.02
28 June 1979	Nesjø	*Bosmina longispina*	$\text{No.} = -147d + 1457$	−0.66	<0.05

at each metre down to 17 m. The distributions were random, the clumping factor (c) of *B. longispina* being 0.23 and for the other species <0.14.

However, a distinct horizontal aggregation was usual. In 1979 the horizontal clumping factor of *B. longispina* in Nesjø varied between 0.49 and 2.15, and was occasionally 0.50–1.00 for the other species (Table 8). *C. scutifer*, the most abundant species, was most evenly distributed. The situation in Essand was similar. A tendency for decreasing numbers with increasing depth existed in June 1979 (Table 9).

Size and fecundity

The extreme minimum adult length of *H. gibberum* was 0.89 mm in Nesjø and 0.83 mm in Essand. The corresponding figures for *B. longispina* were 0.59 mm and 0.55 mm. The overall variation in minimum adult length of both species was <0.1 mm. *D. galeata* minimum adult length increased from ice-out to the end of July, and then decreased again. Long-term changes are shown in Fig. 7 as the seasonal maximum mean adult lengths. The adult cladocerans in Nesjø were always larger than those in Essand. They were especially large in 1971–73. The weight differences were considerable. For example, the maximum mean weight of adult Nesjø *D. galeata* was 41 µg in 1972, compared to 22 µg for the Essand population.

The mean length of the different stages of copepods from Nesjø in 1979 are presented in Table 10. No significant differences were found

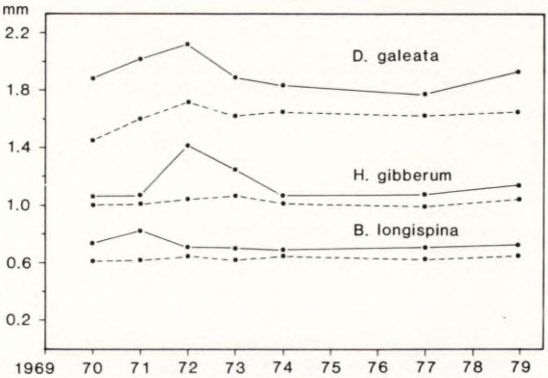

Fig. 7. Annual maximum mean adult length (mm) of the dominant cladocerans in the Nesjø (solid lines) and Essand (broken lines) reservoirs.

Table 10. Mean length (mm) of the different stages of Copepoda in Nesjø reservoir in 1979, significance levels (P<0.05) within ±2 %.

Species	C1	C2	C3	C4	C5	male	fem.
Arctodiaptomus laticeps	0.50	0.65	0.82	1.04	1.21	1.39	1.55
Mixodiaptomus laciniatus						1.13	1.35
Acanthodiaptomus denticornis						1.35	1.61
Heterocope saliens	0.80	1.08	1.38	1.65	2.00	2.45	2.50
Cyclops scutifer	0.50	0.60	0.71	0.87	1.10	1.05	1.27

between the populations of the two reservoirs, nor between data from 1970 and 1979.

Fig. 8 gives examples of some other population characteristics of the cladocerans based on the 1979 data. The adult proportions of *H. gibberum* and *B. longispina* were generally above 60 % in both reservoirs. For Nesjø *H. gibberum* it fell steadily throughout the season, whereas that of Essand *B. longispina* showed a distinct minimum in July. The adult proportion of *D. galeata* was smaller, with a drop in July and another decline in September–October.

Except for *B. longispina* in June, the mean clutch size was highest for the Nesjø populations. It declined generally throughout the season, and in particular for *D. galeata* from June to July. The same, but more distinct, trends existed for the mean number of eggs per individual, as the proportions of egg-carrying adults was also generally higher for the Nesjø populations.

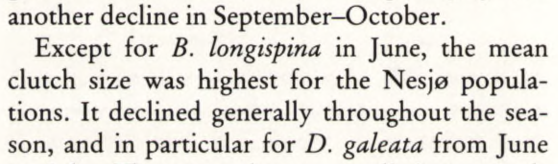

Fig. 8. Percentage of adults (solid lines), mean clutch size (broken lines) and mean number of eggs per individual (dotted lines) for the dominant cladocerans in 1979.

The reproductive capacity was especially high in 1979. The basic trends were, however, valid for the whole research period. Nesjø *H. gibberum* generally carried most eggs. Its maximum mean clutch size was 10.4 in July 1973. The figures for Nesjø *D. galeata* in June 1979 were never exceeded. Its high fecundity in June was often followed by a distinct drop in July. The July proportion of egg-carrying individuals was 0 in 1972, 2 % in 1973 and 12 % in 1979.

The clutch size (C) generally increased with length in mm (L), as shown for *D. galeata*:

Nesjø $C = 4.61\ L - 4.44$ ($r = 0.43$, $P < 0.001$) (16)
Essand $C = 4.06\ L - 3.33$ ($r = 0.39$, $P < 0.001$) (17)

This partly explains why the Nesjø populations carried more eggs. However, below a length of 2.0 mm Essand *D. galeata* carried more eggs than Nesjø *D. galeata*.

Biomass variations

Three species of diaptomids were present in Nesjø (Table 11). In 1970 the predominant species of the former tarns, *A. denticornis*, was most numerous in Nesjø, followed by *M. laciniatus*. They gave way to the only Essand diaptomid *A. laticeps* in 1971, but recovered in 1972–73. Later their number declined again, and that of *A. denticornis* most abruptly. They were absent in 1977, but appeared again in 1979. *A. laticeps* after 1970 was still the only diaptomid in Essand, with the exception of 1973 when *A. den-*

Table 11. The occurrence of the different species of Diaptomidae in Nesjø reservoir in 1970–79, as a percentage of the total adult forms.

Species	1970	1971	1972	1973	1974	1975	1977	1979
Arctodiaptomus laticeps	11	86	19	20	72	74	100	88
Mixodiaptomus laciniatus	17	1	37	39	20	26	0	11
Acanthodiaptomus denticornis	72	13	44	41	8	0	0	1

ticornis represented 15 % and *M. laciniatus* 2 % of the adults.

The midsummer biomass of crustacean plankton usually was about 60 mg m^{-3} (d.w.) in Essand, equivalent to 0.72 g m^{-2} over the mean depth (Fig. 9). Higher values occurred in 1970 and 1979, and lower in 1971 and 1975. Generally, cladocerans made up 50–70 % of the biomass, but copepods predominated on some of the early and late sampling dates.

The large-scale variations were parallel in Nesjø. Except for 1974, the seasonal biomass maximum observed was always higher than in Essand. In July 1970 it reached 219 mg m^{-3}, 98 % of which was cladocerans. It was 75–100 mg m^{-3}, equivalent to 0.90–1.20 g m^{-2} over the mean depth, throughout 1971–73. In 1979 the biomass maximum was 156 mg m^{-3} compared with 103 mg m^{-3} in Essand. In 1970 the Nesjø crustacean plankton was almost entirely a community of continuously reproducing cladocerans. The copepods present either had inhabited the impounded tarns or had been transported from Essand. The density of copepods grew gradually until 1972, and from then on the biomass of both cladocerans and copepods was generally larger than in Essand.

H. gibberum, *B. longispina*, and *C. scutifer* made up the bulk of the crustacean biomass in Essand throughout the research period (Fig. 10). All these species contributed to the high biomass in 1970 and 1979. In 1973 and 1979 the biomass of *C. scutifer* declined through the season, as large numbers survived from the year before. The remaining three species represented a much smaller biomass. The largest numbers of *D. galeata* occurred in 1970, 1977 and 1979.

About five weeks after ice-out in 1970, *H. gibberum* represented 123 mg m^{-3} and 56 % of the biomass in Nesjø. Its numbers and biomass declined steadily to a low level in 1974–75, but increased again in 1977 and 1979. The fate of *B. longispina* was similar, but its numbers were low throughout 1972–75. The numbers and biomass of *D. galeata* and the calanoids increased steadily from 1971 to 1973, were low in 1974–75, and

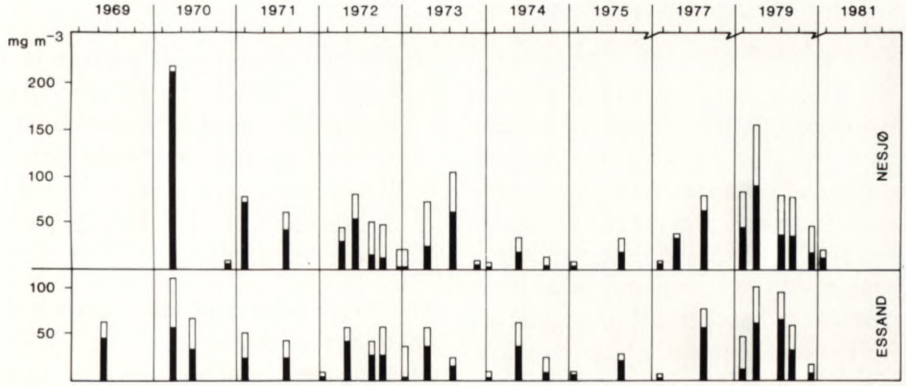

Fig. 9. Biomass (mg m^{-3} d.w.) of planktonic cladocerans (black columns) and copepods (white columns) in June-October.

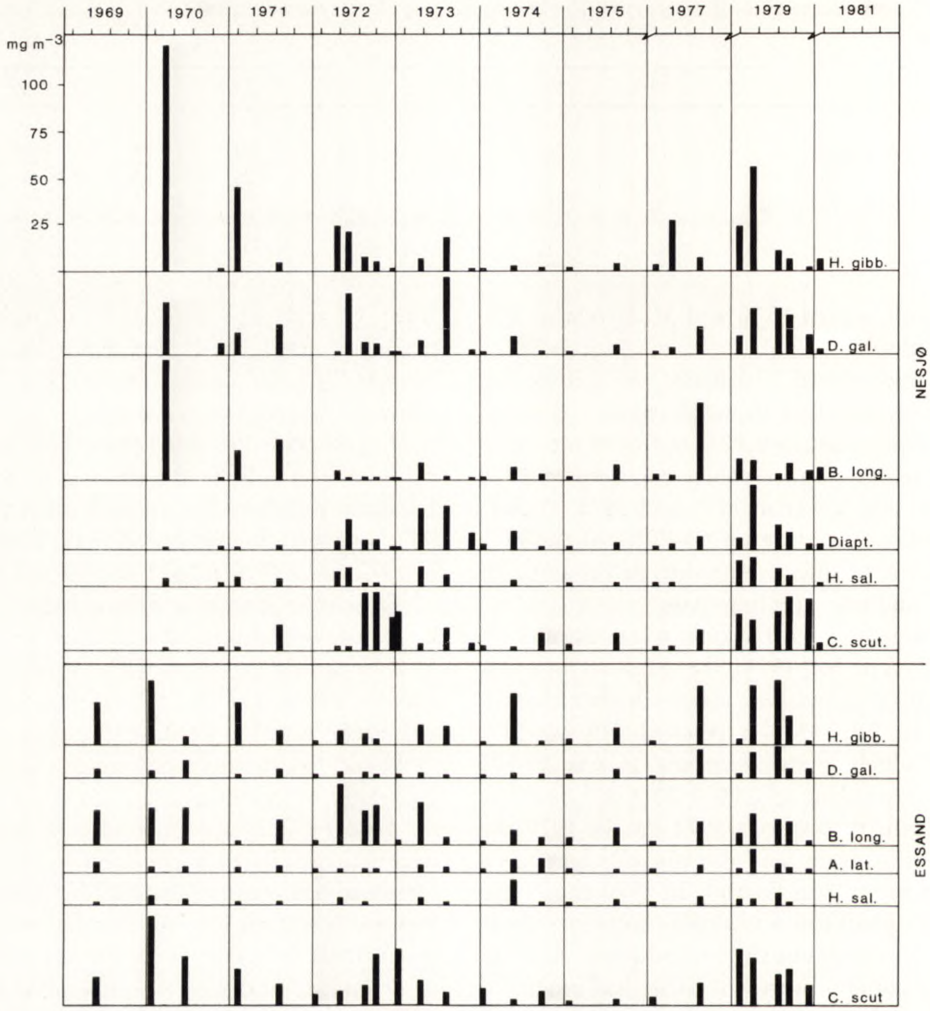

Fig. 10. Biomass (mg m^{-3} d.w.) of the different species of planktonic crustaceans in June–October.

increased again in 1977 and 1979. The biomass maximum of *D. galeata*, 42 mg m^{-3}, was recorded in September 1973. *C. scutifer* showed a similar pattern. Compared with the Essand population, Nesjø *C. scutifer* seemed to overwinter in smaller numbers, but the success of the survivors was better and they produced a larger biomass. Since 1972 the two populations have otherwise shown rather parallel fluctuations. Both had, for example, a positive biomass curve in 1972 followed by a negative one in 1973.

The biomasses of the cladocerans and the new generations of copepods present in Essand in June or early July as mg m^{-3} d.w. (B), were significantly and positively correlated with the simultaneously recorded water temperature in °C (T):

Cladocera: $B=5.3T-31.2$ ($r=0.82$, $P<0.02$) (18)
Copepoda: $B=2.1T-11.0$ ($r=0.77$, $P<0.05$) (19)

The Nesjø populations have shown similar correlations since 1973:

Cladocera: $B=6.0T-31.9$ ($r=0.86$, $P<0.05$) (20)
Copepoda: $B=5.1T-25.9$ ($r=0.88$, $P<0.05$) (21)

Table 12. The net production P (mg m^{-3} d.w.) of Copepoda in the period 15 June–15 October 1979 and corresponding $P/\bar{B}$ coefficients, where $\bar{B}$ is the mean seasonal biomass.

	Nesjø		Essand	
	P	$P/\bar{B}$	P	$P/\bar{B}$
Diaptomidae	39	3.1	12	2.9
Heterocope saliens	23	2.7	10	3.6
Cyclops scutifer	52	2.3	51	2.4

According to the equations a temperature of 5–6°C was required to induce population growth.

Some individuals of the large, carnivorous species *B. longimanus* occurred in most samples from Nesjø, most numerously in 1972. In Essand it was only found in stomachs of fish.

Some littoral species were recorded in the plankton samples from both reservoirs. *Eurycercus lamellatus* (O. F. Müller), *Polyphemus pediculus* (L.), *Sida crystallina* (O. F. Müller), and *Acroperus elongatus* (Sars) occurred frequently but in small numbers, *Acroperus harpae* (Baird), *Alona affinis* (Leydig), *A. quadrangularis* (O. F. Müller), *Alonella nana* (Baird), *Ceriodaphnia* sp., *Chydorus* spp., *Eucyclops Lilljeborgi* (Sars) and *Macrocyclops* sp. only occasionally.

Production

The net production of *C. scutifer* in the ice-free period of 1979 was about 50 mg m^{-3} in both reservoirs (Table 12). Some additional production took place in winter. The production of the calanoid species was lower, especially in Essand. These figures and the corresponding $P/\bar{B}$ values are probably somewhat too low. The intervals between sampling were too long to give representative numbers of nauplii and the first copepodite stages.

$P/\bar{B}$ values for assessing production in 1972 and 1979 (Table 13) were selected after evaluating results from oligotrophic lakes (Alimov et al. 1972, Andronikova et al. 1972, Latja 1974), and especially Norwegian ones (Jensen 1976, Larsson 1978, Langeland and Reinertsen 1982, Ålbu 1983). 1979 was obviously an optimal year for crustacean plankton production, with estimates of 586 mg m^{-3} in Nesjø and 445 mg m^{-3} in Essand (Table 13), equivalent to 7.0 and 5.3 g m^{-2}, respectively, over the mean depths of 12 m. Cladocerans represented about 75 %, with *H. gibberum* as the most productive species. 1972 represents a more usual level, with 4.3 g m^{-2} in Nesjø and 3.6 g m^{-2} in Essand.

Bottom fauna

The few bottom samples from the Nesjø reservoir show that its macrobenthos (Table 14) was composed of Chironomidae larvae, some Oligochaeta and scattered specimens of a few other groups. The stomach contents of fish also proved the presence of some Lymnea, Hydra-

Table 13. Selected $P/\bar{B}$ coefficients, mean biomass $\bar{B}$ (mg m^{-3} d.w.), and net production P (mg m^{-3} d.w.) based on the preceding parameters in the period 15 June–15 October 1972 and 1979.

		Nesjø 1972		Essand 1972		Nesjø 1979		Essand 1979	
	$P/\bar{B}$	$\bar{B}$	P	$\bar{B}$	P	$\bar{B}$	P	$\bar{B}$	P
H. gibberum	10.0	14.3	143	4.5	45	19.5	195	17.2	172
D. galeata	9.0	11.6	104	2.1	19	18.0	162	8.8	79
B. longispina	10.0	1.8	18	18.5	185	7.7	77	10.2	102
Diaptomidae	4.0	7.9	32	1.1	4	12.7	51	4.1	16
H. saliens	4.0	4.9	20	1.3	5	8.5	34	2.8	11
C. scutifer	3.0	16.7	50	13.9	42	22.2	67	21.6	65
Cladocera		27.7	265	25.1	249	45.2	434	36.2	353
Copepoda		29.5	102	16.3	51	43.4	152	28.5	92
Total		57.2	367	41.4	300	88.6	586	64.7	445

Table 14. Macrobenthos of the Nesjø reservoir as number (No.) and gram (w.w.) per m^2.

St.no.	Depth	Oligochaeta		Chironomidae l.		Trichoptera l.		Planorbidae		Pisidium		Sum	
	m	No.	g	No.	g	No.	g	No.	g	No.	g	No.	g
						18 May 1978							
1	13	20	0.17	1090	2.96							1110	3.13
2	14	30	0.21	1180	4.66							1210	4.87
3	13			970	2.85							970	2.85
4	13	30	0.03	1650	7.89							1680	7.92
5	14	30	0.10	2750	17.84							2780	17.94
						20–21 June 1980							
6	2	150	0.44	250	0.04							400	0.48
6	4	150	0.31	80	0.11							230	0.42
6	7	680	0.58	380	2.25	30	0.50	30	0.57	30	0.17	1150	4.07
6	12	150	0.14	280	0.77							430	0.91
7	2			1210	4.90					30	0.04	1240	4.94
7	4	150	0.23	880	0.40							1030	0.73
7	6	50	0.46	900	1.50							930	1.96
7	8	80	0.10	1450	4.69							1530	4.79
7	9	100	0.13	780	2.34							880	2.47
8	1	80	0.18	1800	1.11							1880	1.29
8	2	130	0.69	80	0.05							210	0.74
8	4	80	0.03	430	0.31			30	0.36	30	0.13	570	0.77
8	6	150	0.37	480	0.57							630	0.94
8	8			550	0.77							550	0.77

dephaga, larvae of Trichoptera, Ephemeroptera and Plecoptera.

In May 1978 Chironomidae larvae were found in numbers ranging from 970 to 2,750 per m^2. Their biomass varied between 2.85 and 17.84 g m^{-2} (w.w.), with a mean of 7.24 g m^{-2}. They represented 98 % of the total biomass. Their mean individual weight was then 4.7 mg compared with 2.1 mg on 20 June 1980, when they also were less abundant. In all years, but especially before 1979, intense hatching of chironomids took place in Nesjø from ice-out to the middle of July.

Fish

Catch per unit effort

Except for midsummer 1972, Arctic char gave the highest biomass per net in Essand (Fig. 11). From 1967 to 1971 these catches were 570 to 960 g net^{-1} in early summer and midsummer, and 1,400 to 1,780 g net^{-1} in the spawning period in September. The summer catches were lower in 1972–73 and higher in 1977 and 1979. The September catches, representing spawners, grew steadily from 1971 to 1977–79. Only a few, mainly small, char were caught in Essand in June 1983.

Before 1972 only small quantities of brown trout were taken in Essand. More were caught in 1972–73, with a maximum of 630 g net^{-1} in July 1972. Later the catches fell to the initial level. The catches of burbot in Essand were also higher in 1972–79 than before. However, a few large burbot represented the maximum in autumn 1979.

In Nesjø the catch in July 1970 was 680 g net^{-1} of trout and a few char and burbot. It increased to 2,500 g net^{-1} of trout in autumn 1970. Later the proportion of trout declined, and after 1973 only a few were taken. Only occasional char

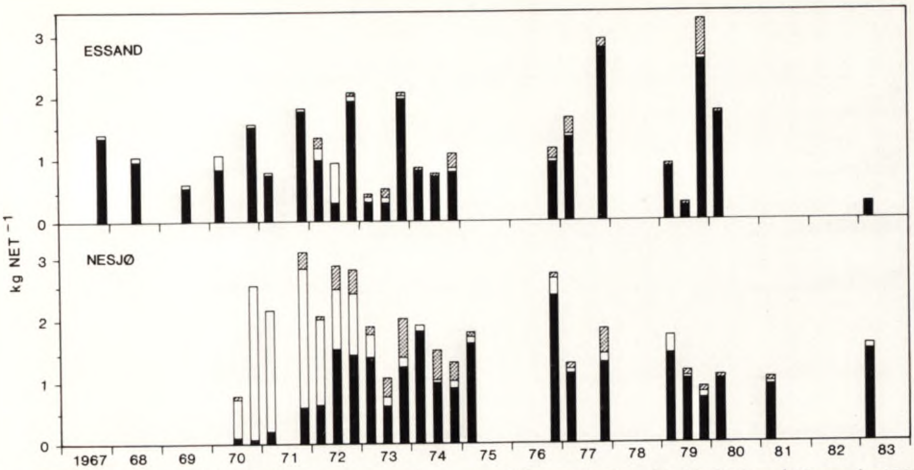

Fig. 11. Catch per effort (kg net^{-1}) in the littoral zone as the mean of the mesh sizes 26, 29, 31.5 and 35 mm in 1967–83, in early summer (before 5 July), midsummer (5 July–20 August) and autumn (21 August–30 September). Black columns represent Arctic char, open brown trout, and hatched burbot.

were caught in Nesjø before the water reached Essand in July 1971. Apart from some seasonal variations, the catch of char increased from then until September 1976 when the maximum of 2,380 g net^{-1} was obtained. Later it decreased to about 1,000 g net^{-1} in 1979–81. The catch in June 1983 was again higher, 1,500 g net^{-1}. The burbot catch usually increased through the season. The September catch increased from 1970 to 1973, reaching a maximum of 640 g net^{-1}. Afterwards it declined and was <90 g net^{-1} in 1979–81.

Fig. 12 shows the corrected numbers caught per series of nets (N_c) of the different species and their length frequencies. N_c of Nesjø trout and its length distribution in July 1970 was almost identical to that of the river Nea trout from August 1968, most fish being <24 cm. In autumn 1970 N_c increased to a maximum of 80, and the peak length to 24–27 cm. After that N_c declined and the general length increased until June 1973. The length frequency in autumn one year and early summer the next year was very similar, but N_c declined during winter. The winter loss was 40 % both in 1971–72 and 1972–73. Since 1974 only occasional trout have been taken in Nesjø, a parallel to the Essand situation.

In September 1971 a strong class of burbot of length 18–24 cm suddenly appeared in Nesjø. Age analyses proved them to be two years old. They could be followed as a peak of increasing length throughout 1972–73. More strong year classes followed, and N_c of the autumn catches in 1972–76 was comparable, 47–57. After 1976, the burbot population collapsed and N_c was only 7 in September 1979.

The initial N_c of Essand char was about 50 for June catches and 100 for September catches. Only very few char were >30 cm. From 1972 to 1976 N_c of both June and September catches fell. The small catch of June 1973 is obviously not representative. It is probably a result of the specially low water temperature. During the same period N_c of the Nesjø catches increased from 3 in October 1970 to a maximum of 65 in September 1976. Many of the Nesjø char were >30 cm, the majority in June 1971–74. Some of these returned in September to the spawning grounds in Essand, from where they had mainly disappeared again the following June. N_c of the Essand char suddenly increased to the maxima of 66 in June and 151 in September 1977. From then it declined to a minimum of 26 in June 1983. Simultaneously, N_c of Nesjø char fell to half of the former level in 1977, remained like that until 1983 when it suddenly increased to 42. After 1975 the number of char >40 cm declined.

Compared with trout and burbot it was more difficult to catch char <20 cm. However, some

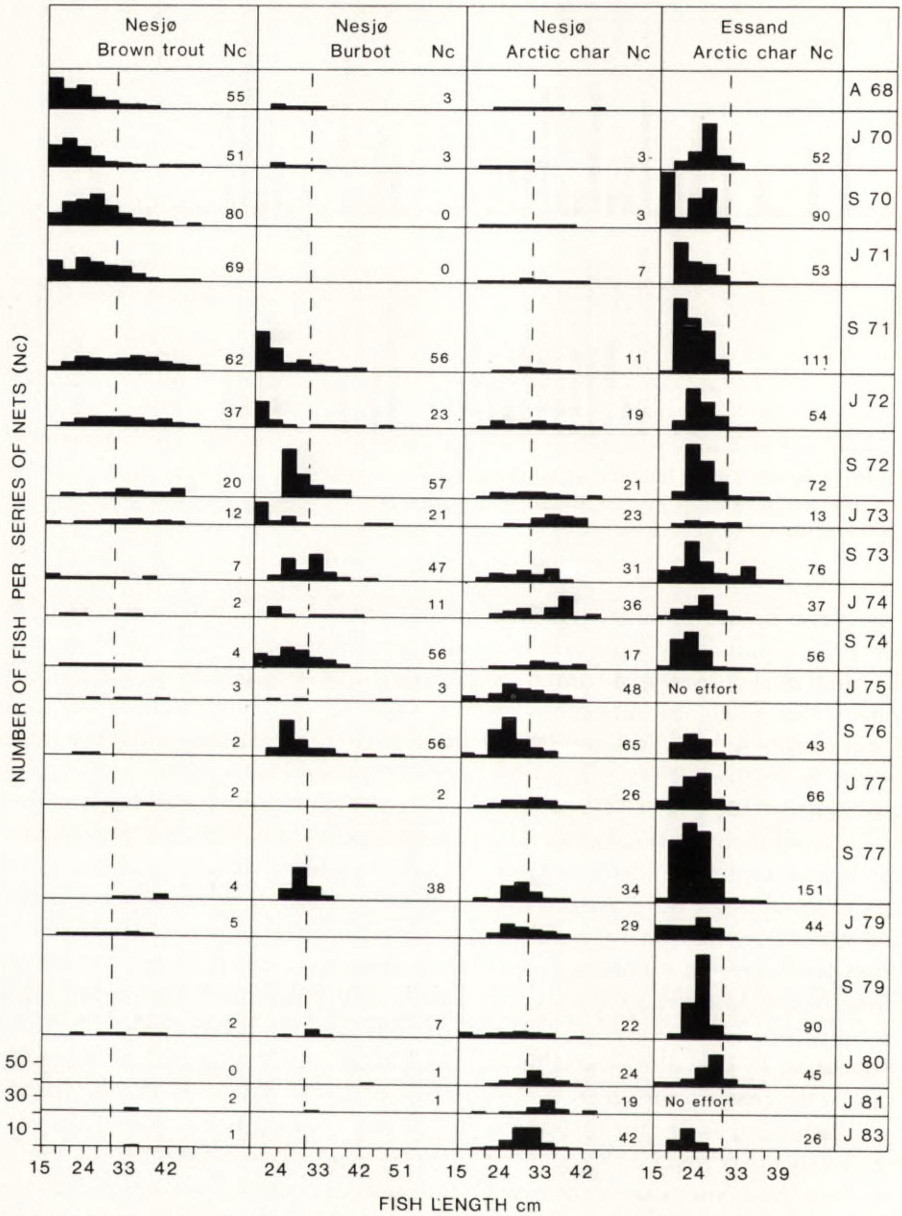

Fig. 12. Number of fish caught per series of nets in the littoral zone and corrected for efficiency relative to fish length (N_c), pooled in 3 cm length classes. The catches were taken in June or early July (J) and September (S) 1970 to 1983 in the Nesjø and Essand reservoirs, and in August 1968 in the river Nea (A68). The September results include the Nesjø catch of October 1970.

classes of young char can be identified. For example, that of peak size 15–18 cm in September 1970 can be traced through 1971–72. That length group was also noticeable in 1973 and 1979.

N_c of Essand trout reached a maximum of 10 in July 1972, but was generally 1–3. For Essand burbot the September N_c had a maximum of 24 in 1974, and otherwise oscillated between 5 and 10 from 1973 to 1977, and was only 0–4 before and after that period.

Floating nets were used on 11 occasions from

Table 15. The total numbers (No.) caught using floating nets from 1972 to 1980, and mean length L (cm) of Arctic char.

	Brown trout No.	Arctic char No.	Arctic char L	Burbot No.
Nesjø	1	192	28.6	0
Essand	0	269	23.7	1

1972 to 1980. The catches showed that the char also lived in the open water, whereas trout and burbot were restricted to the bottom or the littoral zone (Table 15). The mean length of Nesjø char was always significantly higher than that of Essand char. The difference declined from 10.1 cm in July 1972 to 1.2 cm in July 1979.

Food

The differences between the diets of Nesjø char caught in the littoral zone and in open water were small (Table 16). They were more marked in Essand, where the first group took more Chironomidae larvae versus pupae, various aquatic animals versus surface organisms, and in late September its own roe versus plankton.

Fig. 13 presents the diet of the main groups of salmonids. The presentation is both qualitative and quantitative, as the unit is a stomach fullness of 1.0 for a sample of fish. Unless otherwise specified, the "various" groups represent Trichoptera larvae, Hydradephaga larvae and imago, and a few other aquatic insects and snails. Chironomidae include larvae and pupae, the adults being grouped with surface organisms. In June and the first 2–3 weeks of July surface organisms were almost exclusively adult chironomids. Later in summer they comprised various insects and some Araneae, always with a predominance of Diptera.

In July 1970 the Nesjø trout were feeding on survivors of the former river fauna and earth-

Table 16. Stomach contents as mean per cent volume of Arctic char caught in bottom (b) and floating (f) nets on the same day.

Date	Net type	Planktonic crustaceans	Chironomidae larvae	Chironomidae pupae	Surface org.	Various
			ESSAND			
27 July 1972	b	30	15	8	15	32
	f	41	0	31	8	0
27 July 1979	b	23	1	8	48	20
	f	9	3	16	67	5
9 Aug. 1974	b	32	1	3	53	11
	f	28	1	5	65	1
4 Sep. 1977	b	95	0	0	4	1
	f	58	0	0	40	2
25 Sep. 1974	b	56	0	0	3	41
	f	98	0	0	0	2
			NESJØ			
29 July 1973	b	1	14	17	34	34
	f	9	3	22	66	0
10 Aug. 1974	b	35	3	18	35	9
	f	33	5	26	23	13
9 Sep. 1972	b	100	0	0	0	0
	f	100	0	0	0	0
7 Sep. 1977	b	84	1	0	0	15
	f	99	1	0	0	0
29 Sep. 1974	b	86	6	0	0	8
	f	86	13	0	0	1

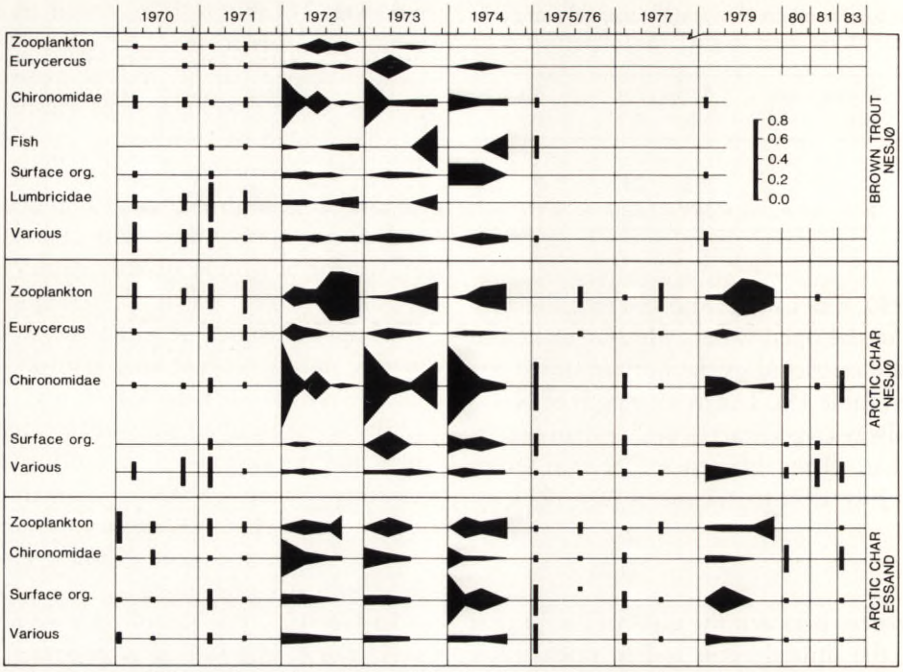

Fig. 13. Stomach contents of Nesjø salmonids and Essand Arctic char in June–October calculated as 0.01 V F, where V is mean per cent volume of the stomachs examined, and F mean fullness of all stomachs in a sample. Unit is a fullness of 1.0.

worms (Lumbricidae). Larvae of the Ephemeroptera *Siphlonurus lacustris* Etn. comprised 41 %, other insect larvae 30 % and earthworms 25 % of the food. In October various aquatic insects made up 46 %, earthworms 24 % and *B. longimanus* and *E. lamellatus* 20 %. In early July 1971 earthworms were at their maximum with 52 %, but in September they had declined and the trout again took more of *B. longimanus*, *D. galeata*, *E. lamellatus* and Chironomidae larvae. The 1972 results give detailed information about a food pattern which, with some variations, existed until 1975. In late June the stomachs contained large quantities of Chironomidae larvae. In early July chironomids, now mainly represented by pupae, were declining. Entomostraca were increasing to culminate in mid-August. From late September to early November earthworms and fish predominated. In this period fish meant burbot yearlings exclusively, some char <20 cm being taken earlier in the season. The trout took most zooplankton, *B. longimanus* and *D. galeata*, in 1972–73. Most *E. lamellatus* were consumed in 1973, comprising 57 % in July. Chironomidae larvae were eaten in equal amounts in 1972 and 1973. They decreased in 1974, but consumption of adult chironomids meant that the importance of the group was maintained. Juvenile burbots were intensively consumed in September–October, comprising 67 % in 1973 and 69 % in 1974. In addition to adult chironomids, other insects drifting on the surface were specially important in 1974.

In July 1970 Arctic char fed mainly on planktonic crustaceans (52 %), and otherwise on *E. lamellatus*, various water insects and a few earthworms. The relative proportions of Entomostraca and the other groups switched in October. Entomostraca and Chironomidae increased and other aquatic insects declined in 1971. Entomostraca, mainly planktonic ones, made up 92 % in early September. From 1972 until 1980 the Nesjø char, too, showed a regular pattern of food intake, chironomids again playing a very dominant role. From ice-out in 1972 the stomachs were almost filled with Chironomidae larvae, mean fullness being 0.77. These declined in importance through the season, *E. lamellatus* being at a maximum and planktonic cladocerans increasing in early July. From early September the char fed almost exclusively on zooplankton. In 1973 more chironomids and less plankton were consumed. Surface organisms made up 46 % in late July. 1974 was a repetition of 1973, but *E. lamellatus* was on the decline. Throughout 1975–79 the stomachs were less full, but the quality pattern was maintained. The "various" group comprised in general the same organisms as were eaten by trout, but *Pisidium* contributed a constant, but small, proportion. In contrast to trout, char never ate many earthworms, the maximum of 9 % occurred in July 1971. In June 1981 Trichoptera larvae of the species *Agrypnia obsoleta* (Hag.) made up 57 % and Chironomidae larvae only 13 %. In June 1983 the char had again turned to chironomids.

Except for the earthworms, animals of terrestrial origin were of minor importance as fish food during the flooding phase, as they never exceeded 1 %. The main representatives were larvae of various Coleoptera, Diptera and a few Araneae.

In the whole period from 1970 to 1983, the food pattern of the Essand char was qualitatively similar to that found in Nesjø from 1972. 1970 was an exception, as zooplankton was the main food as early as June. More surface insects were eaten, and they were especially important in 1974 and 1979. The "various" group comprises the same organisms as taken by the Nesjø char, and in addition a few *E. lamellatus*. The Essand char always had less food in their stomachs than the Nesjø char.

In samples from 1 April and 12 May 1973 Chironomidae larvae comprised 50–60 % of the stomach contents of Essand char. The fullness was 0.23 and 0.27, but digestion is slow at winter temperatures.

The Essand trout fed mainly on Trichoptera larvae in early summer and surface organisms and yearlings of burbot later (Fig. 14). The diet of Nesjø burbot in 1973–79 was similar to that of trout, but included fewer surface organisms and no zooplankton. The mean fullness of their stomachs was low, as a high proportion was always empty.

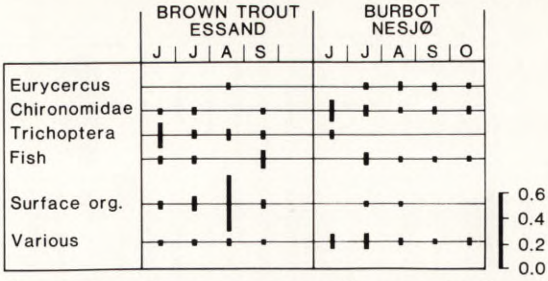

Fig. 14. Stomach contents as monthly means for Essand brown trout in 1970–79 and for Nesjø burbot in 1973–79, calculated as 0.01 V F, where V is mean per cent volume of the stomachs examined and F mean fullness of all stomachs in a sample. Unit is a fullness of 1.0.

The consumption of planktonic crustaceans by char is presented at the species level in Fig. 15. The Nesjø char ate mainly *D. galeata*, and in large quantities during the second half of the growth season. *B. longimanus* predominated in September 1971, and *B. longispina* in early July 1972. At other times these two species and *H. gibberum* were more or less constant, but unimportant, elements of the diet. Essand char predation was directed towards all cladocerans present. A dominant pattern existed, involving the taking of *B. longispina* in early and *D. galeata* in late summer. *H. gibberum* was a more constant prey of less importance. *B. longimanus* was eaten sporadically, in small quantities. The Essand char also turned to copepods in 1972–73. In both years a few adult *Diaptomus* were eaten in June. Later in the summer a few char had turned exclusively to adult and Cop. 5 *H. saliens*. Their stomachs were much fuller than those of the char feeding on cladocerans.

Table 17 presents the consumption of the various prey accumulated over certain growth seasons, 15 June to 30 September. Chironomids were the most important food of Nesjø trout in 1972–73. Other main groups were zooplankton in 1972 and *E. lamellatus* in 1973. Trichoptera larvae, fish and various other groups totalled 37–

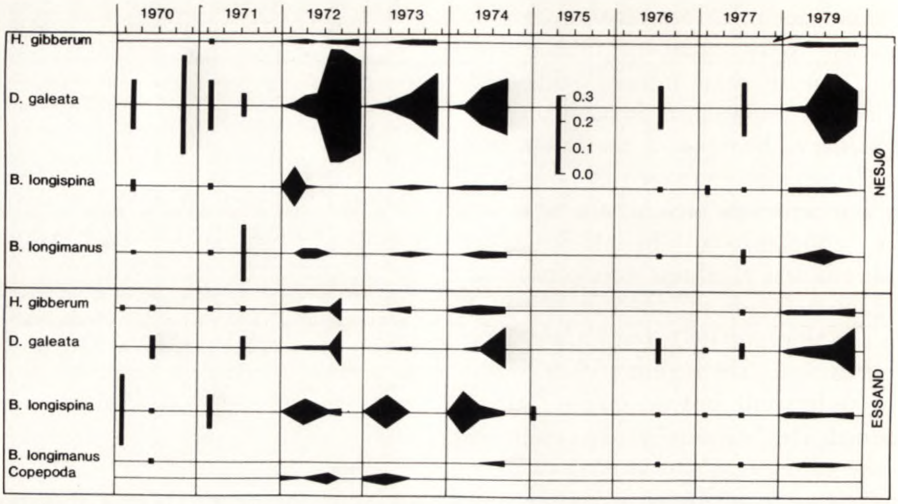

Fig. 15. Planktonic crustaceans in stomachs of Arctic char given as 0.01 V F, where V is mean per cent volume of the stomachs examined and F mean fullness of all stomachs in a sample. Unit is a fullness of 1.0.

44 %. The main food of the Essand trout throughout 1970–79 was surface organisms followed by Trichoptera larvae, together representing 67 %. *D. galeata* and chironomids made up 60–80 % of the food of the Nesjø char. For Essand char these two groups constituted 25–40 %, the difference being compensated for by eating more of the other planktonic crustaceans and surface organisms.

The Nematoda (Table 17) were entozoic parasites of Chironomidae pupae and adults. They occurred in small amounts, never exceeding 1.6 %, in Essand fish throughout the research period. They were first noticed in Nesjø fish in

Table 17. Stomach contents accumulated over the growth period 15 June to 30 September, calculated as Σ 0.01 V F t, where V is mean per cent volume and F mean fullness in a period of t days.

	NESJØ						ESSAND				
	Brown trout		Arctic char				Brown trout	Arctic char			
	1972	1973	1972	1973	1974	1979	1970–79	1972	1973	1974	1979
H. gibberum	—	—	0.6	0.1	—	0.1	—	1.9	2.8	1.8	0.5
D. galeata	2.3	0.1	21.1	7.6	14.3	13.1	—	1.6	1.3	4.3	7.5
B. longispina	—	—	0.3	0.1	0.1	0.3	—	4.0	4.3	4.8	1.3
B. longimanus	4.1	0.9	2.6	0.6	1.0	2.9	—	—	0.1	0.5	0.3
Copepoda	—	—	—	—	—	—	—	3.9	1.4	—	—
Zooplankton	6.4	1.0	24.6	8.4	15.4	16.4	—	11.4	9.9	11.4	9.6
Eurycercus lamellatus	2.9	8.0	6.3	6.9	0.9	3.1	0.4	0.4	0.1	0.4	0.1
Chironomidae l. & p.	9.4	12.8	17.8	24.5	24.6	9.8	1.8	9.6	6.5	4.3	3.4
Trichoptera l.	1.4	3.5	0.5	1.4	—	0.9	5.6	0.3	1.0	0.1	0.5
Pisidium	—	—	0.7	1.4	1.3	2.3	—	1.5	1.0	0.9	1.1
Fish	1.8	0.9	—	—	0.3	—	4.3	—	0.1	0.1	0.3
Nematoda	—	—	—	—	1.5	1.3	—	—	—	0.1	0.3
Surface org.	3.6	3.1	0.2	10.5	8.9	1.0	10.3	4.9	6.9	14.9	8.2
Lumbricidae	1.5	0.4	0.2	—	—	—	—	—	—		
Roe of Arctic char									0.5	0.5	0.5
Various	1.4	3.1	0.5	0.5	1.0	2.1	1.5	2.9	0.4	1.0	2.5
Sum	28.4	32.8	50.8	53.6	53.9	36.9	23.9	31.0	26.4	33.7	26.5

Table 18. The quantity of food (g m^{-2} d.w.) consumed by the Nesjø salmonids during the ice-free period, 15 June–31 October, in 1972 and 1979, based on the consumption by mean-sized fish calculated as in Table 24 and the population estimates.

	1972			1979
	Brown trout	Arctic char	Sum	Arctic char
Daphnia galeata	—	0.86	0.86	0.46
Other Entomostraca	0.17	0.38	0.55	0.10
Chironomidae	0.32	0.94	1.26	0.50
Fish	0.08	—	0.08	—
Other preys	0.21	0.10	0.31	0.37
Sum	0.78	2.28	3.06	1.43

1974, and occurred in increasing quantities until June 1979 when they made up 16 % of the stomach contents, almost every Chironomidae pupa and adult being infected. The abdomen of the hosts apparently contained nothing but nematodes.

The mean fullness of the stomachs of Nesjø char was about 0.5 over the growth seasons of 1972–74. This is a high figure for fish netted over 10–11 hours when all empty stomachs are included. In 1979 the mean seasonal fullness had decreased to 0.34. The stomachs of Nesjø trout contained less, the mean seasonal fullness being comparable to that of the Essand char, about 0.30.

After correction for the effect of digestion and the number of meals per day, the total food consumption of the Nesjø salmonids in the ice-free season was calculated to be 3.06 g m^{-2} (d.w.) in 1972, of which the char took 2.28 g m^{-2} (Table 18). In 1979 the char took 1.43 g m^{-2} or 63 % of the 1972 quantity. Calculated as dry weight, the chironomids outweighed *D. galeata*. From 1972 to 1979 other Entomostraca, including *E. lamellatus*, had declined. Other prey, mainly Pisidium, Nematoda and various insect larvae, had increased.

Sex ratios, maturing and spawning

Spawners and post-spawners of Arctic char were taken in the last two weeks of September. A highly significant predominance of males existed in the littoral zone throughout September, especially in Essand (Table 19) where the maximum of 87 % was recorded in September 1971. Otherwise, the accumulated catches showed no significant difference between the sexes.

The brown trout reached sexual maturity at a minimum length of 25 cm. 9 % of the trout taken in the river Nea in 1968 were mature. This proportion increased to 21 % in 1970, but fell to only 4 and 3 % in 1971–72.

Of the initial Essand char population, more than 70 % of size >25 cm were mature. The smallest mature males were only 18 cm (Fig. 16). In Nesjø, as shown by the example from 1974, the limit for general sexual maturing increased to 30 cm. The proportion of mature char >20 cm was no less than 70% in both reservoirs in 1972 (Table 20). During 1973–74 it decreased to the initial level, but in 1977–79 had again increased to about 60 %, with minor differences between the two reservoirs. With the exception of 1976 and 1977, the proportion of mature char de-

Table 19. The percentages of males and females in total catches. Values significantly ($P<0.05$) different from an equal distribution are marked by *.

Locality	Species	Period	Males	Females
Essand	Arctic char	before 5 Sep.	48.7	51.3
Essand	Arctic char	after 5 Sep.	74.6	25.4*
Nesjø	Arctic char	before 5 Sep.	48.7	51.3
Nesjø	Arctic char	after 5 Sep.	60.2	39.8*
Nesjø	brown trout	all season	52.7	47.3
Nesjø	burbot	all season	47.2	52.8

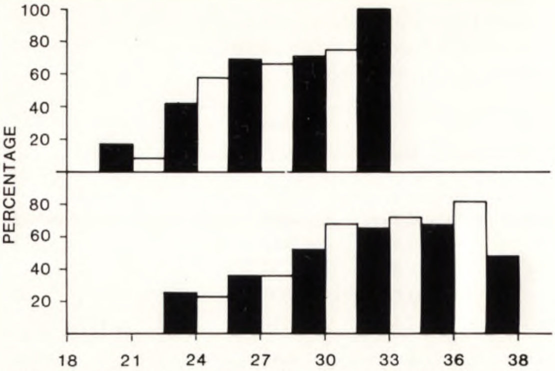

Fig. 16. Percentages of sexually mature females (open columns) and males (black columns) of Arctic char caught before September, above in the Essand reservoir 1971, below in the Nesjø reservoir 1974.

creased in Nesjø and increased in Essand in September. The spawners generally left Nesjø for the spawning areas in the tributaries and along the shores of Essand. Spawning char have never been observed or reported from Nesjø itself, but spawning takes place in its tributaries. Nøsteråa is an Essand tributary (Fig. 1) probably run by several thousands of spawning char. On 30 June 1977, 1 km of Nøsteråa was electrofished. No fish of any species was observed. The fry of the char probably drift downstream as soon as they leave the substratum. The char run apparently prevents any spawning attempts from trout.

Table 20. The percentages of sexually mature Arctic char >20 cm caught in bottom nets before and in September.

	NESJØ		ESSAND	
Year	Before Sep.	In Sep.	Before Sep.	In Sep.
1971	65	33	49	94
1972	75	24	70	93
1973	40	22	58	96
1974	56	10	49	77
1975	43	—	—	—
1976	—	91	—	98
1977	61	72	61	97
1979	53	13	58	99

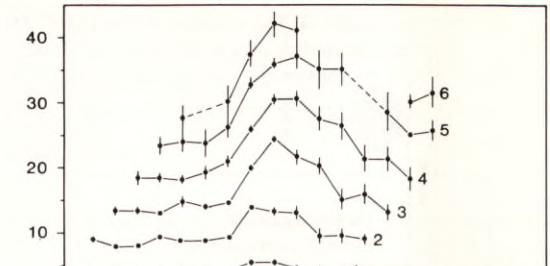

Fig. 17. Mean length of the different age classes of brown trout, Arctic char and burbot at the start of the growth season. Ranges of confidence ($P<0.05$) are shown by vertical bars, except for burbot and 7 year-old char in Nesjø.

Growth

Growth in length: The river Nea brown trout grew almost 5 cm annually throughout their first 6 years (Fig. 17). In 1970–71 the growth increased to more than 11 cm for 3 and 4 year-old trout, and somewhat less for the older ones. The mean length of 6 year-old trout reached a maximum of 42 cm in 1972. Afterwards, growth steadily decreased for all age classes. In 1977–78 it had declined to the initial level for age classes 3 and 4, while older trout still grew somewhat better than before impoundment. The 2 year-old trout were influenced less, and the yearlings almost not at all, by the improved conditions for growth.

In 1970–71 the mean length of Essand char was 21.5 cm by the age of 4. For older char the growth declined with age, so that the mean length of age class 7 was 29 cm. Specimens >30 cm occurred only occasionally. The material selected for growth analysis showed no basic variation from this throughout 1972–83, except for some decreased growth of age classes 3 and 4 in 1978–79. The larger char taken in Essand during this period (Fig. 12) must have returned from Nesjø, as shown by their better growth and higher condition factor. Age class 3 is only represented by fast-growing individuals, because the efficiency of the nets was very low for the smaller ones.

All age classes of Nesjø char increased in length during 1970–72, and those aged 6 and 7 also in 1973–74 (Fig. 17). In 1974 the mean length of 7 year-old char was almost 40 cm. From then the length decreased until 1978, when age classes 3 and 4 equalled Essand char of corresponding age. It again increased somewhat from 1978 to 1983, when all age classes, especially the older ones, were still significantly longer than Essand char of corresponding age.

The analyses based on scale readings show that Nesjø trout and char of initial length 15–25 cm grew 11.6 cm and 10.8 cm, respectively, in 1970. Later their growth decreased parallelly. The individual growth of char and trout was about the same, but the mean length of corresponding age classes of char was less, a consequence of poorer juvenile growth in Essand.

The length of Nesjø burbot decreased from 1972 to 1977, when it seemed to level off. Three and 4 year-old burbot were always longer than salmonids of the same age. The mean length of 3 year-old burbot was 31 cm in 1972. This represents an annual increase in length equivalent to the maximum for Nesjø trout and char. The growth of the larger burbot was much poorer.

Condition factor: Sexual maturation and differences in length had little influence on the condition factor (K) of Essand char in 1970 (Fig. 18). The 1972 situation was typical for the Nesjø fish. Trout >20 cm showed no and burbot only small, random variation with length. The condition factor of the smallest char equalled the initial one of the Essand char. For the larger char it increased with length to K=1.50 for mature char >30 cm. The difference between immature and mature Nesjø char was also small.

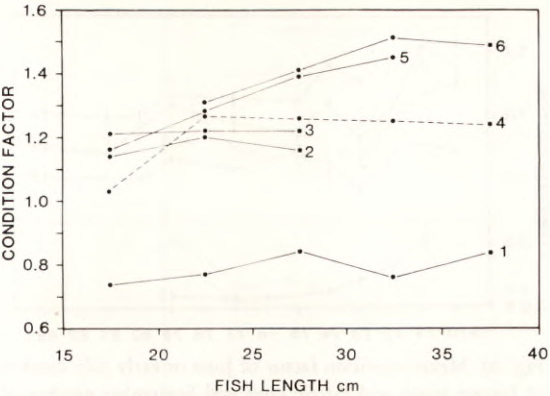

Fig. 18. Mean condition factor of fish grouped in 5 cm length classes. 2 is immature and 3 mature Arctic char from the Essand reservoir on 20 August 1970. 1 is burbot, 4 brown trout, 5 immature and 6 mature Arctic char from the Nesjø reservoir on 28 July 1972. Limits of confidence ($P<0.05$) $<\pm0.08$.

Significant seasonal variation in the condition factor was found for all groups of fish, as shown by the data from 1972 (Fig. 19). Mean K of burbot decreased slightly during the summer, and started to increase again in October. For trout it increased from ice-out to a maximum of 1.26 by the end of July, and then decreased to 1.13 in October. An increase took place for all groups of char until September. Later there was some decrease, which only in the case of Essand char included the effect of post-spawners. The differ-

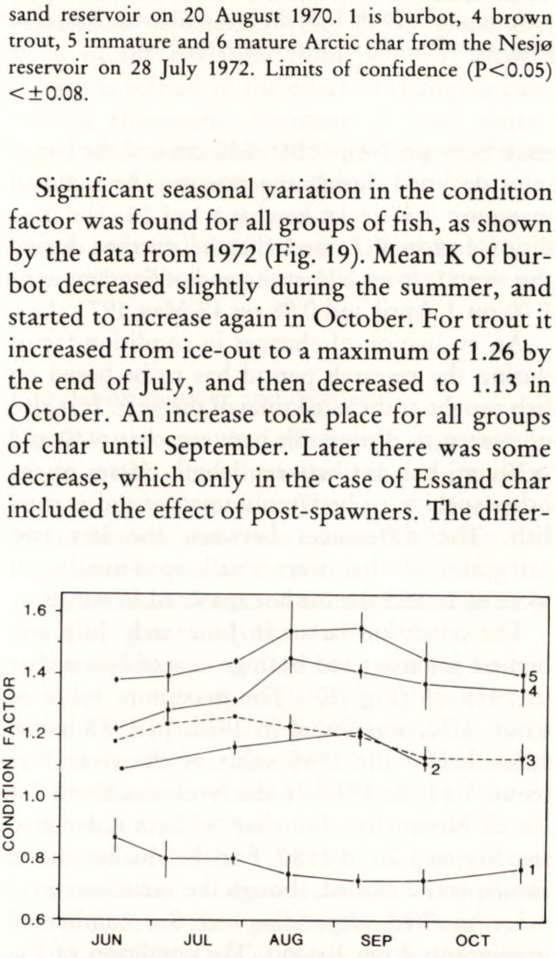

Fig. 19. Mean condition factor in the ice-free period of 1972. 2 is Arctic char ≤30 cm from the Essand reservoir. 1 is burbot, 3 brown trout ≥20 cm, 4 Arctic char ≤30 cm and 5 Arctic char >30 cm from the Nesjø reservoir. Ranges of confidence ($P<0.05$) are shown by vertical bars.

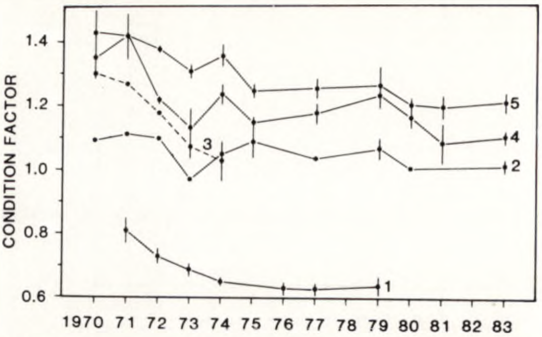

Fig. 20. Mean condition factor of June or early July catches of brown trout and Arctic char and September catches of burbot. 2 is Arctic char ≤ 30 cm from the Essand reservoir. 1 is burbot, 3 brown trout ≥ 20 cm, 4 Arctic char ≤ 30 cm and 5 Arctic char >30 cm from the Nesjø reservoir. Ranges of confidence ($P<0.05$) are shown by vertical bars.

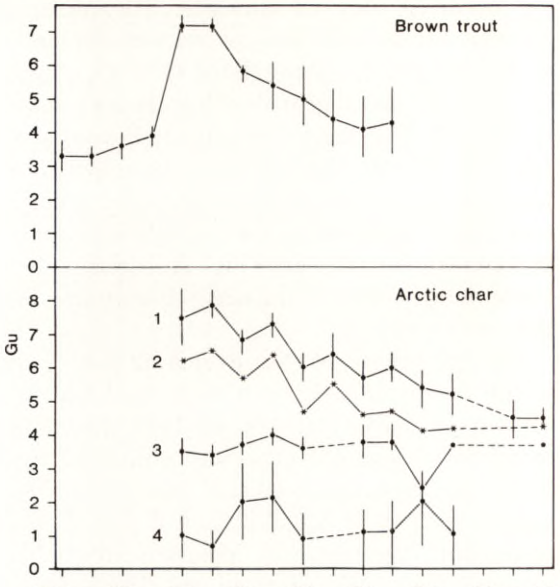

Fig. 21. Mean size-independent growth rate in weight as % day^{-1} (G_u) in the period 15 June to 30 September, for Nesjø brown trout of initial size 15–25 cm and Arctic char of the following categories: 1 Nesjø char of initial size 15–25 cm, 2 Nesjø char of initial size 25–30 cm, 3 Essand char of initial size 15–20 cm, 4 Essand char of initial size 25–30 cm. Ranges of confidence ($P<0.05$) are shown by vertical bars, except for Nesjø char of initial size 25–30 cm.

ence between Nesjø char ≤ 30 cm and the larger ones declined during the season. The seasonal maximum for the larger char was 1.54. The condition factor of Essand char fell further during the winter, from 1.11 at the end of September to 1.00 on 1 April and 0.98 on 12 May 1973.

An evaluation of changes in condition factor during the research period has to be based on fish caught at the same time of the year. It is also necessary to distinguish between char ≤ 30 and >30 cm, but not between length classes of the other species, or between immature and mature fish. The differences between the last two categories of char were small, spawning trout were rare, and the burbot spawned in winter.

The condition factor in June–early July was highest for trout and both groups of Nesjø char in 1970–71 (Fig. 20). The maximum value of trout, 1.30, was found in 1970. In 1973 it had fallen below the 1968 value of the river Nea trout, 1.11. In 1970–71 the level was about 1.4 for all Nesjø char. For char >30 cm it declined steadily to 1.20 in 1980. For the smaller char a similar trend existed, though the variations were more marked, depending on the number of immigrants from Essand. The condition of Essand char varied between 1.11 and 1.01, with a slightly falling trend throughout the research period. The seasonal peak values in 1970–73 were of the levels shown in Fig. 19. The condition factor of Nesjø char >30 cm was at its maximum of 1.59 in September 1971. In 1979 it had fallen to 1.38, and was 1.35 for the smaller char. It was especially low for all groups of char in 1973.

The condition factor of Nesjø burbot taken in September showed a similar trend to that of trout, falling from 0.81 in 1971 to 0.63 in 1976, when it levelled off.

Growth in weight: The mean size-independent growth rate in weight (G_u) of river Nea trout of initial length 15–25 cm over the period 15 June to 30 September was 3.3–3.6 % day^{-1} (Fig. 21). In 1970–71 it reached 7.2 % day^{-1} for Nesjø trout, steadily declining thereafter to a level just above 4 % day^{-1} in 1977. Low numbers of trout caused wide ranges of confidence in later years. G_u of Essand char of initial length 15–20 cm was close to 3.5 % day^{-1}. throughout the research period, except for 1978 when it fell

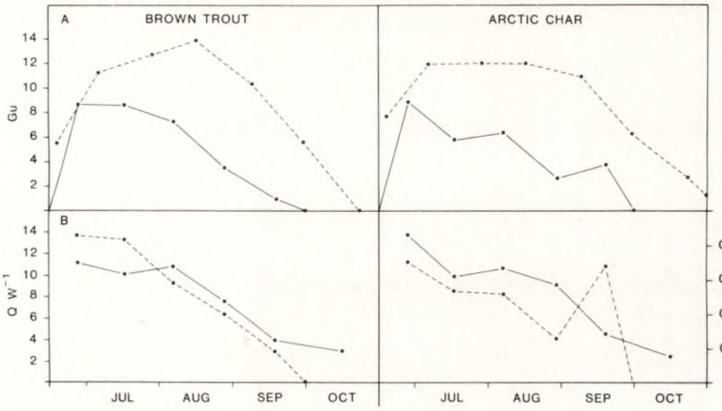

Fig. 22 A. Potential size-independent growth rates in weight as % day^{-1} (G_u) for salmonids of initial length 20 cm, calculated from equations (10) and (11) and the recorded temperatures in the Nesjø reservoir in 1972 (broken lines), and the corresponding achieved rates (solid lines).

B. Daily food consumption as mg d.w. per g round fish weight ($Q\ W^{-1}$) for Nesjø salmonids of initial length 20 cm in 1972 (solid lines), and the corresponding periodical gross food conversion efficiency (k_1).

to 2.4 % day^{-1}. For Essand char of initial length 25–30 cm it was generally about 1 % day^{-1}. The highest G_u, 7.9 % day^{-1}, was recorded in 1971 for Nesjø char of initial length 15–25 cm. Later this decreased steadily to 4.5 % day^{-1} in 1983. G_u of Nesjø char of initial length 25–30 cm was constantly 1.5 units below that of the smaller char until 1978, when it levelled off. In 1983 it was just below that of the smaller char.

The coefficient of size-dependent growth is unknown for burbot. The annual mean growth rate in weight (G) of Nesjø burbot of initial length 15–20 cm decreased from 0.31 % day^{-1} in 1971 to 0.25 % day^{-1} in 1977.

In 1972 the size-independent growth rate of both Nesjø salmonids was highest just after ice-out (Fig. 22 A), when it reached 8.7 % day^{-1} for trout and 8.9 % day^{-1} for char. It declined to zero at the end of September, rather evenly for the trout and more stepwise for the char. No growth took place at temperatures below 7°C. Char grew better than trout at temperatures below 11°C, and less when the water was warmer, even with fuller stomachs (Fig. 22 B). The potential maximum growth rate in relation to temperature was only achieved in June. For the rest of the growth period an evenly increasing deviation existed between the potential growth rate of trout and the one achieved. The growth rate achieved by char fell to 48 % of the potential one already in the middle of July, to recover to 55 % in September. The seasonal growth rate patterns were influenced by declining food consumption and declining gross food conversion efficiencies (Fig. 22 B). Generally, 80 % of the deviation from potential growth rates was related to the effect of changing conversion efficiencies. Shortage of food contributed to no more than 20 % deviation for trout in July and char in September.

The trout had obtained 43 % of its seasonal length increase on 15 July 1970 and 21 % on 7 July 1971, which agrees with the 1972 growth cycle.

Population number and biomass

Fig. 23 presents the relative development in numbers (N_c) and the estimated density numbers of the salmonids. The initial density of Nesjø brown trout was about 2,000 km^{-1} of shoreline. It was at its peak of 3,000 km^{-1} in 1971, and had decreased to the Essand level of about 100 km^{-1} in 1974.

The September catches of spawning Essand char are not comparable with other catches. Based on the June–early July catches, the initial Essand density was almost 200 ha^{-1}. From 1972 to 1976 the density declined to about half the initial, while that of Nesjø increased steadily to a maximum of 235 ha^{-1}. In 1977 the proportions between the reservoirs were completely changed. From then on the Essand density declined steadily. That in Nesjø decreased slowly to 75 ha^{-1} in 1981, to increase to 150 ha^{-1} in 1983.

Initially burbot were caught only occasionally. The Nesjø catch in September 1971 included a large number of small burbot. In Sep-

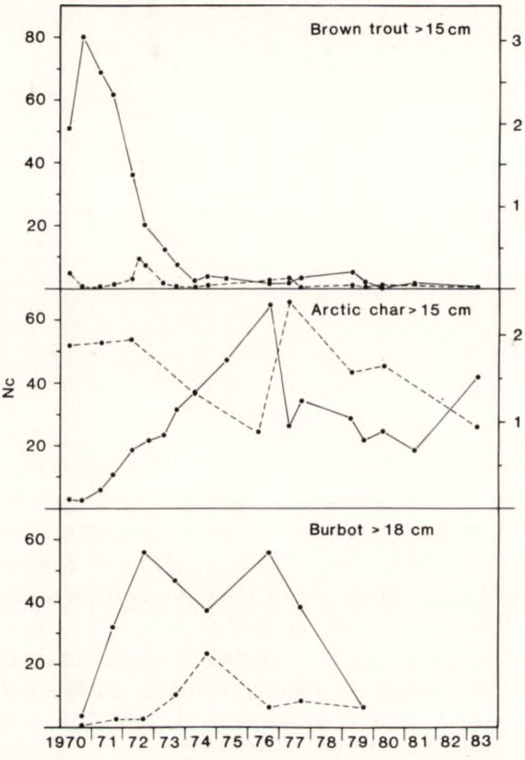

Fig. 23. The numbers of fish caught per series of nets in the littoral zone and corrected for efficiency relative to fish length (N_c) in the Nesjø reservoir (solid lines) and the Essand reservoir (broken lines). Density estimates of brown trout related to shoreline (No. km^{-1}) and of Arctic char related to area (No. ha^{-1}), based on the relationships in Fig. 3. Data for Essand char are based on June or early July catches, for burbot on September catches, and for the others on catches from both periods.

tember 1972 N_c of burbot >18 cm was 57. It declined to 37 in 1974, partly due to emigration to Essand, where N_c increased to a maximum of 24. In Nesjø the 1972 level was again reached in 1976. Later the density fell to the initial Essand level. In 1980–83 N_c of June catches was 0–1, compared with more than 20 in 1972–73.

The number of Nesjø trout reached its peak in 1971 at an estimated 150,000 (Fig. 24). Since 1974 it has been around 10,000. The total population of char reached its maximum in 1976, equivalent to 1 million, with 78 % in Nesjø. It declined between 1976 and 1979 to a number somewhat above the initial one of 450,000. After 1979 the number increased again, and was estimated to be 770,000 in 1983.

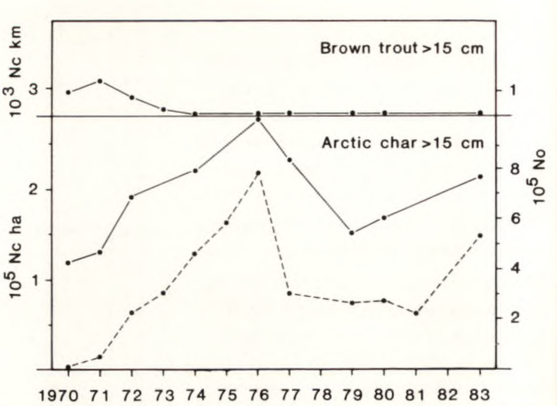

Fig. 24. Changes in Nesjø (broken line) and total population numbers (solid line) of salmonids >15 cm based on catches from June or early July. Relative scale is number per series of nets, corrected for efficiency relative to fish length (N_c), and multiplied by the length of the shoreline (km) for brown trout and surface area (ha) for Arctic char. Population numbers are based on the densities in Fig. 23.

The biomass density of Nesjø trout was at its maximum in 1971–72 with 12 kg per series of nets, equivalent to 500 kg km^{-1} (Fig. 25). That of char occurred in 1974, as the decrease in mean weight influenced more than the increase in number from 1974 to 1976. The peak value of

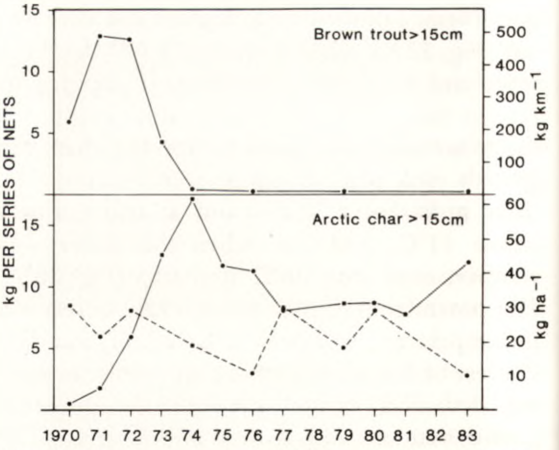

Fig. 25. Changes in Nesjø (solid lines) and Essand (broken line) biomass of salmonids >15 cm, based on catches from June or early July. Relative scale is kg per series of nets. Biomass as kg km^{-1} of shoreline for brown trout and kg ha^{-1} for Arctic char is based on the densities in Fig. 23 and mean weights of N_c.

Table 21. Population numbers of Arctic char ≥20 cm, catches in 1974–75 calculated from population numbers and fractions recaptured, reported catches of angling in 1978–80, and (in brackets) net catches in 1978–80 assuming that the effort was identical to 1974 and the catch per effort linear to population fractions exploited by nets.

	NESJØ			ESSAND		
	Population	Netted	Angled	Population	Netted	Angled
1974	462,000	45,000	21,000	335,000	4,000	7,000
1975	589,000	35,000	27,000			
1978	277,000	(20,000)	26,000	403,000	(5,000)	19,000
1979	264,000	(17,000)	18,000	283,000	(3,000)	13,000
1980	271,000	(28,000)	11,000	333,000	(4,000)	8,000

17 kg per series of nets is equivalent to 62 kg ha^{-1}. The initial June biomass level of Essand char was about 30 kg ha^{-1}. It fell below this during periods of intense emigration to Nesjø, but equalled the initial level in 1977 and 1980. At its peak in 1971–72 the biomass of Nesjø trout was found to be equivalent to 30,000 kg. The corresponding figure for the total char population was 270,000 kg in 1974, 82 % being in Nesjø.

Harvest

The intensity of fishing in Nesjø was low in 1970. As people learned about the high catches obtained, it gradually increased. Since 1978, 30 boats have been available in an organized hiring scheme. Only angling takes place from these boats, net fishing being reserved for the local fishermen.

Rough estimates of the harvest of Arctic char have been made, based on results from tagging experiments in 1973–74 described in the chapter on migrations. Ten char tagged in the Nøsteråa tributary and recaptured in its outlet, constituting high fractions of small catches, were disregarded when harvest was calculated. The other 13 Nøsteråa char recaptured in Essand represent a harvest there of 3.1 % of char ≥20 cm. About equal numbers were netted, angled through the ice and angled in summer. The 19 recaptures of Nea char in Nesjø give a harvest there of 18.1 % of char ≥29 cm. 75 % of these were netted and 25 % angled. Nesjø char <29 cm were assumed to have been angled with the same efficiency as the larger ones, and exposed to a harvest of 4.5 %.

The numbers angled before 1978, calculated from population numbers and percentages of recaptures, correspond with the records of 1978–80 (Table 21). In 1978 the harvest had increased from 4.5 to 9.4 % in Nesjø and from 2.1 to 4.7 % in Essand. This was a logical effect of the boat hiring and the increased fishing. These figures therefore support the reliability of the population numbers calculated for 1974–75. Further support is given by the following figures. In June-September 1974 our mean catch in Nesjø with mesh sizes 39 and 35 mm, those mainly used by the fishermen, was as high as 3.5 char per net. In October 1974 it was 10.8. At that time two men could net more than 300 char in a night. Only one of the 423 tagged in 1973 was among the 385 char of adequate size caught by us in Essand in 1974.

From 1978 to 1980 the catch per effort by angling declined, but increased again thereafter. The net catches given for 1978–80 are based on the assumptions that the effort was equal to 1974, and that the catch per effort was linear to the population numbers exploited by nets.

Based on the mean weights of char caught with 35 mm and larger meshes in Nesjø, 29 and 26 mm meshes in Essand and the angled ones, numbers caught were converted to weights. The limits for the annual harvest in Essand are then 2,000 and 4,700 kg, equivalent to 0.7 and 1.7 kg ha^{-1}. The Nesjø harvest declined from 38,000 kg in 1974 to about 18,000 kg in 1980, representing

9.8 to 4.7 kg ha^{-1}. The calculations refer to maximum surface areas. The Nesjø angling records varied from 2.2 kg ha^{-1} in 1978 to 1.2 kg ha^{-1} in 1980.

Migrations between the reservoirs

Movement of char between the two reservoirs was proven by tagging experiments. On 18–20 September 1973, 423 spawning char were caught in and just outside the Nøsteråa tributary, tagged and released in Essand (Fig. 1). On 18–21 September 1974, 105 char from the Nea tributary were tagged and released in Nesjø. Of the Nøsteråa char 31 (7.3 %) were recaptured, 8 of them in Nesjø. 10 were recaptured in the outlet of the Nøsteråa tributary in the spawning periods of the next two years. The Nea char were more stationary in Nesjø, as only one of 20 recaptures was in Essand. The localities of recapture reflected the intensity of fishing, located as they were along stretches sheltered from westerly winds.

Fig. 12 shows how the Nesjø char population was gradually recruited from Essand, and that a migration pattern was set up, the larger Nesjø char returning to the spawning grounds in Essand in September. Only a few of these were found in Essand the following June, when their number was generally at its maximum in Nesjø. They must therefore have left Essand sometime between October and June. In September 1973, 25 % of the spawning char in Essand had a condition factor higher than the former maximum, 1.35. Twenty % of these were also longer than the former maximum length. The figure of 25 % corresponds exactly with the fraction of spawners tagged in Nøsteråa and recaptured in Nesjø.

A connection existed between the water depth at the sill and the number of char moving between the reservoirs. In 1971–76, when the char population of Nesjø was growing, the sill made hardly any barrier (Fig. 4). In June 1977 the number of char in Nesjø suddenly fell by 60 %, and stayed at this level until June 1983. Throughout 1977–81 the char had the possibility of crossing the sill from October to February–March, but apparently did not do so. The water level fluctuations in 1982–83 were similar to those in 1971–76, and the number of char in Nesjø was doubled. Therefore the char probably moved from Essand to Nesjø in spring, perhaps when the ice was breaking up.

Interactions between planktonic crustaceans and Arctic char

The few Essand char feeding exclusively on Cop. 5 and adult *H. saliens* in 1972–73 showed a high preference for this copepod, then present in

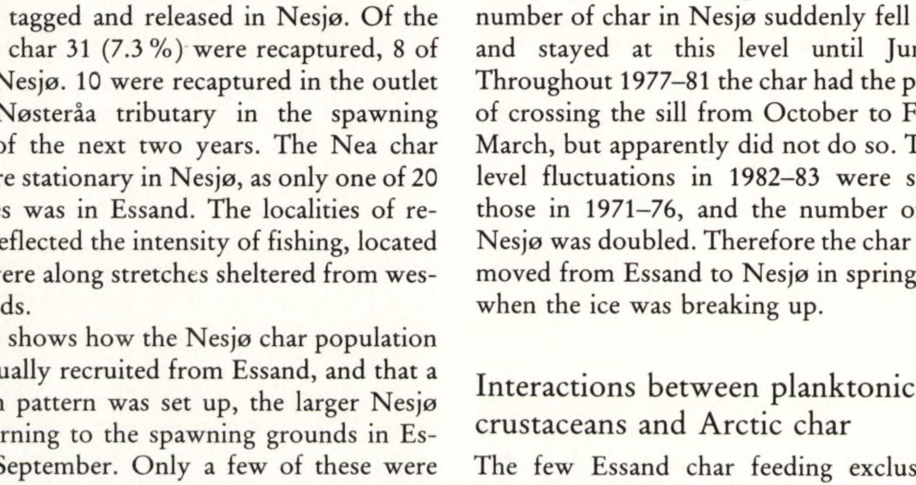

Fig. 26. The electivity-index of Ivlev (1961 a) for the dominant cladocerans eaten by Arctic char.

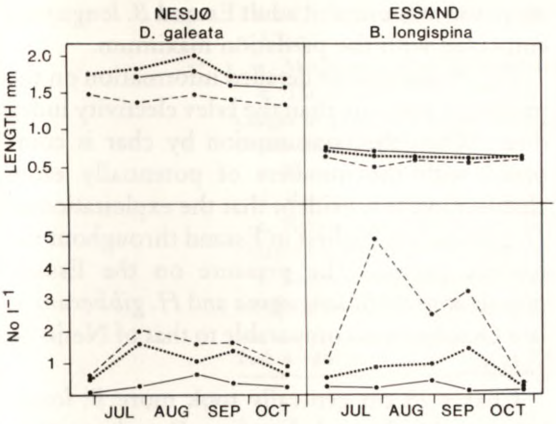

Fig. 27. Above: mean population length (broken lines), minimum length of those eaten by Arctic char (solid lines) and mean adult length (dotted lines) of Nesjø *Daphnia galeata* and Essand *Bosmina longispina* in 1979. Below: total density (broken lines), density of sizes potentially eaten by Arctic char (dotted lines) and density of sizes actually eaten (solid lines).

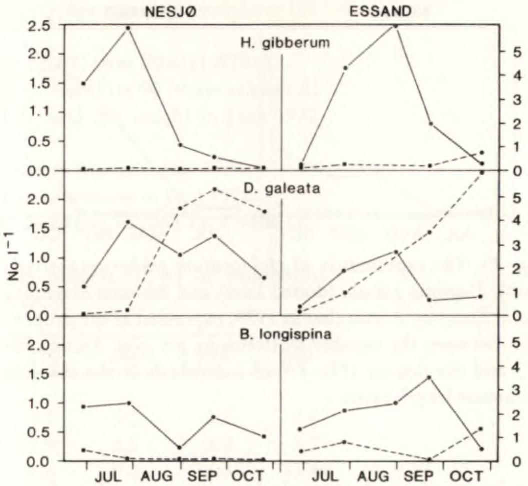

Fig. 28. Density of the predominant cladocerans of size ⩾ the absolute minimum length taken by Arctic char (solid lines), and their number in stomachs of Arctic char per g fish, P_i (broken lines), in 1979.

numbers from 10 to 100 m^{-3}. Otherwise the density of copepods was never influenced by the fish.

Except for June, the Nesjø char showed a clear preference for *D. galeata*, often with a high electivity index (Fig. 26). For *H. gibberum* the index was always negative and generally close to –1, with a small tendency to increase during the growth season. Highest values for *B. longispina* were recorded in June, and in June 1977 and 1979 they were positive. Later in the season the index was mainly –1.

The Essand *H. gibberum* reached a positive index some years, with particularly high values in 1972. *B. longispina* was positively selected early in the season, especially in 1970–72. A clear preference always existed for *D. galeata* in the second half of the growth season, except for 1973.

From the general results on plankton crustaceans and food it appears that both salmonids preferred *B. longimanus* to any other species. On 4 September 1971 it made up 17 % of the food of Nesjø char and on 8 September 1972, 26 % of that of trout.

The 1979 data show that Nesjø char selected adults and some of the largest juveniles of *D. galeata* (Fig. 27). The minimum length of consumed individuals was always a little below the minimum adult length, and followed the seasonal length cycle. The situation was much the same in Essand, but here the minimum length of the *D. galeata* eaten was 1.28 mm on 21 September and 1.24 mm on 24 October. Only the largest adults of *B. longispina* were taken. The mean adult length and the minimum length of those consumed decreased during the season. Both intersected with mean population length in October, when reproduction had almost come to an end.

While the total number of Essand *B. longispina* was much higher than that of Nesjø *D. galeata*, their numbers in the size range potentially eaten by char were comparable in the ice-free period (Fig. 27). Their numbers in the size range actually eaten were low. For Nesjø *D. galeata* it reached a maximum of 700 m^{-3} by the end of August and fell to 200 m^{-3} in October. The maximum of Essand *D. galeata* was 220 m^{-3} in September and that of Essand *B.longispina* 450 m^{-3} by the end of August. From late July these numbers of both species in Essand were lower than those of *A. laticeps*, then present as Cop. 5 or adults (Fig. 6). Thus the char defi-

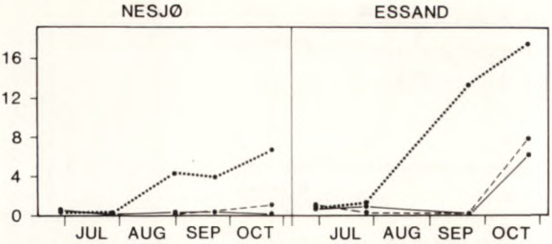

Fig. 29. The exploitation of *Holopedium gibberum* (broken lines), *Daphnia galeata* (dotted lines) and *Bosmina longispina* (solid lines) by Arctic char in 1979, expressed as the proportion between the number in stomachs per g of Arctic char (P_i) and the density (No. l^{-1}) of individuals $\geqslant$ the absolute minimum length eaten.

nitely preferred the cladocerans, as the diaptomid occurred in comparable numbers and sizes.

Turning to the densities of cladocerans larger than the absolute minimum sizes eaten, *H. gibberum* occurred in highest numbers in both reservoirs (Fig. 28). It lived almost untouched by the char. Nesjø *B. longispina* was also eaten in small quantities, still it was less abundant here than in Essand. From late September predation by char might have largely caused the collapse of both species in Essand. At that time they carried resting eggs and were present in numbers of 100–300 m^{-3}. *D. galeata* was heavily preyed on in both reservoirs from late July. Its numbers were highest in Nesjø, as was its consumption by char until October. Predation on *D. galeata* seemed to be triggered by its increasing density. At a certain level the predation depressed its numbers, especially in Essand. This effect on the adults was even more distinct (Fig. 8). Furthermore the minimum of adult Essand *B. longispina* coincided with the predation maximum.

Table 22. The numbers of the dominant species of planktonic Cladocera per stomach of Arctic char of length $\geqslant$25 cm and <25 cm, as means for 10 samples from each reservoir in 1970–79.

	NESJØ		ESSAND	
Length of char	≥25	<25	≥25	<25
Holopedium gibberum	15	5	137	125
Daphnia galeata	1541	912	439	521
Bosmina longispina	21	62	184	271

Fig. 29 gives more detailed information on the predation pressure than the Ivlev electivity index does. When the consumption by char is compared with the numbers of potentially eaten cladocerans, it is evident that the exploitation of *D. galeata* was highest in Essand throughout the ice-free period. The pressure on the Essand populations of *B. longispina* and *H. gibberum* in late October was comparable to that of Nesjø *D. galeata*.

Char <25 cm generally took more *B. longispina*, and in Essand also more *D. galeata*, than the larger ones (Table 22). However, char ≥25 cm were able to eat more crustaceans in Nesjø than in Essand and hence to grow better in the second half of the season.

Relations between food consumption and salmonid growth

For 237 Nesjø salmonids the proportion wet weight of stomach contents in g (Q) to round fish weight in g (W) was linearly related to mean fullness (F):

$$QW^{-1} = 0.0190\ F - 0.0007\ (r = 0.62,\ P < 0.001) \quad (22)$$

Another relationship existed between these three parameters:

$$QF^{-1} = 0.538\ W^{0.38}\ (r = 0.42,\ P < 0.01) \quad (23)$$

Ignoring the second component of equation (22), combining with equation (23), and solving for Q gives:

$$Q = 0.101\ FW^{0.69} \quad (24)$$

expressing that the weight of food increased linearly with mean fullness and decreased relatively with fish weight.

In the range 6.6 to 13.3°C Elliott (1975c) found that brown trout took maximum rations in g w.w. (Q_m) related to fish weight (W) and temperature in °C (T) thus:

$$Q_m = 0.0130\ W^{0.759}\ e^{0.133T} \quad (25)$$

Q_m has been transformed to w.w. from a mean d.w. of 22.3 % of his experimental food (*Gammarus*).

Table 23. Wet weight of food rations in g (Q) for salmonids weighing 100 to 500 g.

a. Maximum rations of brown trout at 12.2°C after Elliott (1975 c).

b. The same at 7.1°C. The other data are based on 90 Nesjø salmonids caught in July 1971 (water temp. 12.2°C) and 204 caught in June 1972 (water temp. 7.1°C).

c. Rations taken by the 11 % with fullest stomachs in July 1971.

d. Rations taken by the 14 % with fullest stomachs in June 1972.

e. Rations taken by the remaining 86 % caught in June 1972 back-calculated for 7 hours to Q_o (equation 13).

f. Rations back-calculated from mean fullness (F) of all salmonids caught in June 1972 by the same procedure.

Fish weight g	100	200	300	400	500
a.	2.2	3.7	5.0	6.2	7.4
b.	1.1	1.9	2.5	3.2	3.7
c. $Q = 0.112\ W^{0.77}$	3.9	6.6	9.0	11.3	13.4
d. $Q = 0.039\ W^{0.91}$	2.6	4.8	7.0	9.1	11.1
e. Q_o from $Q = 0.035\ W^{0.71}$	2.1	3.4	4.6	5.6	6.6
f. $Q_o = 0.101\ F_o\ W^{0.69}$	3.5	5.6	7.4	9.0	10.5

The 11 % of Nesjø salmonids with fullest stomachs caught in July 1971 had taken almost twice, and the corresponding 14 % caught in June 1972 more than twice, the maximum rations Elliott found brown trout to take at indentical temperatures (Table 23). These fractions probably represent fish netted shortly before the nets were drawn. The rations of the remaining 86 % caught in June 1972 were also larger than the maximum ones found by Elliott. When back-calculated for 7 hours, which in this case is a definite underestimate, they approach the quantities taken by those with the fullest stomachs. The rations of all salmonids caught in June 1972, similarly back-calculated from mean fullness of all stomachs, were 10–20 % smaller than those of the salmonids with the fullest stomachs. This standard procedure therefore seems to give reliable results.

To avoid underestimating food consumption in the following calculations, empty stomachs were excluded. In 1972 trout and char took most

Table 24. Mean round weight (W), periodical mean food consumption Q (d.w.) and mean weight increase P (d.w.) of Nesjø salmonids of initial length 20 cm in 1972, and the corresponding food conversion efficiency (k_1). Food consumption was calculated from equation (12), corrected for the effect of digestion (equation 13) and the number of meals in a day (equation 14). Empty stomachs were excluded.

Date	18 Jun.		5 Jul.		27 Jul.		15 Aug.		8 Sep.		29 Sep.		1 Nov.	15 Jun.–30 Sep.
Brown trout														
W g	94		130		188		239		276		284		284	
Q g day^{-1}		1.24		1.59		2.31		1.92		1.09		0.83		1.61
P g day^{-1}		0.53		0.66		0.67		0.39		0.10		0.00		0.44
k_1		0.43		0.42		0.29		0.20		0.09		0.00		0.27
Arctic char														
W g	106		146		186		230		257		292		280	
Q g day^{-1}		1.70		1.64		2.21		2.20		1.24		0.71		1.80
P g day^{-1}		0.59		0.45		0.58		0.28		0.42		0.00		0.43
k_1		0.35		0.27		0.26		0.13		0.34		0.00		0.24

food in July–August and in August–early September, respectively (Table 24). The maximum consumption of fish of initial length 20 cm was 2.2–2.3 g day^{-1} (d.w.) for both species. Calculated as mg (d.w.) per g live weight of fish, the consumption was highest before mid-August (Fig. 22B). The daily mean through the growth season, 15 June–30 September, was 8.6 for trout and 9.5 for char. The daily weight increase was also highest before mid-August (Table 24), but the char approached this level again in late September. The gross food conversion efficiency (k_1) of trout was 0.42 in June–early July, declining to zero by the end of September. k_1 of char was 0.35 in June, below that of trout in the warmest period, and approached the initial level again in late September. Both species obtained a mean k_1 of about 0.25 over the growth season.

Discussion

Abiotic factors

The differences in the recorded water qualities between the Nesjø and Essand reservoirs were minor, as were variations in the ice-free season and between years. So far, their water qualities do not deviate from those of natural lakes in the area. The slightly acid, yellow water is a consequence of the high proportion of bogs in the catchment area. The lower pH of 6.4–6.5 in Essand in 1972–73 may reflect acid precipitation, which severely affects southern, and penetrates northwards across eastern, Scandinavia (Overrein et al. 1980, Bernes 1986). A specific conductivity <3.5 mSm^{-1} is typical for Norwegian lakes, when limited areas of certain bedrock or definite marine influence are excluded (Kjensmo 1966, Nou 1983).

The reservoirs are not stratified in summer, a consequence of the large surface areas relative to volumes and the steady, often strong winds. These factors also cause the late freezing date, resulting in low winter temperatures. Since all the fish are exposed to the same temperatures, the situation is favourable for analyzing fish growth.

Crustacean plankton

The planktonic crustaceans of Nesjø were recruited from the communities of Essand and some small, now flooded, tarns. A succession took place within the Nesjø diaptomids, with *A. laticeps* as the ultimate one. Otherwise, the specific composition was established already in July 1970. The zooplankton of the Rzeszów reservoir (Poltorak 1982) and the Neberdzhai reservoir (Goryainova et al. 1969) were similarly selected from species present in former, smaller water bodies. As with benthos, the number of niches is obviously higher in number of smaller water bodies than in a larger, regulated one. There were far fewer alterations in the crustacean community of Nesjø than Elmore and Bunting (1979) or Munro and Bailey (1980) observed in more eutrophic impoundments. In 1980 the same four species of cladocerans and three of copepods were found in Essand and Nesjø. According to Lötmarker (1964), Langeland (1972), Jensen (1985) and Nøst et al. (1986), the number and selection of species is typical for Scandinavian mountain lakes.

The cladocerans were typical summer forms, with none or only very few parthenogenetic females present in winter. In Målsjøen, at an altitude of 165 m in the same catchment area, *D. galeata* was acyclic and did not produce resting eggs (Jensen 1985c). However, it had similar cycles as regards length and fecundity, which also are known from Base Line Lake, Michigan (Hall 1964) and Esrom, Denmark (Petersen 1983).

All Essand-Nesjø calanoids were univoltine. The few representatives of a second generation died in late autumn. In Målsjøen *A. laticeps* survived the winter as adults, producing eggs the following spring (Jensen 1981). Cycles more like that of Essand-Nesjø are known from Swedish lakes (Lindström 1952, Lötmarker 1964), and an identical one is described from the Ransaren reservoir at 65°N in Sweden (Axelson 1961a). The cycles of the Essand-Nesjø populations of *C. scutifer* were very distinct. Although the reproductive period extended from late June through September, the two generations present in summer were clearly distinguishable. There was no indication of two population fractions having different winter stages, as observed in some Swedish lakes (Lindström 1952, 1958, Axelson 1961 b, Lötmarker 1964), nor of the complex 2- or 3-year cycles mainly known from colder or deeper lakes (McLaren 1964, Halvorsen and Elgmork 1976, Elgmork et al. 1978, Elgmork 1981, 1985). According to Elgmork (1985), the mean summer temperature, the start of the reproductive period and the depths of the reservoirs should imply a 1-year cycle. Cycles similar to those of the Essand-Nesjø populations have been found in many Scandinavian lakes (Lötmarker 1964, Steine 1969, Larsson 1978, Langeland 1982, Elgmork 1985). The population depression between January and May may indicate that fractions of Cop. 4 and 5 diapaused, a phenomenon known from many lakes in southern Norway (Elgmork 1985). Diapausing *C. scutifer* as mainly been found in lakes with periodical oxygen depletion, but also where oxygen conditions were similar to those of Nesjø (Elgmork et al. 1978). The reasons for the delay in the Essand population relative to the Nesjø one are obscure. This is an interesting case as their environments, including temperature regimes, are almost identical. *M. gigas* was found as nauplii only in Essand from January to June, and was otherwise hardly traceable. Its maximum in 1973 was 8,500 m^{-3} and occurred in April. A parallel cycle existed in Øvre Heimdalsvatn at an altitude of 1,090 m in southern Norway (Larsson 1978), but there the maximum number was only 360 m^{-3} and occurred in May. It is difficult to see why *M. gigas* did not appear in Nesjø.

The Nesjø cladocerans were larger and carried more eggs than those in Essand. These differences were most distinct in 1971–73 when the mean adult length of *D. galeata* was close to 2.2 mm. The simultaneous bloom of *Asterionella*, also known from the flooding phase of the Swedish Ransaren reservoir (Axelson 1961 a) and the Barrier reservoir, Alberta (Nursall 1952), indicates that the release of nutrients from the flooded ground was at its maximum. In this period Nesjø was also richer in allochthonous material than Essand, and this was of different quality. After 1974 the differences between the two reservoirs, especially as regards *D. galeata*, are also related to the effect of predation by char of different size.

These assumptions on trophic levels are supported by the somewhat higher general biomass level in Nesjø. However, the only outstanding biomass figure here was the 214 mg m^{-3} d.w. (2.6 g m^{-2} over 12 m mean depth and 6.4 g m^{-2} over 30 m maximum depth) of cladocerans in July 1970. This was four times the corresponding figure in Essand and comparable to the mean level of warmer and more eutrophic reservoirs in southern England (Munro and Bailey 1980) or Oklahoma and Arkansas (Smith and Moen 1983). In Ransaren the seasonal biomass maximum increased from an initial level of about 0.6 g m^{-2} to 3.8 g m^{-2} over 40 m depth the second year after impounding was completed (Axelson 1961 a). In contrast to Nesjø, there was not only an increase of copepods but also of cladocerans during the first eight years of the Neberdzhai reservoir (Goryainova et al. 1969).

The increase of the cladoceran populations, and of *H. gibberum* in particular, in Nesjø over 4–5 weeks up to the numbers present on 17 July 1970, demonstrates their tremendous reproductive capacity. The univoltine copepods, on the other hand, needed two years to reach numbers corresponding to the carrying limits of the reservoir. In 1970 Nesjø *H. gibberum* and *B. longispina* reached numbers which were never achieved by any cladoceran later. They were most probably carried from Essand in larger numbers than *D. galeata* and could take advantage of their high fecundity. In 1971–73 their numbers declined. One probable reason was increasing competition from *D. galeata* and the diaptomids.

The mean seasonal biomass of crustaceans in 1972, an average year, was 41 mg m^{-3} (0.5 g m^{-2}) in Essand and 57 mg m^{-3} (0.7 g m^{-2}) in Nesjø. This is comparable to the level of more mesotrophic lowland lakes in central Norway (Jensen 1976, Ålbu 1983). It is higher than in lakes of more comparable altitude or temperature regimes, for example Øvre Heimdalsvatn (Larsson

1978), Krivoe and Krugloe on the coast of the White Sea (Alimov et al. 1972) and the subarctic Swedish lakes Hymenjaure and Stugsjön (Persson 1975). The relatively high biomasses of the Essand-Nesjø system may be partly caused by a large supply of allochthonous organic material and constant water turbulence, preventing sedimentation of organic material and recycling nutrients in the vegetative period.

The temperature in June-early July had a major effect, exceeding that of predation by char, on the biomass level of all species. High temperature in that period triggered an early growth, followed by a high biomass for most of the summer. Low temperature delayed the biomass maximum to late August or September. The coldest summers were 1974 and 1975, when most species occurred in low or very low numbers.

The constant circulation should result in the random vertical distributions observed in September 1975 being typical for both reservoirs. The horizontal aggregation was, however, high, and made it difficult to obtain significant mean numbers.

Bottom fauna

Ten years after formation the macrobenthos of the Nesjø reservoir was composed of 80 % or more of Chironomidae larvae, some Oligochaeta and a few, scattered individuals of other groups. Based on the stomach contents of fish, the quantity of chironomids was at its maximum in 1972–74. It was still above the Essand level in 1980, when chironomids were important prey for fish in both reservoirs. The diet of the fish showed that the benthos of the flooded rivers disappeared during the first two years. A qualitatively poor bottom fauna is typical for regulated reservoirs, and the predominance and high numbers of chironomids are common characteristics of impoundments. Such conditions have been reported from Norway (Jensen 1982), Germany (Meinel et al. 1983), the Russian Neberdzhai (Goryainova et al. 1969), Tsimlyansk (Miroshnichenko 1979) and Volga reservoirs (Mordukhai-Boltovskoi et al. 1972), Yugoslavia (Janković 1972), England (Armitage 1977), Manitoba (Wiens and Rosenberg 1984), Ontario (Paterson and Fernando 1970), Alberta (Nursall 1952, 1969), Wisconsin (Kaster and Jacobi 1978), Ohio (Paxton et al. 1981), Arkansas (Aggus 1971), Arizona (Rinne 1978), California (Ali and Mulla 1976), Ghana (Petr 1972) and Australia (King 1979). Where the benthos succession has been studied, the biomass maximum has occurred in the second or third year after impoundment. In the Barrier reservoir, Alberta, the predominance changed from *Chironomus* during the first two years to species of smaller size (Nursall 1952). Based on the size of the chironomids eaten by the fish, a similar succession took place in Nesjø.

In the Norwegian Gautsjø reservoir, very similar to Essand, the benthos, mainly chironomids, exceeded that of the original lake by five in number and two in biomass 25 years after impoundment (Jensen 1982). The high production of chironomids in impoundments must be based on the storage of plant material of terrestrial origin. When the impoundment includes bogs, as in the Essand, Nesjø and Gautsjø cases, fragmented peat constitutes a high proportion of the bottom sediments. Peat deposits are still found in reservoirs impounded 60 years ago, and fragments are eroded and spread across the reservoir bottom. Thus, the seasonal biomass maximum of chironomids may be kept at 5–10 g m^{-2} for 100 years or more. This is a high level in relation to the quantities of benthos recorded in most Norwegian lakes (Økland 1963).

Various species of chironomids have survived in the littoral zone of reservoirs exposed to air and frost for 90 days (Nursall 1969) and a few species for 172 days (Paterson and Fernando 1969). Grimås (1961) reported that 80 % of the benthic animals, mainly chironomids, in the regulated zone of the Kultsjön reservoir were still alive in April after 4 months exposure to ice cover. Experimentally Olsson (1981) found that Chironomidae larvae tolerated a temperature of –4°C for five months. Recording the temperature at the sediment surface at three points in the ice- and snow-covered zone of the Norwegian

Granasjø reservoir at an altitude of 650 m, I found a minimum of –2.0°C following three days with a minimum air temperature of –25.0°C. Chironomids can therefore be expected to survive in the regulated zone of the Essand-Nesjø reservoirs, too. Indeed, the fish which had eaten Chironomidae larvae were mainly caught there. The production of chironomids is most certainly not limited to the area corresponding to the lowest water level.

Fish

Compared with other Norwegian lakes and reservoirs populated by salmonids, the mean catches per net in Essand were high, and those in Nesjø were among the highest recorded. Of 128 cases J. W. Jensen (1979) found 80 % to be roughly normally distributed below a mean of 1.0 kg net^{-1}. In 20 % of the cases the catch was 0.6–0.9 kg net^{-1}. Before 1972 the Essand catches were of the last category. The Nesjø catches were always above 1.0 kg net^{-1}. Catches like those taken in 1970–76, 2.5–3.0 kg net^{-1}, have elsewhere in Norway only been obtained in impoundments during the first 2–3 years of their existence, for example Namsvatnet (J. W. Jensen 1979), Granasjø (Bergan 1985) and Innerdalsvatnet (Koksvik 1985). Almost emptying and reducing the area of Nesjø by 95 % in early 1971 did not seem to affect the trout population. Its loss that winter did not exceed that of the following winters.

The corrected numbers (N_c) caught per series of nets and their length distributions show that the numerous trout present during the first few years were the population from the former river system. The subsequent scarcity of trout must be connected with the limited capacity of its only spawning river.

Burbot predominated the corrected Nesjø catches in 1972–74. It was certainly underestimated relative to the salmonids. Burbot is known to live in the littoral zone as well as in deeper water, as it does in Selbusjøen (Langeland et al. 1986) and Målsjøen, both in the Nesjø river system. The new reservoir offered excellent conditions for juvenile burbot. This may be related to the abundance of Chironomidae larvae. However, the 1970 class was the strongest one, and chironomids did not become important fish prey until 1972. Sorokin (1968) found that burbot <3.1–3.6 cm lived in very shallow water and fed exclusively on Entomostraca, whereas the larger ones turned to benthos. The temporary success of Nesjø burbot was more probably a result of a successful survival at a very early stage based on the rich occurrence of *E. lamellatus*. The recruitment failure of burbot coincided with declining quantities of *E. lamellatus* in salmonid stomachs from 1974–75. In contrast to chironomids, *E. lamellatus* was never an important prey in Essand where the number of burbot was very low. At its maximum in 1972, the growth in length of the youngest Nesjø burbot equalled that of the salmonids, but the decrease from the age of 3 was more distinct. The growth was then similar to that of burbot in the Norwegian lake Mjøsa (Sandlund et al. 1985) and comparable to the usual growth in oligotrophic lakes in Canada (Scott and Crossman 1973).

The Arctic char succeeded much better than the other two fishes. It set up a migration pattern, feeding in the new reservoir and returning to the spawning grounds in the old one. It also spawned in all but one tributary. Spawning in Nesjø has not been observed. Nor has any char shown a growth reflecting a life spent entirely in Nesjø, which raises a question concerning the success of the spawning in the Nesjø tributaries. The char lived both in the littoral zone and the open water, and exploited the food organisms present more intensively. The population of char >15 cm in Nesjø grew gradually to a biomass maximum equivalent to 62 kg ha^{-1} in 1974 and to a maximum in number of 235 ha^{-1} in 1976. Later it levelled off at about 100 ha^{-1} and 30 kg ha^{-1}. The latter equals the initial Essand level. Meanwhile, the number in Essand declined until the migrating char were locked there in 1977 because of a low water level. This doubled the number of char in Essand, probably causing the poorer growth of age classes 3–4 in 1978–79. The reliability of these figures depends on the validity of the relationships between catches and numbers. The trout were limited both in Målsjøen and Essand-Nesjø to the littoral zone. A general significant relationship was found between char catches in the littoral zone and in open water. Fish are more easy netted in the littoral zone of a small lake than in a larger one and the efficiency of nets declines with increasing catches. These factors would lead to an underestimate of the Essand-Nesjø numbers. In number the maximum density of Nesjø char was higher than the records of equal-sized fish in large lakes in southern Norway and Finland which have several pelagic species (Qvenild 1987). It exceeded the brown trout population in Øvre Heimdalsvatn (Jensen 1977). The later Nesjø level was comparable to the density of char in the fertilized Langvatn (Langeland 1982) and in Målsjøen, both belonging to the Nesjø river system. The corresponding biomass level of 30 kg ha^{-1} was about twice the records from Øvre Heimdalsvatn, Langvatn and Målsjøen, and that of kokanee, *Oncorhynchus nerka* (Walbaum), representing 90 % of the catches in the Pend Oreille reservoir, Idaho (Bowler 1980).

30 % of 180 Swedish lakes gave in 1913–17 a higher yield (Nordquist 1918) than the about 5 kg ha^{-1} estimated for Nesjø in 1980. This level corresponds to the highest yields of oligotrophic lakes and reservoirs in northern Sweden (Lindström and Bergstrand 1979) and Norway (Aass 1984, Aass and Borgstrøm 1987, Qvenild 1987). The maximum of about 10 kg ha^{-1} is comparable to the average for char lakes in Iceland (Kristjánsson and Adalsteinsson 1984). By increasing the harvest to 30 % of char >20 cm, the Essand-Nesjø reservoirs could probably give a lasting yield of 8 kg ha^{-1}.

During the first two years the Nesjø salmonids mainly fed on earthworms, cladocerans and survivors of the former river fauna. Afterwards a distinct feeding pattern, similar to that in Essand, was established. Chironomid larvae and pupae, planktonic cladocerans and surface organisms made up 80 to 90 % of the food of the char accumulated over the growth season. The fullness of the stomachs was at its maximum in 1972–74, but was still higher than in Essand at the end of the decade. The char exploited the food organisms better than the other two fish species, taking more Chironomidae larvae in early summer and turning to cladocerans in late summer. The trout and burbot were more dependent on larger insects, snails, fish and surface organisms, especially in the oldest reservoir. The large quantities of Chironomidae larvae present were obviously the key to the high production of char. They were the main food at the start of the growth season, when the growth of the char was at its maximum. Indirectly they delayed predation on cladocerans, allowing them to reach such numbers that exploitation by char was not disastrous. Similar seasonal diet patterns of Arctic char are known from other Norwegian lakes (Hindar and Jonsson 1982, Amundsen 1984). However, chironomids have never been such an important food source for fish in Scandinavian reservoirs, where the salmonids have turned to Entomostraca and terrestrial insects (Dahl 1932, Nilsson 1961, 1964, Aass 1969). Outside Scandinavia many parallels to the Essand-Nesjø situation have been reported. Chironomidae larvae and pupae have been the primary or very important prey, often in combination with cladocerans, for various species of fish in reservoirs in U.S.S.R. (Miroshnichenko 1979), Czechoslovakia (Losos 1976, 1977, Albertova 1982), England (Crisp et al. 1978, Moore 1982), Ohio (Paxton et al. 1981) and California (Marrin et al. 1984).

During the ice-free season of 1972 char were found to eat 0.86 g m^2 (d.w.) or 83 % of the estimated production of *D. galeata* in Nesjø. In 1979 they took half that quantity and only 28 % of the production. The mean length of those eaten was 1.9–2.2 mm in both years. *D. galeata* was at its maximum size in 1972 and therefore more exposed to predation. Its production in 1972 may well be underestimated compared to 1979, since temperatures were higher and the bloom of *Asterionella* indicated a higher primary production. The consumption of chironomids represented a live weight of 7.00 g m^{-2} in 1972 and 2.78 g m^{-2} in 1979. The wet weight of the benthic chironomids in May 1978 varied between 2.85 and 17.84 g m^{-2}, with a mean of 7.24 g m^{-2}. Some chironomids were also eaten in August–

September. The general picture of food consumption leaves no doubt about the declining quantities of chironomids from 1972 to 1979. Presupposing that 1 g (d.w.) = 5 kcal, the brown trout population of Øvre Heimdalsvatn consumed 0.74–1.07 g m^{-2} during June–October (Lien 1978). The Nesjø salmonids took 3–4 times these quantities in 1972 and almost twice in 1979.

The annual increase in length of the salmonids in the initial water bodies was about 5 cm, which according to Huitfeldt–Kaas (1927) and Sivertsen (1953) is typical for Norwegian lakes. In Nesjø they initially grew more than twice that much in length and obtained a condition factor of up to 1.5. The low K-values of char in 1973, corresponding with values for April and May, may be connected with the low water temperature of only 3.8°C. Even though scale readings showed no length increase from the end of September to June, the fish may in other years have gained some weight between ice-out and the date of the first catch. Thus, growth rates may be underestimated. The seasonal size-independent growth rate in weight of Nesjø salmonids of initial length 20 cm reached 7–8 % day^{-1} in 1970–71, twice the former level, and was close to 9 % day^{-1} in June–early July 1972. Higher growth rates for salmonids have only been recorded for pink salmon, *Oncorhynchus gorbuscha* (Walbaum) (Brett 1974, Jobling 1983 b), sea-dwelling Arctic char and Atlantic salmon (*Salmo salar* L.) in aquaculture (Jensen 1985 b). The maximum growth rate of brown trout was three times the 2.8 % day^{-1} obtained experimentally by Elliott (1975 a). Like the char they took twice the maximum rations Elliott (1975 c) found for brown trout. The same has been recorded for Arctic char in Takvatn, northern Norway, in June (Amundsen 1984). Whereas the growth of the Nesjø salmonids was almost identical, the trout were found to consume less food, this mainly being an effect of more empty trout stomachs. This agrees with the results of Amundsen (1984), who found that the rate of gastric evacuation in Arctic char was somewhat lower than Elliott (1972) obtained for brown trout. Thus, the food consumption of the Essand-Nesjø char is probably somewhat overestimated.

To avoid underestimating food consumption when calculating food conversion efficiency (k_1), empty stomachs were excluded, giving more equal values for the two salmonids. The procedure can still be expected to underestimate food conversion efficiency of the char. These calculations are necessarily based on a series of assumptions. The most speculative of these is the number of meals taken per day. Within the most relevant temperature interval, 10–13°C, the equation chosen (Elliott 1975 b) gives about two meals a day. This is in accordance with field data on brown trout and rainbow trout, *Salmo gairdneri* Richardson, (Elliott 1973) and walleye, *Stizostedion vitreum vitreum* (Mitchill), (Swenson and Smith 1973). Expressed as mg food (d.w.) per g live weight of fish, the daily mean food intake from mid-June to 30 September 1972 was 8.6 for trout and 9.5 for char of initial length 20 cm. It was 1.8 for char of comparable size in Takvatn, where the condition factor and growth of the char were considerably poorer (Amundsen 1984). The food conversion efficiency (k_1) of both Nesjø salmonids was about 0.25 over the 1972 growth season. This is median in the range 0.13 to 0.35 which has been found for various species of fish (Ricker 1946, Winberg 1960, Ivlev 1963). The 1972 figures correspond with the results on walleye in the temperate Lake of the Woods, which fluctuated around a seasonal mean of 0.22 (Swenson and Smith 1973).

The temperatures in Essand-Nesjø were favourable for the growth of the salmonids present. Swift (1961) and Elliott (1975 a) found 12–13°C to be optimal for the growth of brown trout. Jobling (1983 b) assumes a corresponding one of 14°C for Arctic char. Based on the fact that Arctic char grew better than brown trout in Nesjø at temperatures below 11°C and less at higher temperatures even with a higher food intake, the circumpolar distribution of the Arctic char, and the maximum sea temperatures at the southern limit of distribution of anadromous Arctic char on the Norwegian coast, Jensen (1985 b) found 11–12°C to be a more probable range. Based on the fast growth in June–early

July 1972 at temperatures below the optimal ones, Jensen (1985b) predicted the potential size-independent growth rates of 13.8 % day^{-1} for brown trout and 11.6 % day^{-1} for Arctic char, and formulated equations for their maximum growth in relation to temperature and weight.

After 1972 the growth of the Nesjø salmonids declined towards the more usual Essand levels. But in 1983, the size-independent growth of Nesjø char >25 cm was still like that of the smaller ones and four times that of Essand char of equal size. This may be related to somewhat better food conditions and the low or non-existent competition with char <15 cm.

The Nesjø salmonids were not found to grow in length at temperatures below 7°C. For brown trout this is in accordance with field observations of Egglishaw (1970) and experiments of Wingfield (1940). Growth has taken place at lower temperatures (Swift 1961, Jensen 1978), and in experiments even at 4°C (Elliott 1975a). The declining growth rate of Nesjø trout during the season was to a certain degree related to decreasing food quantities, but mainly to the food conversion efficiency, which declined from a level of the maximum recorded for any species of fish to zero at the end of September. Wingfield (1940) and Swift (1961) also found that brown trout grew faster at temperatures below 12°C when the temperature was rising than when it was falling. The seasonal growth pattern of the Arctic char was similar, but both food conversion efficiency and growth rate decreased when the temperature exceeded 11°C, to recover in September at temperatures between 11 and 7°C. In any case, the salmonids had to use more energy searching for food, as they turned from the abundant chironomids to less abundant or smaller prey during the growth season.

The increased growth delayed sexual maturation of the Nesjø trout. It did not have a similar effect on the char, whose maturation seemed to be determined by age.

The Nesjø char were gradually recruited from Essand. The first individual visit in Nesjø was probably a result of random movement. The majority of these char returned to the spawning grounds in Essand in September and then went back to the better feeding areas in Nesjø, probably the next spring. The individual char seemed quickly to learn an optimal behaviour. A clear connection existed between the number of char moving from Essand to Nesjø and the possibilities for crossing the sill between them, especially at the time the ice broke up. Char migrations are known from other reservoirs (Runnström 1964, Aass 1970, 1984), where the char also moved from spawning sites to areas exposed to currents or other feeding areas in the winter. By comparison, the Nesjø burbot and especially the trout were far more stationary.

Arctic char often segregate into two or more phenotypes (Johnson 1980). This has been observed in several Scandinavian lakes (Nyman et al. 1981, Hindar and Jonsson 1982, Klemetsen 1984). In Essand-Nesjø there was no indication of such segregation from information on colour, growth, general ecology or spawning time. However, 32 % of the recaptured char tagged in the Nøsteråa tributary, occurred in small catches taken in its outlet in September the following two years. This strongly indicated that a subpopulation of char was spawning in this tributary.

Interactions between planktonic crustaceans and Arctic char

Planktophagous fish are known to select the larger individuals of the larger species of crustaceans and to prefer cladocerans, and primarily egg-carrying ones, thus reducing their number and size, and eventually eliminating them from the lake (Brooks and Dodson 1965, Nilsson and Pejler 1973, Langeland 1982). Planktonic cladocerans were, in the second half of the growth season, the main food of Arctic char in Essand-Nesjø. Over the whole growth season they regularly made up 35 % of the food of Essand char, with *B. longispina* and *D. galeata* as the most important species. For Nesjø char, *D. galeata* alone accounted for 14 to 42 % of the total. The *D. galeata* populations, and especially the adult fractions, declined when predation set in. The heaviest predation pressure existed on the Essand populations. Predation by the smaller, more numerous char in Essand may to some degree explain the smaller size of Essand *D. galeata* and *B. longispina* in the second half of the research period. Such effects on *H. gibberum* are less obvious, but its smaller size in Essand may reflect a strategy of avoiding predation. The higher egg numbers of Essand *D. galeata* <2.0 mm may also be part of such a strategy. The exploitation of Essand cladocerans carrying resting eggs was especially intense, and took place at densities as low as 160 m^{-3}. It probably caused their lower numbers relative to Nesjø at the start of the growth season, as shown in 1979. However, according to Nilsson and Pejler (1973) the char would not be expected to eliminate any of the species present.

No correlation existed between the biomass density of char and its effects upon the cladocerans. The Essand populations were more heavily exploited than those in Nesjø, even when the biomass density of char was higher in Nesjø. Biomass densities of char in Essand varying by a factor of 3 did not seem to have any influence. The Nesjø population of *D. galeata* increased from 1971 to 1973, when the biomass of char increased by a factor of 7.

The different predation pressure in the two reservoirs could be related to char of different size, as the smaller Essand char took more and smaller cladocerans than the larger char. In ten lakes Langeland (1978b) found that the populations of *D. galeata* and *H. gibberum* declined in number and size with the declining size of Arctic char. Where the mean size of the char, as in Nesjø, was >300 g, the characteristics of the crustacean populations and the pattern of predation were almost identical to those in Nesjø. Where the mean size of the spawning char was like that of Essand, about 230 g, the importance and the mean length of *D. galeata* declined and the char turned more to other species of cladocerans. With further decline in char size the effects of predation were intensified. The extreme case was Langvatn, then populated by Arctic char of mean size 70 g at spawning and planktophagous stickleback, *Gasterosteus aculeatus* (L.). The mean adult length and the clutch size of the Langvatn cladocerans was about half the corresponding Nesjø data of 1979, and *D. galeata* was on the edge of elimination (Langeland 1982). Fertilizing Langvatn increased the biomass of these populations above those of Nesjø, but their length and fecundity were still well below. Likewise in Øvre Stavåtjønna, populated by small char (Langeland 1982), the effects of predation were far more distinct than in Essand-Nesjø. Compared with the quantities eaten per g round fish by Nesjø char in 1972, the Takvatn char ate 30 % in June, but only 11 % in September (Amundsen 1984). The Takvatn char, about 90 % of which were <23 cm, were mainly feeding on *B. longispina*, *C. scutifer* and *Eucyclops graciloides* (Lillj.) in September. The predation pressure of a population of Arctic char seems more closely related to the size of the fish than to its biomass. Several small fish of a given combined weight are capable of collecting more and smaller objects and can take more food relative to weight, than one larger fish of the same weight. The biomass density of Essand and especially Nesjø char was probably higher than in most Scandinavian lakes. The successful interaction between char and planktonic crustaceans in Essand-Nesjø can mainly be related to the size of the char, allowing the cladoceran populations to exist in such numbers and sizes that their production was maintained at a relatively high level. It was also positively influenced by the consumption of chironomids at the beginning of the growth season, allowing the cladoceran populations to flourish before predation set in. In Takvatn the consumption of crustacean plankton started at ice-out, reached its maximum in mid-July, and declined through the rest of the growth season (Amundsen 1984).

The difficulty of catching small Arctic char is a general one (Johnson 1980). In temperate lakes the young char are known to live in deep water (Svärdson 1976, Hindar and Jonsson 1982). This seem to be the situation in Essand, too, and juveniles are assumed not to have had any influence on the crustacean plankton.

The recruitment of the char population was controlled by some obvious factors. The Essand char and especially the river spawners ate much of their own roe. Burbot are also known to be heavy predators of char roe (Langeland 1987). Roe deposited in the exposed zone may freeze or be damaged in other ways.

Concluding remarks

The recorded water qualities of the man-made Nesjø reservoir differed very little from those of the 30 year older Essand reservoir or natural lakes in the district. Mass occurrence of *A. formosa* indicates that some nutrients were released from the flooded ground in 1972–73.

The crustacean plankton in Nesjø deviated, especially before 1975, from those of other reservoirs and lakes with comparable temperature regimes in having larger cladocerans and a somewhat higher biomass. These parameters were influenced by the size of the planktophagous char.

Nesjø has the qualitatively poor bottom fauna and high numbers of chironomids typically found in impoundments in various parts of the world. Judging by the quantities eaten by the salmonids, the chironomids were at their maximum in the first and second year after impoundment was completed. A lasting Chironomidae production at the 1983 level, based on the peat deposited in the reservoir, is predicted for a long period, say 100 years.

A temporary predominance of brown trout and then of burbot came to an end after 5 years because of failing recruitment. The fish diversity decreased as the Arctic char was superior to the other fishes as regards reproduction and the exploitation of the food organisms present, mainly planktonic cladocerans and chironomids. The growth rate in weight of brown trout and Arctic char in the first two years was close to the maximum recorded for any salmonid.

Throughout its first decade, the Nesjø reservoir offered the best known lake fishing on salmonids in Scandinavia, and attracted many anglers from Norway and Sweden. A succession towards the qualities of the Essand reservoir took place. However, the catches and the quality of the Essand char are better than in most Scandinavian fresh waters, including partly impounded ones. So far, the Nesjø char have been mainly, perhaps entirely, recruited from the Essand population by individuals generally >15–20 cm. As long as this situation exists, Nesjø will probably produce char of the size 300–500 g. The mean weight of those angled in 1986 was 350 g. By increasing the harvest in both reservoirs to 30 % of the char >20 cm, a lasting yield of 8 kg ha^{-1} is expected. This would enhance the possibilities for maintaining the size of the char and thus the existing successful interaction between the char and the planktonic cladocerans.

In the first decade, the crustacean plankton, the benthic fauna and the fish populations of the Nesjø reservoir passed through the usual successions following impounding as described by Mordukhai–Boltovskoi et al. (1972), Baxter (1977) and Baxter and Glaude (1980). However, an early-stage flourishing of planktonic crustaceans was only noticeable the first summer. Later their biomass was primarily controlled by temperature and seasonally influenced by predation from char. By the end of the research period the yield and individual size of the fish were still higher than in most Scandinavian reservoirs and oligotrophic lakes. At its maximum the yield was comparable to the level of a later and stable stage of succession in more eutrophic Russian reservoirs (Mordukhai–Boltovskoi et al. 1972, Hrbáček 1984).

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Freshwater Eel *Anguilla anguilla* (L.) from North Norway, with Emphasis on Occurrence, Food, Age and Downstream Migration

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Abstract

Eels were sampled from six lakes along the outer North Norwegian Coast, employing long lines and fyke nets. Long lines gave catches of 2–10 eels per 100 hooks per night. The fyke nets gave very poor catches, possibly due to the light midnight sun conditions. The catches document the presence of eel populations in N. Norwegian watercourses. No density gradient was found from S to N within the sampling area. Catches were low compared to those reported from southern parts of Europe.

The sex ratios showed a strong preponderance of females. Postlarval ages determined by densitometry were 3–5 years. Growth rates were from 6–12 cm yr^{-1}. The age structures and growth rates were close to those in samples from South Norway.

From 221 eels, three eels had vertebrae counts within the range reported for the American eel *Anguilla rostrata*.

The principal food items of the eel were the snail *Lymnaea peregra*, the amphipod *Gammarus lacustris*, large insect larvae and three-spined sticklebacks *Gasterosteus aculeatus*. Stickleback nests with eggs were frequently eaten. Negative selection indices were found for oligochaetes, chironomid larvae and pea mussels *Pisidium* spp. In N. Norway eels seem to feed more actively at lower temperatures than do eels from more southern locations.

In Skogsfjordvatn, the emigration of silver eels largely took place between mid-August and mid-September. The mean weight of silver eels was 368 g, and 93 % were females. The mean fat content in muscle samples of silver eels was 26.2 %; this seems comparable to measurements from central parts of Europe.

The eel, considered a warmwater fish, has in North Norway to sustain long periods of relatively low temperatures (2–4°C). Despite this, it appears remarkably well adapted to the presumably suboptimal conditions for feeding and growth, close to the northern limits of its geographical distribution.

Introduction

North Norway lies close to the margin of the eel's north-eastern continental distribution (Fig. 1). Occurrence of eels is known around Kola Bay and in the river Dvina (Schmidt 1909, 1925, Berg 1965, Konstantinov and Sorokin 1960). Berg (1965) reports that eels are caught in the lower tributaries of the river Pechora.

In North Norway, the occurrence of yellow and silver eels is well known, and they are frequently caught by anglers. Only one observation of ascending fry (elvers) is published (Collett 1905, Schmidt 1906). The eel is rarely fished, and it has no commercial value. No research on the species has been carried out, and very little recorded information exists on its distribution and biology.

The present contribution reports a study of yellow eels from six North Norwegian coastal lakes. Emphasis is placed on their food, which is discussed in relation to records from other

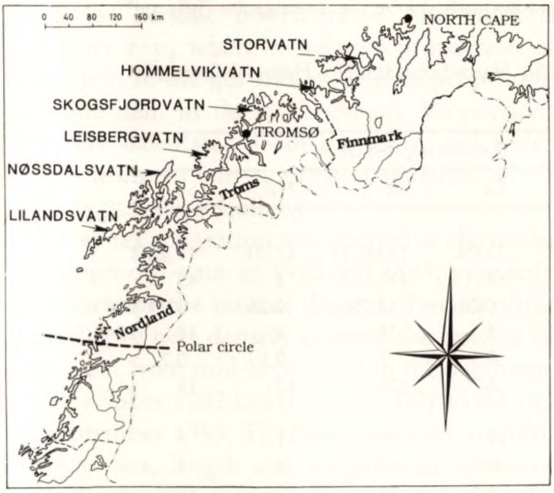

Fig. 1. The sampling localities (six lakes).

European lentic habitats. Occurrence and relative densities, size, growth, sex ratios and vertebrae counts are briefly discussed. From one of the lakes the seasonal development of silver eel emigration is indicated.

Methods

Eels were sampled from six lakes along the outer North Norwegian coast (Fig. 1, Table 1). The lakes are evenly spread, covering a coastline of about 500 km (Fig. 1).

Simple limnological observations were made for lake description. From these, the trophy of the lakes is indicated (Table 1). The lakes are quite unequal with regard to size, depth, trophy and distance from sea. A supplementary description of the lakes is found in Bergersen (1984).

Fishing was carried out the summer of 1982, employing long lines and paired fyke nets, commonly used by eel fishermen in Ireland. The fyke nets had three funnels and were linked two and two by a leading net, 6 m long and 50 cm high. Mesh size decreased from 16 mm in the leader to 10 mm in third funnel. The common use and construction of fyke nets are discussed in Moriarty (1972) and Tesch (1977). The long lines had 100 hooks and were baited with earthworms. Long lines and fyke nets were put mostly at depths of 2–5 m along the lake shores, and were lifted the following day. Fishing periods, efforts made and definitions of unit efforts are given in Table 2.

For basic stock parameters sex, length and weight were recorded from all eels.

Age readings were made from otoliths, using the densitometry method of Deelder (1976). The method requires a thin slice of the otolith to be illuminated. A graph then describes the optic density along the otolith's radius. The resulting graphs were interpreted as described by Deelder (1976), and were made by comparing two independent readings of each graph. The graphs were used for back-calculating the lengths at all ages in the individual life histories and combining these values in a growth curve.

The interpretation of eel otoliths is a matter of controversy, especially regarding the treatment of supernumary zones. Several variations of conventional techniques are used (Moriarty 1973, Moriarty and Steinmetz 1979, Vøllestad 1985). The densitometric technique can be critizised for giving too low estimates of age. Realizing this, we present the results mainly for comparison with South Norwegian material, which was also read by densitometry (river Imsa, Haraldstad 1984). In present study, otoliths from all lakes were combined. The age distributions were very similar between lakes, and the length/age observations were rarely significantly different (Sommerseth 1984).

Stomachs from all eels were conserved in 96 % ethanol. Upon opening, each stomach was given a fullness index. After identification, the volume of each food item was assessed using the points method of Hynes (1950) slightly modified. Prey importance is documented by combining frequency of occurrence and mean stomach fullness; both terms are discussed and defined by Hyslop (1980).

At the sites of fyke nets and long lines, bottom samples were taken by an Ekman grab (gap area 225 cm^2), in order to compare the bottom fauna with stomach contents. Strauss' index of food selection (Strauss 1979, 1982) was calcu-

Table 1. Lake characteristics and limnological observations made during the investigation (July and August 1982).

Li: Lilandsvatn, Nø: Nøssdalsvatn, Le: Leisbergvatn, Sk: Skogs-fjordvatn, Ho: Hommelvikvatn, St: Storvatn.

	The investigated lakes					
	Li	Nø	Le	Sk	Ho	St
Map reference (M711)	1031I	1233II	1333I	1534I/IV	1735I	1936III
Catchment area (km²)	12	8	1	137	1	43
Area of lake (km²)	1.00	0.86	0.04	11.75	0.05	0.23
m. a. s. l.	15	22	5	20	8	10
Distance to sea (km)	8	7	0.1	2	0.1	0.2
Maximum depth (m)	6	4	6	100	12	18
Lake temperature (°C)						
surface	16	13	12	8	11	9
bottom	12	12	6	5	5	9
Secchi disk transparency	6	>4	5.5	15	10	13
Water colour	Yellow	Yellow	Brown	Green	Yellow	Green
pH (average)	7.1	6.9	6.1	6.9	6.5	6.3
Specific cond. (average)	53	55	26	36	36	31
Dominating bottom vegetation:						
Potamogeton natans	x					
Myriophyllum spp.		x			x	
Isoetes lacustris		x		x		
Nitella spp.	x				x	
Dead organic matter			x			*
Fish species:						
Anguilla anguilla	x	x	x	x	x	x
Salmo trutta	x	x	x	x		x
Salmo salar	x	x		x		x
Salvelinus alpinus	x	x		x	x	x
Gasterosteus aculeatus	x	x	x	x	x	x
Platichtys flesus	x					
Lake trophy (tentative)	Eu-	Meso-	Dys-	Oligo-	Oligo-	Oligo-

* Polluted by household sewage

Table 2. Fishing periods, effort, eel catch and catch per unit effort (CPUE). Unit efforts: One longline of 100 hooks, or two linked fyke nets, in one night.

	Fishing periods (1982)	Effort		Catch		CPUE	
		fyke nets	long lines	fyke nets	long lines	fyke nets	long lines
Lilandsvatn	1/7– 5/7	82	3	5	18	0.06	6.0
Nøssdalsvatn	8/7–11/7	84	6	3	15	0.04	2.5
Leisbergvatn	12/7–16/7	84	5	9	15	0.11	3.0
Skogsfjordvatn	19/7–23/7	63	6	2	27	0.03	4.5
Hommelvikvatn	27/7–30/7	0	5	—	48	—	9.6
Storvatn	1/8– 4/8	21	5	6	26	0.29	5.2
Total		334	30	25	149	0.07	5.0

lated for benthic invertebrates. The index is given by r–p, where r = relative proportion of food item in the gut and p = relative proportion of same item in the environment. Proportions are here calculated from numbers, and index ranges from −1 (strong negative selection) to +1 (strong positive selection).

Silver eel emigration was studied at the outlet of Skogsfjord-vatn in 1982 and 1983, primarily to determine the time of descent. Twenty-three paired fyke nets densely covered the bottom of the outlet from mid-September to the beginning of November 1982 and from mid-July to the end of September 1983. The fyke nets were emptied weekly. Sex, length and weight were observed for all eels. The fat content of muscle samples was measured from 13 yellow eels and 43 silver eels in 1983.

Vertebrae counts were made from X-ray photographs, employing X-ray photography equipment at the Zoological Museum, Oslo. Counts were made according to Schmidt (1913) and Boëtius (1976, 1980).

Results

Catches of yellow eels

The presence of eel was demonstrated for all six lakes. The total catch was 174 eels, ranging from 18 in Nøssdalsvatn to 48 in Storvatn (Table 2). No systematic trend in the catches per unit effort (CPUE) between lakes was apparent. Long line catches were 2–10 eels per 100 hooks per night, with a median of 5 eels. The fyke nets gave very poor catches. The highest CPUE value was 0.29 eel per net per night. Most CPUE values were below 0.1.

Only one male was registered in the material from all six lakes. Six small specimens could not be sexed in the field. All the remaining fishes were females.

Age and growth of yellow eels

Postlarval ages of the eels ranged from 2 to 7 years. Most (91 %) were 3–5 years old. The maximum age observed was 7+ for Nøssdalsvatn, 6+ for Lilandsvatn and Skogsfjordvatn and 5+ for the remaining lakes. There was a close correlation between growth depicted as length for age and the back-calculated value (Fig. 2). Length increments were from 6–12 cm yr^{-1}.

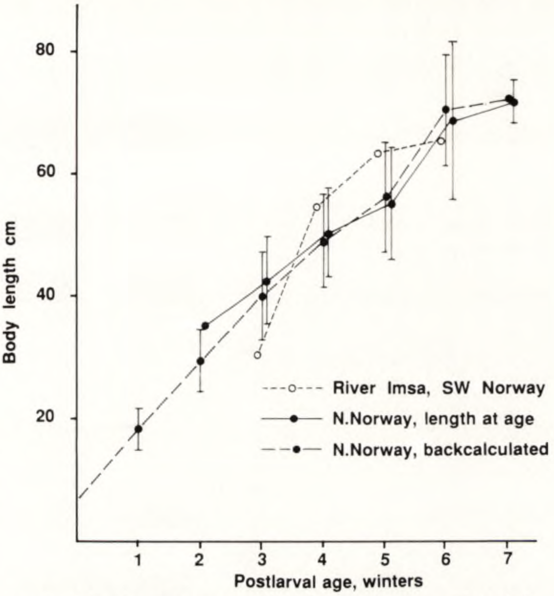

Fig. 2. Growth of North Norwegian freshwater eel (six lakes combined) based on densitometric readings of otoliths. Results from river Imsa in South Norway inserted for comparison (after Haraldstad (1984), standard deviation omitted for clarity).

The sample was compared to South Norwegian material from Imsa, which also was aged by densitometry (Haraldstad 1984, Fig. 2). The length for age in Imsa eel was higher in age classes 4+ and 5+, but the difference was only significant for 5+ ($t=4.07$, $p<0.01$).

Food of yellow eels

Important prey

Stomach contents revealed both similarities and differences between the lakes. Zoobenthos and fish dominated the stomach contents in all lakes (Fig 3). Plankton never occurred and food items of terrestrial origin were exceptional. Among the benthos prey, the snail *Lymnaea peregra*, the

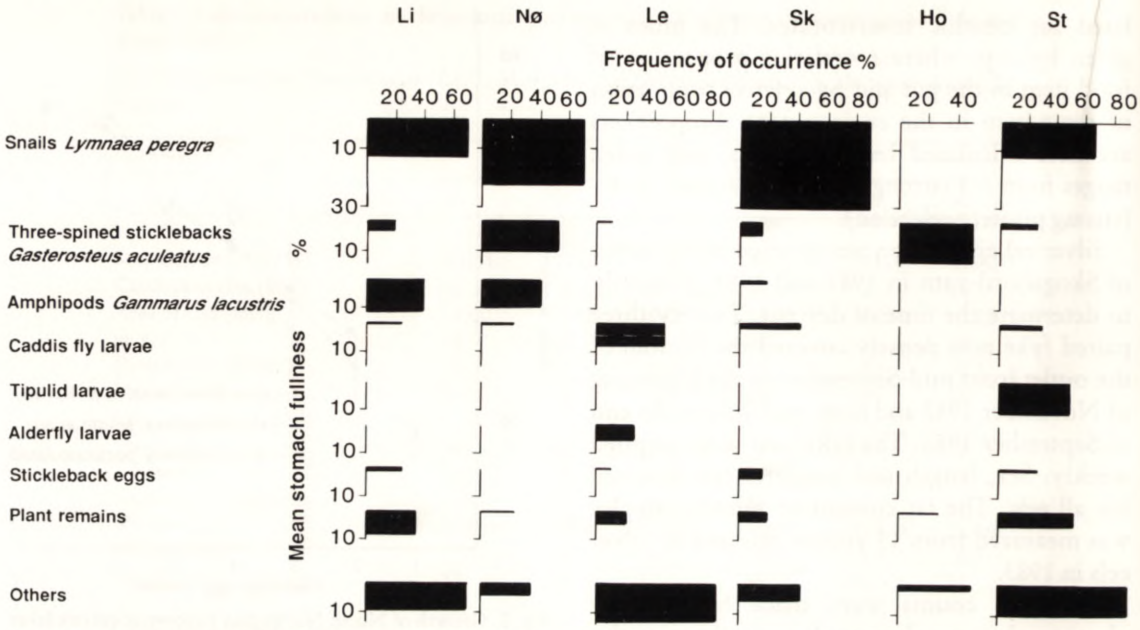

Fig. 3. Food composition of yellow eel from six North Norwegian lakes, summer 1982. Data presented as mean stomach fullness and frequency of occurrence (see Hyslop 1980).

Others include in

Lilandsvatn (Li): *Eurycercus lamellatus*, *Pisidium* sp. and insect larvae (mostly Chironomidae)

Nøssdals-vatn (Nø): Trichoptera pupae and chironomid pupae

Leisbergvatn (Le): *E. lamellatus*, *Pisidium* sp. and insect larvae (mostly Leptoceridae and terrestrial Lepidoptera)

Skogsfjordvatn (Sk): *Pisidium* sp., chydorids, insect larvae (mostly Trichoptera) and a frog *Rana* temporaria

Hommelvikvatn (Ho): *Pisidium* sp. and insect larvae/pupae

Storvatn (St): *E. lamellatus*, *Pisidium* sp., oligochaetes and insect larvae/pupae (mostly Chironomidae).

amphipod *Gammarus lacustris* and immature insects (Plecoptera, Megaloptera, Tricoptera, Tipulidae, Chironomidae) were most frequently eaten. Three-spined sticklebacks (*Gasterosteus aculeatus*) were the only fish prey. Stickleback eggs were of minor importance, but were often accompanied with plant remains in substantial amounts.

One species of snail, *L. peregra*, was the dominant food item where it occurred (Lilandsvatn, Nøssdalsvatn, Skogsfjordvatn and Storvatn). *Lymnaea peregra* is common in North Norwegian watercourses (Økland 1979). It occurs in both eutrophic and oligotrophic lakes and is available as food through all seasons.

The amphipod *G. lacustris* occurred in three lakes and was a dominant food item in two of them, Lilandsvatn and Nøssdalsvatn. This species is also quite common in northern, coastal lakes (Økland 1969). It was an important food item in many of the Irish lakes studied by Moriarty (1972, 1973).

Large insect larvae were eaten frequently in Storvatn (mainly *Tipula* sp.), and they constituted the main food in the dystrophic Leisbergvatn (*Sialis* sp. and Trichoptera). It is interesting to compare Leisbergvatn with Dubh Lochan (Shafi and Maitland 1973), a dystrophic Scottish lake of about the same size. The eels here had much the same length distribution, and

Table 3. Strauss selection indices (Strauss 1979, 1982), indicating food selection of benthic invertebrates. Groups not included in table had indices close to zero.

Li: Lilandsvatn, Nø: Nøssdalsvatn, Le: Leisbergvatn, Sk: Skogs-fjordvatn, Ho: Hommelvikvatn, St: Storvatn.

	Li	Nø	Le	Sk	Ho	St
No. of Ekman samples	13	17	15	17	20	18
Eels examined	23	18	24	29	48	32
Lymnaea peregra	0.4	0.7	—	0.8	—	0.4
Gammarus lacustris	0.3	0.2	—	0.0	—	—
Eurycercus lamellatus	0.2	—	0.1	0.0	—	0.0
Trichoptera, larvae	0.0	0.0	0.2*	0.0	0.0	0.1
Sialis sp., larvae	—	—	0.2	—	—	—
Tipulidae, larvae	0.0	—	0.0	0.0	—	0.2x
Oligochaeta	0.0	−0.2	0.0	0.0	0.0	−0.2
Pisidium spp.	−0.5	0.0	0.0	0.0	−0.1	−0.1
Chironomidae, larvae	−0.4	−0.7	−0.4	−0.8	−0.5	−0.4

* Leptoceridae
x *Tipula* sp.

their main food items were, besides perch (*Perca fluviatilis*), large larvae of the insect genera *Leptophlebia* and *Sialis*.

The three-spined stickleback (*G. aculeatus*) was the only fish species in the stomachs, and it was moderately eaten in five lakes. This fish is very abundant in the coastal lakes of northern Norway (Pedersen 1987). In Hommelvikvatn, sticklebacks were the most important food item. In this lake the length of smallest eel which had eaten sticklebacks was 34 cm, in the other lakes this length ranged from 42–52 cm.

Prey selection

The strongest positive prey selection was for the snail *L. peregra* (Strauss indices 0.4–0.8 in four lakes), but the amphipod *G. lacustris* (0, 0.2 and 0.3 in three lakes) was also selected for (Table 3). These species were not found in the other lakes. Other cases of positive selection indices (0.2) occurred for *Eurycercus lamellatus* in Lilandsvatn, larvae of Leptoceridae and *Sialis* sp. in Leisbergvatn and Tipulidae in Storvatn.

Chironomid larvae were strongly negatively selected in all lakes (−0.4−−0.8). They dominated in many grab samples, but had low importance in the eel stomachs. Pea mussels (*Pisidium* spp.) also showed negative indices in three lakes. Other cases of negative selection (−0.2) were found for oligochaetes in Nøssdalsvatn and Storvatn.

Descent of silver eel from Skogsfjordvatn

The total catch over 8 weeks in 1982 was only 47 eels. The fish were small (Fig. 4) and the majority was classified as yellow eels, probably with home ranges at the outlet end of the lake. There was no peak in the catch pattern. This suggested that the silver eel emigration had largely taken place when the sampling started in September 1982. For this reason, we started earlier the following year (in the middle of July). We also consentrated the nets more in the outlet proper by placing them where the river current became visible. They made up a dense pattern, covering the outlet from bank to bank.

The 1983 catch over 10 weeks was 182 eels (Fig. 5). The majority (88 %) was silver eels. Their size distribution was very different from the 1982 sample, with a peak in the 300–400 g weight classes and the largest eel in the 700 g

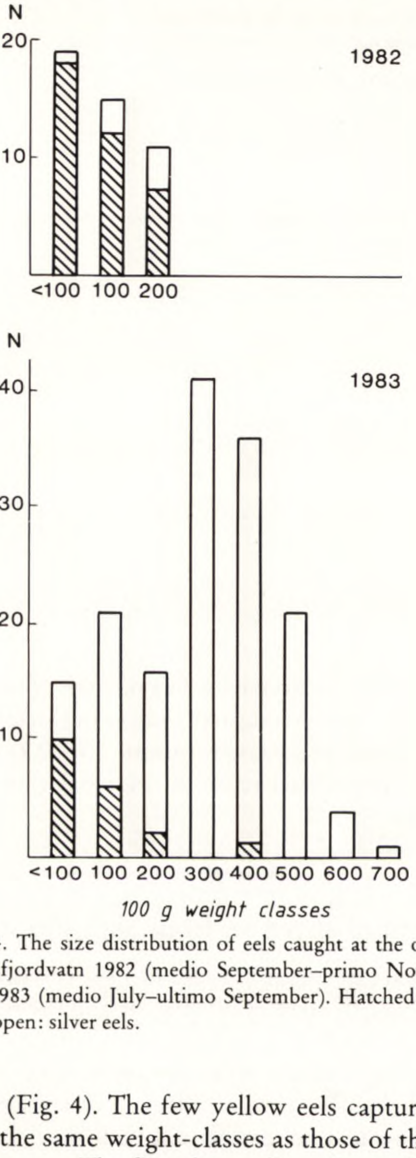

Fig. 4. The size distribution of eels caught at the outlet of Skogsfjordvatn 1982 (medio September–primo November) and 1983 (medio July–ultimo September). Hatched: yellow eels, open: silver eels.

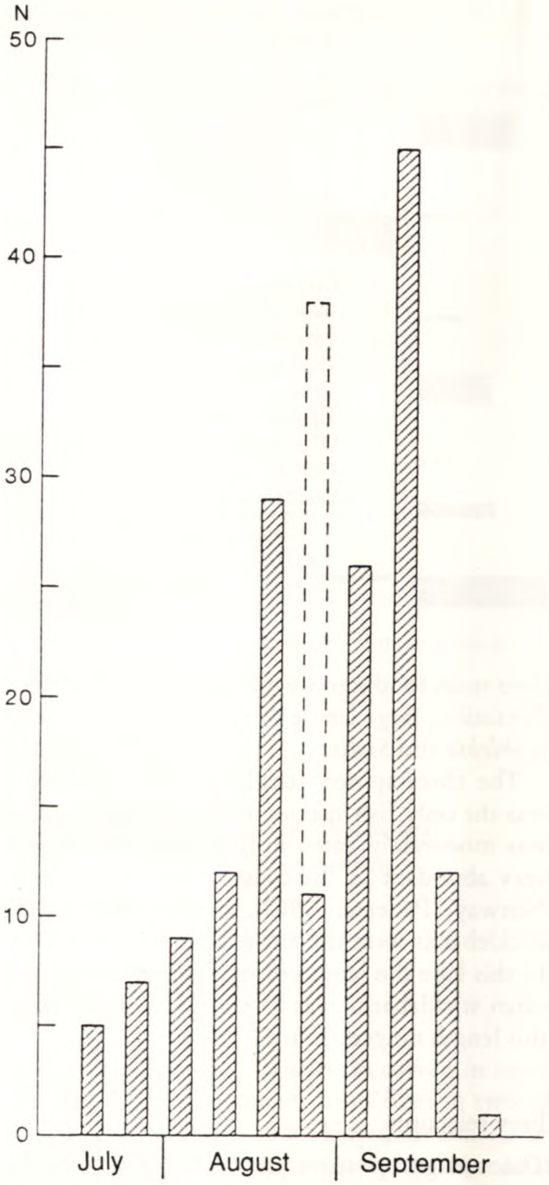

Fig. 5. Number of eels (N) caught per week in 23 paired fyke nets at the outlet of Skogsfjordvatn 1983. An adjustment is made for the last week in August, when some nets were illegally emptied.

class (Fig. 4). The few yellow eels captured fell into the same weight-classes as those of the previous year. The first descending silver eels were caught in mid-July, during the first week of the sampling period. The weekly catch then built up gradually, and the main descent took place from mid-August to mid-September (Fig. 5). After the third week of September the catch fell to nearly zero, and the sampling was terminated. The main descent coincided with a conspicuous rise in the lake water level due to heavy rainfall, but not with any marked temperature changes. Because the main descent lasted for four weeks, no correlation to moon phases was apparent.

The incidence of males in the 1983 material was low (10 fish, 7 %). One small specimen could not be sexed. The remainder were females. The mean weight of the males was 127 g (SD 25.4), and all were silver eels. In comparison, the

Table 4. Fat content of somatic muscle samples of descending silver eels (N=43), Skogsfjordvatn 1983.

	Fat content %						
	<15	15–19	20–24	25–29	30–34	35–40	>40
n	3	8	11	6	8	5	2
%	7.0	18.6	25.6	14.0	18.6	11.6	4.7

total catch of silver eels in 1983 had a mean weight of 368 g (SD 144.2).

The fat content of silver eel somatic muscle varied from 12.5 % to 41.9 % (1983 sample). About 75 % of the eels had at least 20 % fat (Table 4). The mean value was 26.2 % (SD 8.05, n=43, 3 males included). This is significantly higher than for yellow eels in the same sample ($p=0.05$, $t=2.677$). The yellow eels had a mean value of 21.2 % muscle fat (SD 5.08, n=13).

Vertebrae counts

The vertebrae counts from the combined material of 1982-eels (yellow and silver, n=221) ranged from 109 to 119 (Table 5). The mean value was 114.335 vertebrae (SD 1.583). Three eels had 109–110 vertebrae.

Discussion

Yellow eel in lakes

Virtually nothing was known of the biology of the eel in its extreme northern part of its European distribution. Our results confirm that the eel ascend regularly into river systems on the outer coast at least as far north as West Finnmark (71°N). Several year classes were present in all lakes. This documents the presence of eel populations, not only stray individuals. Also, the lack of any decreasing density gradient along the approximately 500 km coastline investigated, supports the conclusion that the eel occurs regularly this far north. This agrees well with Sivertsen (1970) who notes the presence of eel in Finnmark County and with Berg (1965) who states that the species has been caught as far east as the Pechora river in USSR, 1,200 km E of the present region of investigation. A questionnaire study by Eggan and Johnsen (1983) confirms the presence of eel in the majority of the districts in North Norway.

We have been unable to find other studies where longlines have been used as sampling gear. Our general experience does, however, indicate that longline catches are usually low. This is confirmed by the CPUE values for fyke nets. Compared with the catches of Moriarty (1972, 1973) with identical gear in Ireland, our fyke net catches were in general one order of magnitude or lower. Also, Moriarty (1973) states that his catches, commonly in the range of 1.0–1.8 eel per fyke net per night, were low. Even allowing for a low efficiency of fyke nets during the light summer nights of the Subarctic, the densities of yellow eels in North Norwegian lakes appears

Table 5. Vertebrae counts of eels (N=221) from six North Norwegian lakes.

	Number of vertebrae										
	109	110	111	112	113	114	115	116	117	118	119
n	2	1	4	14	47	53	44	40	14	1	1
%	0.9	0.5	1.8	6.3	21.2	24.0	19.9	18.1	6.3	0.5	0.5

to be low, compared to southern areas of Europe. One reason for this may be the North Atlantic Drift, which can be looked upon as a carrier of eel larvae along the European coasts. The further north and east, the less should be the load of larvae left for delivery.

The sex ratios in the present samples always showed a strong preponderance of females. This is common for the freshwater phases of the eel (Tesch 1977, Haraldstad 1987). Descending silver eels in Imsa, SW Norway had 95 % females. The result from Skogsfjordvatn (93 %) is very close to that value.

It is possible that densitometry does not yield correct age readings for eel. The low ages, and the correspondingly high growth rates may therefore be a result of erroneous age estimation. Further development of the techniques is needed to illucidate this. Meanwhile, comparison with results based on other techniques are precluded. However, backcalculation of growth and direct length at age were similar enough to warrant the conclusion that the growth rate of eels in North Norwegian lakes is sustained over many years.

In comparison with eels from Imsa, SW Norway (Haraldstad 1984), the present results are interesting. Using the same technique, the estimations of the age structures of the two samples were very close. Also, the length measurements in Imsa were made in the autumn on descending silver eels, i. e. after a longer growing season. Alltogether, the comparison indicates that North Norwegian eel have a growth which is similar to or slightly inferior to that of eel from Imsa. Compared to North Norway, the watercourses in the SW have a much longer growing season and the temperatures are much higher. This may be taken to indicate that the eel is not as dependent on high temperatures, long summers and high lake trophic levels as is generally believed, in order to feed and grow well. A presumably lower inter- and intra-specific competition for food in North Norway may strengthen this independence.

Food of yellow eel

The main food in all lakes was a combination of four groups: snails (*Lymnaea peregra*), the amphipod *Gammarus lacustris*, large benthic insect larvae and three-spined sticklebacks (*Gasterosteus aculeatus*). Except from the fact that it was mainly thelarger eels (generally >40 cm) which ate sticklebacks, no differences in food choice between small and large eels could be detected. Our impression is that all eels had reached a sufficient size (~30 cm) to search for food among the large, epibenthic prey items. The selection indices support this impression. In none of the lakes did stomach contents reflect the bottom fauna. Small, and also burrowing prey (chironomids, pea mussels and oligochaetes) were avoided, while *G. lacustris*, *L. peregra* and large insect larvae seemed to be selected.

The probable lack of suitable invertebrates in Hommelvikvatn may have forced the eel population here to adapt to a diet of sticklebacks. Similarly, Moriarty (1979) found more fish-eating eels in lakes where *Asellus* and *Gammarus* were lacking. We agree with De Nie (1987) and Tesch (1977) that high occurrence of fish in the stomachs of small (<40 cm) eels reflects poor feeding conditions. Outside Norway sticklebacks have not been reported as important food for eels in freshwater habitats. From a lake in Western Norway, Sagen (1983) reported frequent predation on sticklebacks during springtime. He argues that territorial male sticklebacks are easily captured while watching their nests in the breeding season. Eggs of sticklebacks were of minor importance as food in the present study. However, some eels had eaten a great number of eggs, often accompanied by plant remains. It is likely that eels attack and eat the whole nest. Predation on stickleback nests is reported by Daniel (1968) and Sagen (1983).

A list of species which have served as food for the eel would cover almost the entire freshwater fauna (see summary in Tesch 1977). For larger eels, most authors have found a diet composed mainly of benthic invertebrates and fish. The results from the present study are in agreement with this general picture, although relatively few studies have been carried out in lentic habitats in Europe.

Stomach contents of eels from a lake in southern Norway were dominated by insect larvae, mussels and snails (Sivertsen 1938). Sagen (1983) reports from a West Norwegian lake snails, stickle-backs, eggs of sticklebacks, chironomid larvae, mayfly nymphs, caddis fly larvae and Diptera pupae as being important food through the season. Svärdson (1972) considers the predatory impact of eels on populations of crayfish (*Astacus astacus*). Opuszyński and Leszczyński (1967) studied smaller eels from several lakes in Poland and found a diet composed mainly of chironomid larvae, mussels, snails, caddis fly larvae, mayfly larvae and *Asellus* sp. Mastyński (1984) studied eels from three Polish lakes at the spawning grounds of roach (*Rutilus rutilus*), bream (*Abramis brama*) and bleak (*Alburnus alburnus*). He found a diet composed almost exclusively of equal amounts of fish eggs and insect larvae. In the German lake Chiemsee, oligochaetes, snails, caddis fly larvae, larger crustaceans and fish were the most important food items (Micheler 1967). De Nie (1982, 1987) found in Lake Tjeukemeer, Holland, the most important food items for eels of 250–400 mm length to be fish fry (mainly 0+ of smelt (*Osmerus eperlanus*) and perch (*Perca fluviatilis*)), but also chironomid larvae, molluscs and *Gammarus tigrinus*. Eels from Lake Windermere, England, had snails and mussels as dominant food items (Frost 1946). The eels in this lake are also reported to prey upon eggs of Arctic charr (*Salvelinus alpinus*) (Frost 1952). Moriarty (1972, 1973) studied 10 lakes in Ireland and generally found, among medium-sized eels, a diet of epibenthic invertebrates, mostly chironomid larvae and the genera *Gammarus*, *Lymnaea*, *Asellus* and *Ephemera*. Larger eels fed almost exclusively on fish. In Lake Balaton, Hungary, Biró (1974) found various periphyton-living crustaceans to be the most important food near-shore, while chironomid larvae and pupae, molluscs and fish were eaten in open water areas. In Lake Manzalah, Egypt, Ezzat and El-Seraffy (1977) found eels smaller than about 50 cm to eat crustaceans, chironomid larvae and fish. Larger eels fed mainly on fish.

In general, it must be concluded that the eel is a bottom-dwelling predator feeding mainly on epibenthic and periphytic invertebrates. However, a closer look into the literature from lentic habitats reveals no clear-cut picture. Small eels (<30 cm) seem to prefer benthic insect larvae (often chironomids), bivalve mussels and snails. As eels grow bigger (35–50 cm), a progressively greater amount of errant forms occurs in the diet. This is especially true for *Gammarus* and *Asellus*, but also for larger bivalve molluscs, larger snails (often *Lymnaea*) and large insect larvae. Except for the eels in Lake Tjeukemeer (De Nie 1987), the eel often seems to become piscivorous at lengths of about 35–40 cm. In most lakes only the larger eels have a diet dominated by fish (Micheler 1967, Sinha and Jones 1975, Ezzat and El-Seraffy 1977, Tesch 1977, Moriarty 1979, Sagen 1983, Mastyński 1984).

The eel is considered a warmwater fish, with optimal growth in aquaria at temperatures of about 23–25°C (Nyman 1972, Sadler 1979, Dosoretz and Degani 1987). Ezzat and El-Seraffy (1977) report feeding of eels from Lake Manzalah, Egypt at temperatures above 30°C. Sadler (1979) found a critical thermal maximum of 39°C for eels acclimated at 29°C. Nyman (1972) gives 14°C and other authors (Bruun 1963, Sinha and Jones 1967, Moriarty 1974) about 10°C as lower temperature limits for active feeding. Vøllestad (1986) found yellow eels from brackish water in southern Norway to become inactive at about 9°C.

In Danish streams, Rasmussen and Therkildsen (1979) found eels with stomach contents at 5°C. Øygarden (1982) and Sagen (1983) observed feeding of eels at 5°C and 2.8°C, respectively. Eels with stomach contents (snails) from a frozen lake in Central Norway have been reported to us. They were caught in April, when water temperatures are normally 3–4°C. Sadler (1979) has shown experimentally that eels acclimated to temperatures below 15°C may tolerate temperatures below 1°C.

In the present study, water temperatures generally ranged from 12–13°C in Lilandsvatn and Nøssdalsvatn to 8–9°C in the other lakes, at the sites of fyke nets and long lines. In Skogsfjordvatn, a large oligotrophic lake with prolonged autumn cirqulation due to wind exposure, the eels must sustain long periods of low temperatures (2–4°C).

Larger eels are known to be strictly night-active (Bohun and Winn 1966, Tesch 1977, Veen, Hartwig and Müller 1976, Neveu 1981, De Nie 1987). However, from aquaria in northern Sweden, Müller (1972) has shown eels to be active day and night during the midnight sun period.

In addition to living at low population densities in North Norwegian coastal lakes, the eels here may benefit from having few other fish species (mainly trout and charr) to compete with for food. Regardless of the extent to which eels compete with the salmonids (this subject is discussed by Frost (1946), Sinha and Jones (1967) and Tesch (1977)), they should in northern lakes bebetter able to find a niche, than in lakes with several bottom-dwelling fish species.

Under semi-Arctic conditions eels seem to feed adequately, and by size and condition they appear well adapted to their living conditions.

Silver eel descent

The suggestion, based on the 1982 results, that the silver eel had already emigrated by mid-September, was fully confirmed in 1983. Compared to results further south in Norway, this is unusually early. Wolf trap catches over six years in Imsa, SW Norway (58°N), gave descent peaks in September and October, sometimes even November (Hvidsten 1985, Vøllestad et al. 1986). In two years a significant descent was observed in August. In middle Norway, descent peaks are reported in September at 62°N (Møre coast, Hvidsten 1982) and in September/October at 63°N (Trondheim fjord, Mehli 1974). More observations are needed before it can be concluded that early silver eel descent is typical for North Norway. Considering the extremely long distance to the Sargasso Sea from sub-Arctic Europe, and the probability of an early onset of possible autumnal cues for migration this far north, an early start seems likely.

As could be expected, the silver eels had more fat stored in their muscles than yellow eels. The mean value (26.2 %) is close to the fat level given by Bertin (1956) for silver eels (27–29 %), and also to the values of McCance (1944) for silver eel muscle tissue (26.4–29.8 %). Emigrating North Norwegian silver eels seems therefore to have fat stores comparable to eels from the central parts of Europe. The individual variation was very large (range 12.5 % to 41.9 % muscle fat) in the present material. Neither Bertin (1956) nor McCance (1944) give any variance observations to their values. It is therefore difficult to decide whether the present variation is a typical feature or whether it is characteristic for northern silver eel. Compared to central parts of Europe, N. Norwegian eels have a handicap of 1,400 km or more for the migration back to the spawning areas. It seems doubtful if the more lean individuals will ever make the journey.

Vertebrae counts

American (*A. rostrata*) and European eel have differing distri-butions of vertebrae numbers, overlapping in the 104–110 range. Boëtius (1976) argues that counts of 109 and 110 vertebrae in Europe indicates drift from the *rostrata* population. He also argues that the incidence of possible *rostrata* drift increases towards the north in Europe (Boëtius 1980). His northernmost region includes Iceland and West Norway. The present material therefore should fit into his geographic cline, with an even lower vertebrae count. Our mean value 114.335 (SD 1.583) is lower than that of the Iceland/West Norway material (114.438, Boëtius 1980), but the difference is not statistically significant ($t=0.995$, $p=0.4$). The absolute difference is, however, very close to the differences demonstrated within the cline. These differences were established by data sets of several thousands of eel. Possibly, the analysis of a large sample from subarctic Norway will yield support for the hypothesis of Boëtius (1980).

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Habitat and Food Segregation of two Sympatric Populations of Whitefish (*Coregonus lavaretus* L. *s.l.*) in Stuorajavri, Northern Norway

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Abstract

Two populations of whitefish have been identified in Stuorajavri on the basis of a bimodal distribution of gill raker numbers. The two populations are referred to as benthic and pelagic whitefish. The benthic whitefish has 19–29 gill rakers (mean 24.0), whilst the pelagic whitefish has 29–39 (mean 33.5). The rakers of the benthic whitefish are short and widely spaced, whilst those of the pelagic whitefish are long and closely packed. The benthic whitefish, which is dominant in catches from the littoral zone, feeds mainly on benthic invertebrates. The pelagic whitefish is in excess in pelagic catches, and crustacean zooplankton dominates the diet. The findings are discussed in relation to "the coregonid problem".

Introduction

The whitefish in Fennoscandia occurs in many different forms (Svärdson 1949, 1957, 1979). The different forms (or morphs) are usually separated on the basis of differences in gill raker numbers, which have been found to have a high hereditary component (Svärdson 1952). Frequently two or more morphs of whitefish are found in the same lake (Svärdson 1957, 1979, Rufli 1978, Bergstrand 1982, Kirchhofer and Tschumi 1986), and co-existing forms of *Coregonus* often exhibit profound differences in habitat and food selection (Nilsson 1958, Lindsey 1962, Lindström and Nilsson 1962, Bodaly 1979, Bergstrand 1982). Svärdson (1957, 1979) has described the different forms of whitefish as sibling species, but the systematic status of the coregonids is disputed. In the present study the taxonomically more neutral term "population" has been used.

The present paper describes a study of the whitefish in Stuorajavri, a north Norwegian lake, performed in connection with an intensive fishing programme carried out at the beginning of the 1980's (Amundsen 1988). According to the local fishermen there should be at least two forms of whitefish in Stuorajavri, and Svärdson (1957, 1979) presented evidence for the presence of two different forms in the lake. An important aspect of the whitefish studies in Stuorajavri was therefore to investigate the possible existence of two or more sympatric populations, and to elucidate any differences in habitat and feeding ecology between the forms.

Material and methods

Stuorajavri (69°08'N, 22°47'E) is an oligotrophic and slightly humic lake, situated 374 meters above sea level in Finnmark county, northern Norway (Fig. 1). The lake area is 25 km^2, and the approximate average and maximum depths are 5 and 30 m, respectively. The lake is dimictic, and the icefree season normally lasts from mid June to mid October. The drainage area is 1,170 km^2 and is dominated by a birch wood landscape with stretches of boggy land. The fish

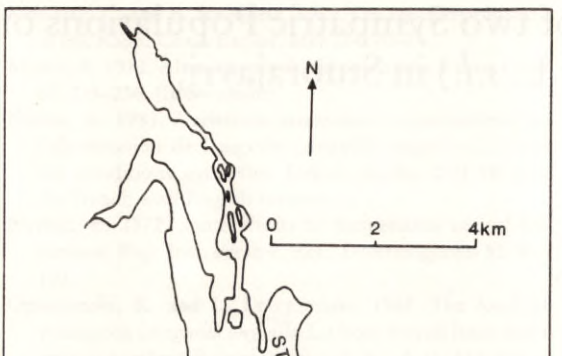

Fig. 1. The study area.

community of the lake is dominated by whitefish, but perch (*Perca fluviatilis* L.), burbot (*Lota lota* L.), pike (*Esox lucius* L.), Arctic charr (*Salvelinus alpinus* L.), brown trout (*Salmo trutta* L.) and minnow (*Phoxinus phoxinus* L.) are also present. Whitefish constitute more than 90 % of the catchable fish stock. Aspects of growth and parasite infection of the whitefish in Stuorajavri have been described by Amundsen (1988).

Sampling was carried out twice a year (July and September/October) from 1981 to 1986. Whitefish were collected using bottom gillnet series of 10 nets with mesh sizes from 10 to 52 mm (knot to knot), and floating gillnet series of 7 nets with mesh sizes from 10 to 45 mm. From 1981 to 1983 some additional samples were taken from commercial catches with beach and wedge-shaped seines. The bottom gillnets and beach seines provided benthic catches from the littoral zone, while floating gillnets and wedge-shaped seines were used to catch fish in the pelagial zone. Each fish was weighed and measured (fork length). The gill rakers on the first, left branchial arch were examined and a sub-sample was counted. Stomachs were preserved in ethanol and later examined. In the laboratory, stomachs were opened, food items were identified and the relative contribution of each prey type to the stomach fullness was estimated (Hyslop 1980). A total of 5,136 whitefish were sampled during the 6 years period, and 747 stomachs of whitefish larger than 18 cm have been examined for the present study.

Results

Gill raker numbers and whitefish forms

On the basis of a bimodal distribution of gill raker numbers, two different populations of whitefish have been identified in the lake (Fig. 2). The populations are designated pelagic whitefish and benthic whitefish based on differences in ecology. The benthic whitefish had 19–29 gill rakers (mean 24.0) on the first, left branchial

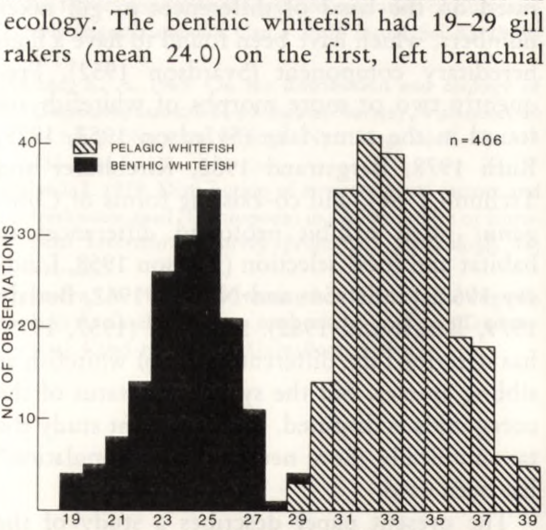

Fig. 2. Distribution of gill raker numbers of whitefish in Stuorajavri. The two different forms are indicated by different hatchings.

Fig. 3. Morphology of gill rakers on the first left branchial arch of benthic (lower) and pelagic whitefish (upper).

arch, while the pelagic whitefish had 29–39 rakers (mean 33.5). The two forms can be separated easily in the field due to differences in the morphology of the gill rakers on the first branchial arch (Fig. 3). The rakers of the benthic whitefish are short and widely spaced, whilst those of the pelagic whitefish are longer and more closely packed. There were few dissimilarities between the two populations with respect to other morphological traits.

Habitat

Whitefish was well represented in both benthic and pelagic catches, but the proportions of the two populations in the catches differed markedly. In July, the high-rakered, pelagic whitefish

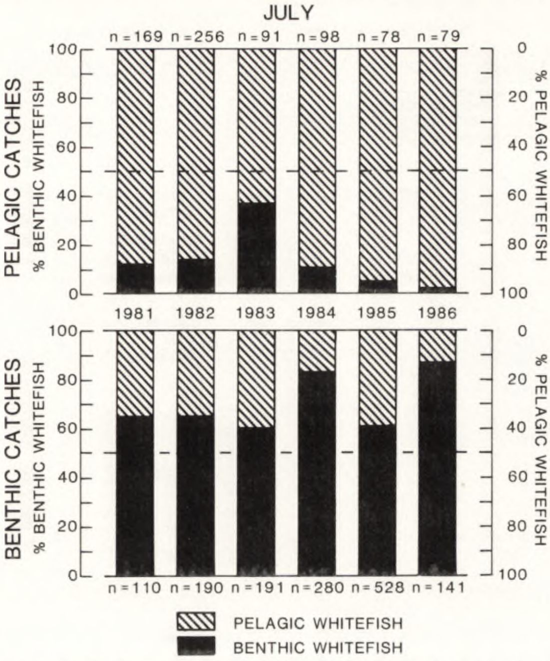

Fig. 4. Relative occurrences of the benthic and the pelagic whitefish populations in benthic and pelagic catches taken in July.

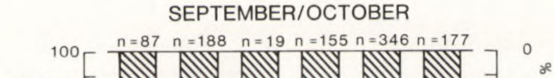

Fig. 5. Relative occurrences of the benthic and the pelagic whitefish populations in benthic and pelagic catches taken in September/October.

population dominated catches from the pelagial zone, whereas the low-rakered, benthic whitefish were taken predominantly in littoral fishing gears (Fig. 4). Usually specimens of the pelagic whitefish population constituted 80 % or more of the whitefish numbers in pelagic catches, whilst more than 60–70 % of the benthic catches consisted of individuals of the benthic whitefish population.

In the autumn samples, there were an even stronger segregation of the two whitefish populations (Fig. 5). With the exception of 1981, there were more than 85 % pelagic whitefish in the catches from the pelagial zone, and more than 80 % benthic whitefish in littoral catches. In the autumn of 1981, however, there were slightly more of the benthic than the pelagic whitefish population in pelagic catches.

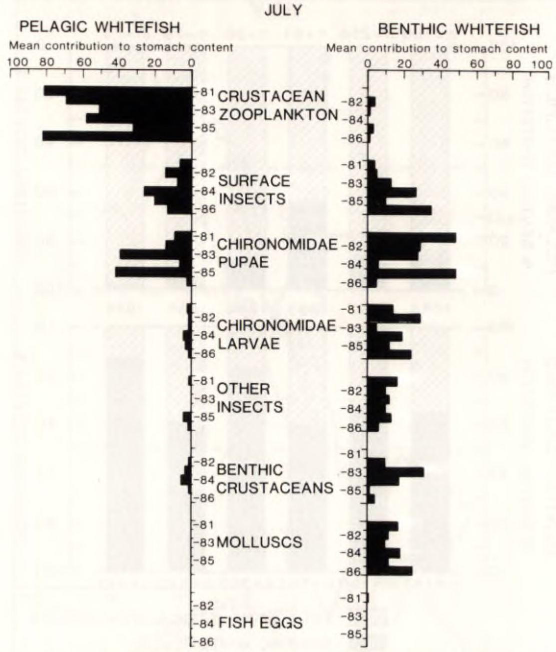

Fig. 6. Diets of benthic and pelagic whitefish in July samples.

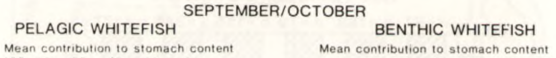

Fig. 7. Diets of benthic and pelagic whitefish in September/October samples.

Feeding

Crustacean zooplankton dominated the diet of the pelagic whitefish in the July samples, whereas benthic invertebrates were the major prey of the benthic whitefish (Fig. 6). Chironomid pupae and surface insects also contributed significantly to the diets of both populations.

The autumn diet of the pelagic whitefish was composed almost exclusively of crustacean zooplankton (Fig. 7). The autumn diet of the benthic whitefish was usually dominated by benthic invertebrates with benthic crustaceans, especially *Eurycercus lamellatus*, being particularly important. The stomach contents of the benthic whitefish in the autumn of 1981 differed from the general pattern in being dominated by crustacean zooplankton.

The zooplankton diet of both whitefish populations was mainly composed of *Cyclops scutifer*, *Eudiaptomus graciloides*, *Bosmina longispina* and *Daphnia cristata*. Also *Heterocope appendiculata*, *Holopedium gibberum* and *Bythotrephes longimanus* were occasionally recorded in the stomachs. The benthic crustaceans in the diet, although dominated by *E. lamellatus*, were also infrequently represented by other smaller chydorids and *Sida crystalina* and *Gammarus* sp. In addition to chironomids, larvae of Trichoptera, Plecoptera, Tipulidae and *Sialis* sp. were the main benthic insects identified in the diet. The molluscs in diet were *Pisidium* sp., *Sphaerium* sp., *Valvata* sp., *Planorbis* sp. and *Lymnea* sp. Molluscs and fish eggs were never found in the stomachs of the pelagic whitefish.

Discussion

The bimodal distribution of gill raker numbers indicates the presence of two distinct populations of whitefish in Stuorajavri. The two populations correspond to *Coregonus nasus* and *C. lavaretus* as described by Svärdson (1957, 1979). Svärdson (1957) presented data of gill raker counts for 152 whitefish collected from Stuorajavri in 1953–54. The mean number of gill rakers of fish in Svärdson's sample was 24.8 and, except for two counts of 32 and 34 gill rakers, the distribution of gill raker numbers ranged between 20 and 29. This corresponds very closely to the gill raker distribution found for the benthic whitefish in the present study. Svärdson (1979) argued that fishes with gill raker numbers up to 29 belonged to one pool, wheras the two specimens with 32 and 34 rakers belonged to another population. This latter population appears to correspond to the pelagic whitefish. The reason why fish of this population were poorly represented in Svärdson's (1957) samples, may be that the samples were probably taken using a beach seine, which in the past was the most commonly used fishing gear in Stuorajavri. Results obtained in the present study demonstrate that the pelagic whitefish is poorly represented in beach seine catches.

The two populations exhibited a clear-cut segregation in habitat choice, the benthic whitefish being most commonly caught in the littoral zone and the pelagic whitefish in the pelagic zone. There were, likewise, marked differences in feeding habits between the two populations. These differences were also reflected by differences in parasite infections. Plerocercoids of *Triaenophorus crassus* Forel and *Diphyllobothrium ditremum* Creplin, which both have planktonic copepods as first intermediate hosts, had the highest prevalence of infection in the planktivores pelagic whitefish (Amundsen 1988). The segregation with regard to both habitat and diet was most pronounced in the autumn. In early summer, there was a certain diet overlap, as both populations exploited chironomid pupae and surface insects to some extent. Nilsson (1965, 1967) proposed that food segregation of two related species (or populations) is interactive, with segregation being most pronounced when food is scarce and being broken down in periods of food abundance. Following this concept, the niche overlap in early summer may be the result of a high food abundance at this time of the year, whereas the stronger segregation in autumn may reflect a seasonally lower food availability.

In contrast to the normal observation of segregation in autumn feeding of the two populations, there was a conspicuous diet overlap in the autumn of 1981. At this sampling, the benthic whitefish had crustacean zooplankton as dominant food, concurring with an enhanced pelagic habitat choice. The strong overlap in zooplankton feeding between the two populations is apparantly inconsistent with the interactive segregation concept. However, the reasons for these observations on the benthic whitefish are probably not to be sought in the segregative mechanisms between the whitefish populations. More likely they are related to the state of the fish stock in Stuorajavri in 1981, as the fish stock at that time was very dense and suffered from stunting (Amundsen 1988). The planktivorous behaviour of the benthic whitefish may thus be the result of heavy intra- and interspecific competition in the littoral zone, related to food shortage from over-exploitation of benthos by several benthophagic fish species. Taking into consideration the disappearance of emerging insects, the benthic food resources were likely to be most limited in the autumn, coinciding with the observed food and habitat shift of the benthic whitefish in 1981. As the intensive fishing programme reduced the fish density (Amundsen 1988), the predation pressure on benthos probably diminished, allowing the benthic whitefish to remain as a, primarly, benthic feeder in the subsequent autumns (Fig. 5 and 7).

The food habits of sympatric populations of whitefish have often been found to be correlated with gill raker numbers, in that populations with closely spaced gill rakers are planktivores, whereas those with widely spaced gill rakers are benthophagic (Svärdson 1952, 1965, 1979, Nilsson 1958, Bodaly 1979, Bergstrand 1982). This is supported by the findings in the present study, and it appears that fishes with closely spaced gill rakers are better adapted to feeding on plankon. However, when evaluating the role of the gill rakers in feeding on zooplankton, it should be noted that the gill rakers of whitefish have been shown not to act as a mechanical sieve in relation to size selection (Seghers 1975). The role of the gill rakers is, therefore, not obvious, but although the whitefish do not appear to filter-feed, the rakers may play a significant role in the retention of prey in the mouth cavity.

Feeding preferences of whitefish have been suggested to have a considerable hereditary component (Svärdson 1979, Bergstrand 1982). If this suggestion is correct, the observed correlations between feeding habits and gill raker number must be the result of a linked inheritance, i.e. the genes of both characters must be located on the same chromosomes. Alternately, and perhaps more likely, the hereditary component of feeding preferences may be related to a dependency of the food choice upon gill raker numbers, which in turn have a hereditary basis (Svärdson 1952).

Provided there is a strong hereditary component in the determination of gill raker numbers, the distinct differences in gill raker distribution between the benthic and the pelagic whitefish indicate a strong reproductive segregation between the two populations. Autumn samples have contained both ripe fish and also some spent spawners of both populations. A segregation in time of spawning is therefore not likely. According to local fishermen, the peak spawning period of whitefish in Stuorajavri occurs after ice covering in autumn. Whether or not the two populations are segregated in place of spawning is not currently known, as sampling has not been undertaken after ice cover. Svärdson (1965) described the isolating mechanisms in whitefish as rather poor, but emphasized size segregation. In Stuorajavri, the benthic whitefish show faster growth rates and achieve larger sizes than the pelagic whitefish, but these differences were not pronounced when the populations suffered from stunting (Amundsen 1988). The factors responsible for isolation of the two populations are, therefore, not clear, although the bimodal distribution of gill raker numbers reveals that the segregation is efficient, as hybrids would have possessed the intermediate raker numbers (Svärdson 1952, 1957). Comparison of the gill raker counts of the present study with those of Svärdson's (1957) samples, indicates that introgression of the benthic whitefish has not occurred during the last 30 years.

Adopting the biological species concept (Mayr 1963), Svärdson (1957, 1979) concluded that the whitefish complex of Scandinavia comprises six species. It is proposed that the species originated allopatrically before or during the last glaciation periods. The large number of different whitefish forms is attributed to introgressive hybridisation in sympatry following deglaciation, and introgression is actually considered to be a factor acting in the evolution of new species (Svärdson 1970). Introgressive hybridisation between the species leads to a dilution of morphological differences, whereas "Since natural selection favours all sorts of ecological differences between sympatric populations, the ecological traits of the species are the last to disappear when introgression is in progress" (Svärdson 1957). In my opinion, this interpretation explains the maintenance of ecological differences between sympatric whitefish populations in the absence of morphological dissimilarities. Assuming that the number of gill rakers is an indirect ecological trait influencing the feeding ecology of the whitefish, the above interpretation may also explain the maintenance of differences in gill raker numbers between sympatric populations. However, whether the origin of the differences in gill raker numbers (and ecology) is due to allopatric or sympatric processes, is disputed. A view contrary to

Svärdson's (1949, 1957, 1979) allopatric speciation of coregonids may be inferred from the paper of Lindsey (1981), who emphasizes the plasticity in gill rakers of coregonids and phrases that "gill raker counts expand to fill the available niches" (Lindsey op. cit.). The origin and systematic status of the two sympatric populations in Stuorajavri is, therefore, open to question.

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Physical Habitat Selection by Brown Trout (*Salmo trutta*) in Riverine Systems

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Abstract

Knowledge about habitat requirements of brown trout (*Salmo trutta*) is important for stream management and impact assessment. Method of observation may influence the habitat suitability results obtained. The best approach may be to adopt a combination of direct underwater observation and electrofishing, if a variety of habitat conditions are studied. A distinction should be made between physical habitat variables affecting in situ habitat choice and habitat variables affecting carrying capacity, i.e. boundary conditions, because their spatio-temporal dimensions are different. Water depth, water velocity, streambed substrate and cover seem to be the most important physical stream characteristics influencing in situ habitat choice by brown trout. Preferred habitat is positively correlated with fish size. Smaller brown trout occupy shallow riffle areas with cobble substrate, while the larger fish prefer deeper stream areas with cobble/boulder substrate and abundant cover. All sizes of fish seek out low water velocity micro-niches to minimize energy expenditure. Different studies emphasize the importance of different habitat variables. This is probably a reflection of the diverse factors modifying habitat selection. Total available habitat should be quantified in all habitat analysis studies, because availability can modify habitat choice strongly. Different habitat characteristics may be the limiting factor(s) in different streams and true habitat preferences cannot therefore be constructed from habitat use data alone. Furthermore, habitat selection may be modified by biological factors such as fish population density and composition, food supply and presence of other species. In addition greater attention should be given to the possible interactions between physical habitat variables.

Introduction

The habitat requirements of brown trout (*Salmo trutta*) in streams are important considerations in stream management, and in assessing future impacts of stream development on brown trout populations. Hence, studies of physical habitat selection by brown trout have been undertaken in a variety of streams, in order to establish objective habitat suitability criteria. However, several studies have emphasized the importance of different habitat variables (Lewis 1969, Egglishaw and Shackley 1982, Shirvell and Dungey 1983, Hermansen and Krog 1984, Wesche et al. 1987a). Thus it appears unclear from the existing literature whether brown trout tend to consistently select similar physical habitats among different streams.

One obvious reason for the apparent inconsistencies is that the studies have to some degree focused on different habitat factors. Uncertainties about which factors might be of significance, and also practical considerations, may have caused important habitat variables to be omitted from the work. It is thus neccessary to find out which physical factors ought to be included in all habitat studies. A second reason may be that most studies have only reported on fish occupancy of habitat. The underlying assumption that habitat not used by fish does not influence habitat actually used, may be false (Moyle and Balz 1985, DeGraaf and Bain 1986). A particular habitat may be used by a fish only because the preferred habitat is in short supply (Moyle and Balz 1985). Identification of limiting habitat factors is important (Bowlby and Roff 1986). Therefore, to find true habitat preferences, the quantification of total available habitat seems necessary. Thirdly, there is the problem of whether physical habitat variables can be considered as independently influencing habitat selection by brown trout. This is apparently an underlying assumption in most studies on the subject. Habitat simulation models developed in recent years, particularly the Instream Flow Incremental Methodology (IFIM; Bovee 1982) which is designed to quantify available habitat for different species of fish, assume preferences for different habitat variables to be independent (Orth and Maughan 1982, Mathur et al. 1985), i.e. actual habitat preference is constant for the species, irrespective of variability in habitat use. On this basic assumption, habitat suitability curves have been constructed independently for a range of habitat variables, based on empirical data for observed habitat use for brown trout (Raleigh et al. 1986). However, the validity of this assumption has been questioned by several authors (Orth and Maughan 1982, Mathur et al. 1985, Moyle and Baltz 1985, DeGraaf and Bain 1986).

In the present paper, I summarize habitat selection by brown trout reported from riverine systems, in order to analyse why several studies apparently report different physical habitat requirements for brown trout in streams. I will discuss the possible effects of not comparing habitat use with habitat availability, and evaluate the criticism about the assumption of habitat variables independently influencing habitat selection by brown trout.

Observation methods

Two approaches have been adopted in field studies of habitat occupancy by brown trout in riverine systems;

(1) the "habitat" approach, in which the physical habitat variables characterizing a stream area, as opposed to stream point, have been measured (Lewis 1969, Bohlin 1977, Egglishaw and Shackley 1982, Hermansen and Krog 1984, Heggenes 1988 a, b)

(2) the "micro-habitat" approach, in which physical characteristics have been measured in a stream point, i.e. the focal point (snout) of the brown trout (Fausch and White 1981, Shirvell and Dungey 1983, Cunjak and Power 1986).

These two approaches require different observation methods. Three observation methods have been adopted in habitat studies;

(1) electrofishing, primarily used in the habitat approach, but also used for studying micro-habitats (Hearn and Kynard 1986, Gatz et al. 1987)

(2) observation from river banks (surface observation), also used in the micro-habitat approach (Shirvell and Dungey 1983), but as well for studying brown trout habitat and behaviour in general (Jenkins 1969, Bachman 1984)

(3) direct underwater observation used only in some micro-habitat studies (Fausch and White 1981, Cunjak and Power 1986).

Electrofishing was the first method adopted for studying trout habitat in general (Tarzwell 1937), and also for studying habitat use by brown trout in particular (Shuck 1945, Boussu 1954, Lewis 1969). The method has been considered convenient for catching territory-holding fish, such as brown trout (Karlström 1977). In most studies sections of a stream with previously described pysical characteristics, have been blocked by stop nets, repeatedly electrofished, and the fish in the sections counted and measured (Boussu 1954, Lewis 1969, Bagliniere and Champigneulle 1982, Egglishaw and Shackley 1982, Kennedy and Strange 1982, Hermansen and Krog 1984). One problem with the described procedure is that it gives a rather rough estimate of habitat use, i.e. number and size of fish observed within a relatively large section of the stream. Positions of individual fish in the stream are not observed, and more detailed analysis is therefore not feasible.

Several authors have indicated that electrofishing is a method less suited for more detailed studies, as it may bias the habitat use observed. If the anode is pulled forward in the water, the electrical field may frighten the fish and thus displace individuals from their original positions prior to capture. This possible bias has been termed "fright bias" (Bovee and Cochnauer 1977). The opposite effect, galvanotaxis, may also produce a bias (Gatz et al. 1987). In order to refine the electrofishing method and reduce the bias, a systematic "point" method of electrofishing has been developed for habitat studies (Balz et al. 1982, Hearn and Kynard 1986), and this modified method has also been adopted for studies of stream-living brown trout (Heggenes 1988 a, b). The anode is not pulled forward in the water, and the approximate position of the fish is ascribed to the area of its first observation. Even though positions of individual fish may be recorded in this way, it may be that for a wary species like brown trout, the method tends to give typical refuge and resting habitats rather than feeding habitat. Bachman (1984) noted that repeated alarm stimuli or a stronger initial stimulus would cause foraging brown trout to flee to deep water or to move under some kind of cover. However, the degree of "fright bias" apparently depends on the type of habitat investigated. In low gradient stream sections with fine substrate and low water velocities the bias will tend to be more pronounced (Heggenes et al. 1989). In high gradient stream sections with coarse substrate, the electro-fishing method may give a better estimate of habitat use than alternative methods (Heggenes et al. 1989).

Observation from river banks or from elevated vantage points have found application in brown trout habitat studies since the 1960's (Jenkins 1969), and also in recent works (Shirvell and Dungey 1983, Bachman 1984). As the fish are not directly disturbed through observation, this method may be unbiased as to the position of the observed fish. However, the method may be biased due to reduced probability of observation under certain habitat conditions, as in deep water or below surface turbulence (Shirvell and Dungey 1983). Observation from the surface apparently is sensitive to even slight surface disruption, which reduces observation probability (Heggenes et al. 1989).

Direct underwater observation by diving or snorkeling is a useful method for observing fish in their natural habitats under as variety of conditions. Hence, this method has gained increasing popularity in recent years for studies of brown trout in riverine systems (Fausch and White 1981, Cunjak and Power 1986). It is particularly suited for observing micro-habitat use. Fish do not appear to be disturbed by the diver, provided he moves carefully and upstream (Fausch and White 1981). Therefore, direct underwater observation has been considered a non-biased method for observing fish. Usually, little displacement of fish due to the diver occurs. For larger trout, underwater observation appears to be a consistent method for estimating fish numbers under certain habitat conditions (Schill and Griffith 1984, Slaney and Martin 1987, Zubik and Fraley 1988). However, a recent study suggests that the method may be biased in high gradient stream sections with relatively high water velocities and coarse substrate, because the observation probability of individual fish by diving is lowered in such habitat conditions (Heggenes et al. 1989). Consequently, too few fish may be observed by diving in this type of habitat. Also, the use of shallow habitat may be underestimated (Keenleyside 1962, Heggenes et al. 1989), which in particular may bias observed habitat use by the smallest fish.

Physical habitat variables studied

Four physical habitat variables have been more consistently studied than others; water depth, water velocity (or stream gradient), streambed substrate and cover (Table 1). This may reflect that these variables are considered the most important habitat variables affecting habitat selection by brown trout. One type of habitat model (IFIM; Bovee 1982) assumes explicitly that these four physical variables are the most important. To my knowledge no criticism has been raised against this assumption (Mathur et al. 1985). One or more of these variables have been demonstrated to correlate with distribution and abundance of brown trout in a number of streams (Shuck 1945, Boussu 1954, Lewis 1969, Binns and Eiserman 1979, Shirvell and Dungey 1983, Gatz et al. 1987, Wesche et al. 1987 a).

Table 1. Some published studies of habitat use by brown trout showing the relative importance of the different physical parameters studied, as estimated subjectively by the author.
0 = no importance, * = some importance, ** = important, *** = most important.

Reference	Observation method	Brown trout size (cm)	Activity studied	Importance of physical parameters									Remarks
				Stream width	Surface area	Water volume	Water depth	Surface velocity	Mean velocity	Snout velocity	Sub-strate	Cover	
Shuck 1945	Electrofishing	> 21.4 < 21.3		0	0 0	***	**	0[a]					Imprecise descript. of habitat var.
Lindroth 1955	Electrofishing	0+ 1+					**		**		**		Qualitative description
Lewis 1969	Electrofishing	> 17.5			*	*	*		**			***	Only pool-areas
Bohlin 1977	Electrofishing	0+ 1+					*** ***				** **		
Karlström 1977	Electrofishing	< 2+					**		***		***		
Bagliniere and Champigneulle 1982	Electrofishing	0+ > 1+					** ***		**		**	 ***	
Egglishaw and Shackley 1982	Electrofishing	0+ 1+		0 0	0 0	0 0	** **	0 0			0 0	* *	
Kennedy and Strange 1982	Electrofishing	0+ 1+					** ***						Gradient: * Gradient: *
Hermansen and Krogh 1984	Electrofishing	> 15		***[b]			**		*[c]		**		Gradient: ***
Gatz et al. 1987	Electrofishing	> 1+					*		***		***	**	
Heggenes 1988a 1988b	Point electro-fishing	$\bar{X}$=17.8 $\bar{X}$= 8.1 $\bar{X}$=14.9					*** ** ***		* ** *		** ** **	** * **	
Butler and Hawthorne 1968	Surface observation[d]											**	
Baldes and Vincent 1969	Surface observation[d]	$\bar{X}$=21.3		*	*					***[e]		**	
Shirvell and Dungey 1983	Surface observation	$\bar{X}$=42	Feeding Spawning				** **			*** ***	 **		
Fausch and White 1981	Underwater observation		Feeding Resting				** **			** **		 ***	Low water temp.
Cunjak and Power 1986	Underwater observation	0+ > 1					** **			** **		** **	
Heggenes and Saltveit 1989	Underwater observation	$\bar{X}$= 9					**	**	**	**	**	*	

[a] Velocity not specified, assumed to be surface velocity [b] I.e. wetted perimeter [c] Measured 7cm above the bottom, highly correlated with CV of mean velocity [d] Studies in experimental flume [e] I.e. micro water velocity

A whole range of additional habitat variables have also been studied in trout habitat surveys (Platts et al. 1983), but, except for variables related to water-flow and temperature, which in most studies are considered as implicit boundary conditions, other physical variables are in most cases some kind of refinement of the four basic variables above (Binns and Eiserman 1979, Hermansen and Krog 1984, Bowlby and Roff 1986, Wesche et al. 1987a). Besides, it is necessary to make a distinction between physical habitat variables only affecting carrying capacity (biomass, standing stock), e.g. maximum water temperature or average annual base flow, and variables affecting in situ habitat choice. Their spatio-temporal dimensions are different. With regard to waterflow, particularly during spring and summer, some studies have suggested that it can influence the size of young salmonid populations (Elwood and Waters 1969, Tschaplinski and Hartman 1983, Hume and Parkinson 1987, Erman et al. 1988), possibly by determining a stream's depth and velocity. Young salmonid fry are susceptible to downstream displacement (Heggenes and Traaen 1988a). However, short-time high flows do not seem to affect in situ habitat choice by brown trout (Heggenes 1988b). Binns and Eiserman (1979) tested correlations between standing crop of trout, including brown trout, cutthroat trout (*Salmo clarki*), rainbow trout (*Salmo gairdneri*) and brook trout (*Salvelinus fontinalis*), in 36 Wyoming streams, and 13 physical, 5 chemical and 4 biological fluvial habitat attributes. Significant correlations were found for eight physical variables, of which three might be considered as spatio-temporal boundary conditions not directly influencing actual in situ habitat selection by trout (late summer stream flows, annual stream flow variation, maximum summer stream temperature). The remaining physical factors were stream cover and depth (depth was considered as a type of cover), water velocity, stream substrate, stream width and eroding stream banks, which also may be considered as a type of cover. Similarly trout biomass in 30 southern Ontario streams were correlated with the physical factors percent pool area, which may be considered a singlevalued combined effect of depth and velocity, overhead cover and mean maximum summer temperature (Bowlby and Roff 1986). A habitat suitability index model (HSI) developed in particular for brown trout in riverine systems, includes 18 habitat variables, which are all believed to govern the habitat suitability or carrying capacity for brown trout in streams (Table 2) (Raleigh et al. 1986). Except for average maximum water temperature and average annual base flow, which affect a stream's carrying capacity, but usually not in situ habitat choice by brown trout, the other physical factors are variations of the four basic variables depth, velocity, substrate and cover. Therefore, based on present knowledge about brown trout habitat selection, it seems reasonable to conclude that these four variables are the most important physical factors to include in habitat studies.

Table 2. Suitability index variables for brown trout developed by Raleigh et al. (1986) for the HSI-model.

	Variable
1.	Average maximum water temperature (°C)
2.	Average maximum water temperature during embryo development
3.	Average dissolved O_2 (mg/l)
4.	Average thalweg depth (m)
5.	Average velocity over spawning areas
6.	Percent cover during the late growing season low-water period
7.	Average diameter of substrate components in spawning areas
8.	Percent of substrate components 10–40 cm in diameter
9.	Dominant substrate type
10.	Percent pools
11.	Average percent vegetation
12.	Average percent rooted vegetation
13.	Maximum pH
14.	Average annual flow as a percent of average annual daily flow
15.	Pool class rating
16.	Percent fines
17.	Percent of stream area shaded
18.	Nitrate-nitrogen (mg/l)

Depth is commonly measured in cm with a standard measuring rod, and the variable is easy to quantify objectively. It is usually expressed as total depth, i.e. from stream bottom to stream water surface, but it has also in some cases been expressed as relative or snout depth, i.e. from fish snout position to stream water surface (Cunjak and Power 1986). Focal points are often close to the stream bed, i.e. within 10–15 cm (Shirvell and Dungey 1983, Bachman 1984, Cunjak and Power 1986), and are therefore also an indication of selected water depths. However, this may vary with water velocites (Shirvell and Dungey 1983, Bachman 1984, Fausch 1984), and the assumption may not necessarily be valid in slower flowing water.

Water velocity has been measured in several ways. The most accurate micro-velocity measurement is that of the fish snout position (Fausch and White 1981, Shirvell and Dungey 1983, Cunjak and Power 1986). Most other habitat studies have included the measurement of mean water column and/or surface velocity. Although water velocites are easily quantifiable and presumably objective, there are some inherent problems in their measurement. They may vary not only with fish positions, but also with the type of flow-meter used. Indeed, different studies may report different snout water velocities preferred due to application of different measuring devices, e.g. midget Bentzel current speed tubes compared to Ott flow meters fitted with a propeller. Even with similar measuring devices, differences may be found if the areas of the measuring surface exposed to the water current are different. It is likely that reported differences in snout water velocities preferred by juvenile Atlantic salmon (*Salmo salar*), were an artifact of measuring velocities with a 0.8 cm propeller compared to earlier measurements with a 3 cm propeller (Heggenes and Saltveit 1989).

Streambed substrate has been measured in a variety of ways. Substrate sizes are reported in several scales, and no standardized classification has been adopted (Bovee 1982, Platts et al. 1983). Bain et al. (1985) suggested a modified Wentworth scale be used, and this scale may be well suited for habitat analysis studies. Most methods have been based on a visual assessment of the percentage composition of the streambed substrate by fraction at the habitat area of interest (Bovee 1982, Bain et al. 1985). However, the problem of subjectivity associated with this procedure tend to invalidate it. A better method is to visually assess only the dominant substrate component within a specified area (Platts et al. 1983, Bain et al. 1985). Although this method results in some loss of information, it will tend to be unbiased with a large enough sample. Substrate data obtained in this way are categorical. This is inconsistent with the physical habitat variables of depth and water velocity which are measured on a continuous scale. For a more detailed substrate description of a habitat area, Bain et al. (1985) developed a measurement method which quantifies the central value estimate of surface coarseness and a measure of substrate heterogeneity. The dominant substrate category is described at several consecutive points along an axis to give several coded observations. A mean (index of coarseness) and standard deviation (index of heterogeneity) can then be calculated, and the data can be treated as continuous. This procedure circumvents the problems associated with the percentage composition method, but is of less use in describing points or minute areas which may be of interest in microhabitat studies.

Cover is apparently the most difficult variable to quantify in habitat analysis studies. First of all there is no standard definition of cover, and different authors have defined what they consider as cover in different ways (Binns and Eiserman 1979, Fausch and White 1981, Cunjak and Power 1986, Wesche et al. 1987a). Based on the previous discussion I would suggest that both depth and substrate be considered as variables on their own, and are not included in cover. Thus the variable cover would be limited to overhead cover in the sense it has been used in experimental (Butler and Hawthorne 1968, Baldes and Vincent 1969, DeVore and White 1978, Heggenes and Traaen 1988b) and some field studies (Harshbarger and Bhattacharyya 1981, Cunjak and Power 1986, Heggenes 1988a,b). In some field studies overhead cover has been taken to include both instream cover, surface turbulence, shade and overhead riparian vegetation, and expressed as a single-valued function (Cunjak and Power 1986, Heggenes 1988 a, b). It might, however, be useful to distinguish in-stream cover as distinct from riparian cover (Gatz et al. 1987). Like streambed substrate, the assessment of cover is usually based on a visual rating method, which involves a subjective element (Bovee 1982, Wesche et al. 1987 a). As the problems here are similar to those encountered in classifying substrate, it may be fruitful to adopt an approach similar to the one suggested for substrate by Bain et al. (1985).

Physical habitat use by brown trout

Physical habitat use by brown trout may be expected to change with increasing fish size. Several authors have reported an increasing use of deeper habitats with coarser substrate as the size of the fish increases from young-of-the-year (3–8 cm) up to adult fish (>20–25 cm) (Jenkins 1969, Bohlin 1977, Karlström 1977, Kennedy and Strange 1982, Bachman 1984, Cunjak and Power 1986). It is therefore necessary to consider habitat use in relation to fish size.

Experimental and field studies of brown trout have suggested that low winter temperatures may induce a winter hiding behaviour with preferences for greater overhead cover (Hartman 1963, Cunjak and Power 1986, Heggenes and Traaen 1988 b, Heggenes and Saltveit 1989). Substrate providing shelter appears to be more important at low temperatures (Heggenes 1988 c). Consequently, water temperature ought to be considered when habitat analysis studies of brown trout are reported and compared.

Whether allopatric or sympatric populations are investigated should be considered, as interspecific competition may influence habitat choice (Fausch and White 1981, Shirvell and Dungey 1983, Moyle and Balz 1985, Gatz et al. 1987). However, brown trout is an aggressive species, and it tends to dominate over other salmonids in sympatry. Brown trout has been reported to dominate over Atlantic salmon (Kalleberg 1958, Karlström 1977, Kennedy and Strange 1986), brook trout (Fausch and White 1981, 1986, Cunjak and Power 1986) and rainbow trout (Gatz et al. 1987), although these general dominance relationships may be modified for example by size differences (Jenkins 1969).

On the other hand strong intraspecific competition characterizes brown trout social behaviour. Larger brown trout dominate smaller, and consequently tend to restrict smaller brown trout to sub-optimal habitat areas (Jenkins 1969, Bohlin 1977, Bachman 1984, Heggenes 1988 a). Similarly, resident brown trout seem to have an "owner's advantage" over introduced fish (Bohlin 1977). Therefore, surveys of total population composition should be included in habitat analysis studies, but this has rarely been done. Usually only a fraction of the total population is included, either adults or young (Table 1). Brown trout may also select different habitats for different activities. In the recent literature, habitats have been divided into the following categories according to the activity involved: (1) refuge habitat (Bachman 1984), (2) feeding or foraging (Fausch and White 1981, Shirvell and Dungey 1983, Cunjak and Power 1986), (3) resting (Fausch and White 1981, Cunjak and Power 1986) and (4) spawning (Shirvell and Dungey 1983). Refuge, foraging and spawning habitats are clearly defined concepts, and the reported studies indicate they may have different physical characteristics. But the definition of resting habitat is more ambiguous, and I suggest it may be more conveniently included in the foraging category if the fish is simply resting on the bottom (Cunjak and Power 1986) or in the refuge category if it is sheltering (Fausch and White 1981). Besides, this detailed classification is probably more pertinent in micro-habitat studies. The generally very restricted movements by trout in streams (Jenkins 1969, Bachman 1984, Heggenes 1988 a), indicate that brown trout select habitats providing both foraging and refuge sites within a small stream area (Bachman 1984). Therefore, in habitat studies focusing on stream areas, as opposed to snout-point positions occupied by trout, a subdivision into foraging or refuge habitats is probably of little use.

Water depth

Several field studies of brown trout have indicated total water depth to be an important physical characteristic determining habitat suitability, especially in smaller streams and for larger fish. Shuck (1945) electrofished a small stream for 4 consecutive years, and found only the volume and depth of water to be significantly correlated with number of larger trout (>21.4 cm) in the different stream sections. Lindroth (1955) observed brown trout fry and parr in the shallow areas (20–30 cm depth) along the river banks in the river Indalsälven. From studying physical parameters of microhabitats occupied by brown trout in an experimental flume, Baldes and Vincent (1969) concluded that brown trout with average length 21.3 cm avoided shallow areas (<5 cm). Karlström (1977) studied habitat selection by brown trout and Atlantic salmon parr by electrofishing sections of 12 relatively large Swedish rivers and 1 Icelandic river for several consecutive years. He observed trout parr more often in shallower water closer to the river bank than salmon parr. The different age-groups of both species were also distributed in gradients from the river banks with the smallest fish in the shallowest areas closest to the river banks. However, Karlström (1977) considered water velocity and bottom substrate more important habitat characteristics than depth. In another small Swedish stream, Bohlin (1977) studied habitat utilization by juvenile anadromous brown trout, also by electrofishing. Depth was emphasized as the more important physical factor in this study, partially in conjunction with particle size of the substrate. A correlation between fish length and depth of habitat used was also reported; the larger fish occupied the deeper stream areas. Egglishaw and Shackley (1982) electrofished a small Scottish stream to investigate the relation between densities of sympatric brown trout and Atlantic salmon populations, and the water depth. They found a positive correlation between densities of 0+ and 1+ brown trout and the variations in area of water deeper than 10 cm. For 1+ this positive correlation became progressively stronger when areas were restricted to those with depths greater than 15, 20 and 25 cm. Similar results were reported for sympatric populations of brown trout and Atlantic salmon in two small Northern Ireland streams (Kennedy and Strange 1982, 1986). Fry of both species were significantly more abundant in shallow water (<20 cm), while older trout (2+ and older) were captured mainly in the deeper areas (>20 cm). Yearling fish were found in highest numbers in the mid-range depths, but occupied all the depth-ranges sampled. Electrofishing was the observation method in this study. In sympatric populations of juvenile brown trout and Atlantic salmon studied by electrofishing on the river Scorff, France, brown trout again had a similar habitat distribution (Bagliniere and Champigneulle 1982). Young-of-the year trout were distributed mainly in shallow rapids with low mean depth (10–40 cm), while older trout (>1+) colonized all types of habitat provided it gave a certain "security", i.e. depth and cover. In the small Danish stream Kvindeback, Hermansen and Krog (1984) found by electrofishing that the densities of brown trout larger than 15 cm to be significantly correlated with mean stream depth. Allopatric, small brown trout (64 and 94 mm in mean total lengths) preferred depths in the 10–20 cm range in a small Norwegian stream, while larger trout (138 and 160 mm in mean total lengths) were more often found in the deepest pools (30–40 cm) (Heggenes 1988b). In another stream, adult brown trout (170 mm and 247 mm in mean total lengths) showed increasingly strong preferences for deeper stream areas (up to 115 cm depth), and the largest trout occupied the deepest areas (Heggenes 1988a). In these two studies a modified method of systematic "point" electrofishing was adopted. Based on diving studies in a river, Heggenes and Saltveit (1989) reported brown trout parr to select depths preferrably in the range 30–60 cm, in sympatry with Atlantic salmon. Shirvell and Dungey (1983) used surface observation for studying microhabitats chosen by large, adult brown trout (mean fork length 42 cm) for feeding and spawning in six diverse rivers in New Zealand. The trout chose positions with optimum combinations of depth and velocity. For feeding preferred mean depth at the position occupied by the fish was 65 cm, but for spawning they preferred a mean depth of 31.7 cm. Contrary to these findings, Gatz et al. (1987) found depth of water only to be important in separating Age 0 and Age >0 brown trout.

All the cited studies have focused on summer habitat use. Cunjak and Power (1986) observed winter habitat utilization by brown trout and brook trout at different sites in an Ontario river by diving. The habitat distribution with regard to fish size was consistent with summer observations; older trout (<1+ mean total length 20.3 and 21.9 cm) generally occupied positions in deeper (and faster) water (mean 53.4±3.2 cm and 75.6±5.96 respectively) than age 0+ (mean total length 11.1 and 11.6 cm) trout (mean depth 46.2±3.34 and 43.1±2.97 respectively). However, no consistent trends between seasons for fish snout water depths utilized was observed. Compared to other studies, 0+ brown trout occupied unusually deep habitats in this river. It is likely, however, that diving may have produced biased results in this study, as most of the fish presumably were hiding in the substrate (Heggenes and Saltveit 1989).

Water velocity

From an energy cost-minimizing point of view, brown trout in running waters would be expected to occupy microhabitats providing low snout water velocities (Fausch 1984). This has been confirmed through field studies. Shirvell and Dungey (1983) reported snout water velocity to be the most important and consistent factor determining positions occupied by large brown trout. The fish preferred lower snout water velocities for feeding, 27±11 cms^{-1}, than for spawning, 39±11 cms^{-1}. Similarly Bachman (1984) studying foraging behaviour of brown trout (total lengths 15–30 cm) in a stream by surface observation (Pennsylvania, USA), stated that "the most distinctive characteristic of positions occupied was the low snout water velocity". However, the velocity reported in that study, about 8 cms^{-1}, was considerably lower than reported by Shirvell and Dungey (1983). Some of this discrepany may be explained by the different fish sizes studied. Heggenes and Saltveit (1989) reported brown trout parr to rarely occupy positions with snout water velocities >20 cms^{-1}, and demonstrated both a seasonal and spatial variation in selected snout water velocities. In winter, lower snout water velocities of mean 4.7 and 2.2 cms^{-1} were found for 0+ brown trout (mean total lengths 11.1 and 11.6 cm), and also at one site for larger brown trout (mean snout water velocity 5.7 cms^{-1}, mean total fish length 20.3 cm) by Cunjak and Power (1986). They also observed considerable differences between snout water velocities selected at two different river sites by larger brown trout (mean snout water velocity 5.7± 1.24 cms^{-1} for 20.3 cm fish at one site, compared to 16.0±1.70 cms^{-1} for 21.9 cm fish at another). Consequently, although there can be little doubt that brown trout select low-velocity microhabitats which presumably minimize energy expenditure, there is some variation as to what velocites are preferred. This may be due to different measurement devices, techniques and accuracies, but it may also be that there is a preferred range of low snout water velocites (Heggenes and Saltveit 1989).

Water velocity may also be a limiting factor in some types of habitat, especially for young salmonid fry, which are susceptible to downstream displacement at comparatively low water velocities (>15 cms^{-1}) (Ottaway and Forrest 1983, Heggenes and Traaen 1988a). Thus fry would be unable to occupy habitats which combine smooth bottom, e.g. sand or bedrock, with even fairly low water velocities.

From a management point of view, a more general description of water velocities in preferred brown trout habitats might be more useful than quantifying micro snout water velocities. The importance of water velocities in defining suitable brown trout habitat has been emphasized by a number of authors. The smallest brown trout (0+) are usually found to occupy the shallow riffle areas with moderate mean water velocities (20–50 cms^{-1}). In larger rivers young brown trout are often observed close to the river banks or in inverts where the water velocities are relatively low and the number of older trout few (Shuck 1945, Lindroth 1955, Bohlin 1977, Karlström 1977, Bagliniere and Champigneulle 1982, Heggenes and Saltveit 1989). There is apparently a tendency for the development of competitive segregation between 0+ and 1+ brown trout, the latter being dominant and expelling the 0+ fry to the shallow riffles. With increasing size the brown trout tend to move to deeper stream areas (Shuck 1945, Bohlin 1977, Karlström 1977, Bagliniere and Champigneulle 1982, Egglishaw and Shackley 1982, Kennedy and Strange 1982, 1986, Cunjak and Power 1986, Gatz et al. 1987, Heggenes 1988b). However, the observations with regard to the effect of water velocity in this respect differs between studies. According to Baldes and Vincent (1969), adult brown trout (average length 21.3 cm) in an experimental flume occupied resting habitats within a mean velocity range (measured 12.7 cm above the bottom) of 12.2–21.3 cms^{-1}, and consistently avoided areas of turbulence, low or high water velocities. Karlström (1977) reported that older brown trout parr select river areas with higher water velocities. Larger trout (mean total lengths 20.3 and 21.9 cm) in an Ontario river generally occupied positions in both faster and deeper water than smaller brown trout (mean total lengths 11.1 and 11.6 cm) (Cunjak and Power 1986). In contrast, several authors have reported that brown trout use more slow-deep or pool-like stream areas with increasing size (Shuck 1945, Bohlin 1977, Egglishaw and Shackley 1982, Gatz et al. 1987, Heggenes 1988a, b). I suggest that this discrepancy may, at least in part, be due to the different sizes of the streams studied. In larger rivers, e.g. those studied by Karlström (1977), the number of pools may be comparatively few. While the shallow, slow-flowing areas close to the river banks are ulilized by the 0+ brown trout, the only deeper areas available to the larger trout will be further out into the river. Although deeper, these areas will also usually have higher mean or surface water velocities. On the other hand, the deeper areas available in small streams, e.g. those studied by Bohlin (1977), Egglishaw and Shackley (1982) and Heggenes (1988a, b), are usually found in pools, which presumably also are slow-flowing. If this hypothesis is correct, depth would appear to have importance over water velocity in assessing habitat suitability for brown trout, except for the snout micro water-velocities experienced by the fish. In that case the size of the streambed substrate would be important.

At low water temperatures in late fall and winter, brown trout apparently seek out habitats characterized by slower water compared to preferred summer habitat (Karlström 1977, Cunjak and Power 1986), and seek shelter in the substrate (Heggenes and Saltveit 1989).

Hermansen and Krogh (1984) found the coefficient of variation in current velocity 7 cm above the bottom to be best correlated with density of brown trout >15 cm. They suggested that this coefficient of variation might be regarded as a composite measure of stream complexity, i.e. the structure of pools, riffles and macrophytes. However, no correlation between mean current velocity 7 cm above the bottom and trout density was found.

Stream bottom substrate

In general brown trout apparently avoid stream areas with fine bottom substrate, i.e. silt, sand, fine gravel, and prefer the coarser substrate, i.e. cobble and coarser, depending on fish size (Lindroth 1955, Bohlin 1977, Karlström 1977, Heggenes 1988a, b, Heggenes and Saltveit 1989). Similarly, in experimental stream-channel studies, brown trout fry preferred the coarse cobble substrate (50–70 mm) to the finer pebble and gravel substrate (<30 mm) (Heggenes 1988c). Bachman (1984) reported submerged rocks to be important characteristics for foraging and refuge sites occupied by brown trout in a stream. Observations by Cunjak and Power (1986) suggest that large stones providing shelter also are an important habitat factor for brown trout at low water temperatures during winter.

The main physical habitat function of streambed substrate is apparently to provide shelter, both from high water velocities and as cover from predators. Due to the low water velocity niches created in the interstitial spaces between the particles and the turbulence close to the bottom, coarse substrate is advantageous from an energyminimizing point of view. Consistent with this, it has been reported that stream-dwelling brown trout spend most of their time at or close to the streambed rather than in midwater or close to the water surface (Baldes and Vincent 1969, Jenkins 1969, Shirvell and Dungey 1983, Heggenes and Saltveit 1989). They specifically select foraging sites where the water flows over and around large embedded rocks, providing micro-niches with low water velocites (Bachman 1984). Especially for small trout fry, low velocity niches provided by the streambed substrate may be critical, as they have limited swimming ability and are susceptible to downstream displacement (Ottaway and Forrest 1983, Heggenes and Traaen 1988 a). The importance of bottom substrate as cover for brown trout has also been emphasized in several studies (Bachman 1984, Cunjak and Power 1986, Heggenes 1988a). To provide cover, the more important characteristic of suitable substrate is apparently that it has adequate interstices which fish can get into (Bachman 1984). This may be particularly important at low water temperatures (Heggenes and Saltveit 1989), and for brown trout fry (Heggenes 1988c). Alexander and Hansen (1983) reported a 40 % increase in young brown and rainbow trout numbers when the sandy bedload sediment throughout a stream area was reduced by 86 %.

Another less obvious function of the streambed substrate, is that it may provide visual isolation. Kalleberg (1958) observed that fry of brown trout held pronounced bottom territories, and the size of the territory depended on the degree of visual isolation within the biotope. Increased visual isolation, i.e. more horizontal cover, as would be provided by coarser substrate, resulted in less aggressive behaviour, smaller average sizes of territories, and presumably higher fry densities.

Cover

In spite of the difficulties encountered when trying to define and quantify cover, this habitat characteristic has attracted attention in numerous studies of brown trout habitat. Some kind of cover, including brush, overhanging vegetation, undercut banks, "broken" surfaces, physical instream structures, shade and miscellaneous (Lewis 1969, Fausch and White 1981, Harshbarger and Bhattacharyya 1981, Bovee 1982, Cunjak and Power 1986, Gatz et al. 1987), are considered by most authors as important especially for brown trout.

In a field study, Boussu (1954) observed a marked increase in trout biomass in sections of a small stream which was supplied with artificial brush cover. Conversely, a decrease was found in sections where natural brush was removed. However, brown trout only made up 2 % of the total biomass in the stream. Hunt (1977) observed a six-fold increase in the abundance of brown trout (>25.4 cm) after adding half-logs to a stream with very little cover. In another small stream where brown trout were the more abundant trout species, Lewis (1969) reported overhead cover to be the single most important habitat factor for brown trout distribution in a stream. Baldes and Vincent (1969) found cover and light to influence brown trout (21.3 cm) microhabitat selection in an experimental flume. Increased mortality rates for brown trout fry in reaches where cover was removed, have been reported from small Danish streams (Mortensen 1977). While 0+ brown trout may occupy shallow riffles, Bagliniere and Champigneulle (1982) suggested that older and larger trout (>1+) would colonize all types of aquatic environment, provided it gave a certain "security", i.e. enough depth and/or cover. In a small stream where trout cover was scarce and a critical resource, brook and brown trout competed for preferred resting positions beneath submerged cover, with brown trout as the dominant competitor occupying the preferred positions under cover (Fausch and White 1981). Amount of overhangig banks and degree of macrophyte cover correlated significantly with densities of brown trout >15 cm in a small Danish lowland stream (Hermansen and Krog 1984). Similar results were reported for five small streams in North-Carolina, USA (Harshbarger and Bhattacharyya 1981). Of the 18 cover variables measured, four key factors only, explained relations between variables in the observed set; area in debris, turbulent water, vegetation (both in and over stream) and overhanging banks. Cunjak and Power (1986) reported brown trout to have a strong preference for positions in association with cover, and even more so at low water temperatures, as was also reported by Hartman (1963). In a comprehensive study of streams dominated by brown trout in Wyoming, USA, Wesche et al. (1987a, b) found the amount of cover together with flow regime, to be the most important habitat variables. But in this study cover was defined in a wider sense than in most other studies, as it included instream rubble and boulder and deep-water (>45 cm) habitat in addition to overhead bank cover. Gatz et al. (1987) reported that cover, defined as overhead vegetation and shade, was the second most important habitat variable for brown trout in five small streams. In two Norwegian streams brown trout (>130 mm) showed a clear preference for habitats providing a high degree of overhead cover (Heggenes 1988a, b).

In contrast, Bachman (1984) reported the "surprising" result that foraging brown trout used overhead cover only to a relatively little degree during daytime. However, time spent under cover must not be confounded with its importance. Brown trout is a particularly wary trout species, and as Bachman (1984) notes, some kind of cover is characteristic of brown trout refuge habitats. This may be essential, even though the actual time spent in the refuge habitat is limited. Contrary to expectation, a poor response of "catchable-size" brown trout to overhead cover enhancement was found in a Pennsylvania, USA, stream (Hartzler 1983). This was however attributed to the presence of abundant natural cover. Other environmental factors apparently determined the density of trout.

Strong preferences for overhead cover by brown trout have also been observed in experimental studies (Butler and Hawthorne 1968, DeVore and White 1978, Heggenes and Traaen 1988b), but care must be taken when interpreting these results. The artificial environment experienced by the brown trout in experimental studies may tend to overemphasize the importance of cover.

Ranking of habitat variables

Different studies rank the importance of the habitat variables differently. It is apparently difficult to agree upon which, if any, of the habitat characteristics are the more important. One obvious reason for this, is that a number of authors have investigated only one or a few of the physical characteristics influencing habitat use by brown trout (Table 1). It might also be asked whether it is reasonable to try to find "the most important" variable from field studies. It seems more sensible to expect that changes in habitat suitability will be accompanied by changes in a host of variables.

An additional problem is that most studies have focused on measuring characteristics of habitats actually occupied by brown trout, without quantifying total available habitat. This may bias the results and invalidate any more general conclusions (Fausch and White 1981, Hartzler 1983). Furthermore, it may in many cases be as important to find out what types of habitats are not occupied or directly avoided by brown trout. I suspect that some of the differences in the assessment of the physical variables between studies may be explained by the simple fact that streams are different (Moyle and Balz 1985), as was suggested by the spatial variation in use of several habitat variables reported by Heggenes and Saltveit (1989) for one river. Different habitat factors may be limiting in different streams. Fausch and White (1981) observed that brown and brook trout competed for resting positions beneath cover, but not for feeding positions. They ascribed this to the fact that submerged cover providing resting positions were a scarce and critical resource, while feeding positions were abundant. Conversely, Hartzler (1983) reported a poor response of brown trout to cover enhancement in a small creek, and attributed this to the presence of abundant natural cover. In a similar way, suitable substrate may be found rather uniformly within a study stream, and consequently no preferences for streambed substrate would be found (Heggenes and Saltveit 1989). On the other hand, a range of water velocities will be present in almost any stream inhabited by brown trout, and water velocity preferences will be easily detected (Shirvell and Dungey 1983, Cunjak and Power 1986, Heggenes and Saltveit 1989). Based on observed variability in habitat selection, Heggenes and Saltveit (1989) hypothesized that the genetic basis allows a certain range to the behavioural response. It is also likely that different stocks of brown trout are adapted to the local habitat conditions found in a stream. Consequently, different stocks may select somewhat different habitats or not have the strongest preferences for the same habitat characteristics. Borgstrøm and Heggenes (1988) suggested that smoltification of sea-trout at short length in a small stream, was an adaption to adverse habitat conditions, i.e. extremely low summer flows.

Few studies of trout habitat preferences exist. Shirvell and Dungey (1983) quantified habitat available in one of six streams studied, by locating 54 transects randomly along an 11 km study area, i.e. on the average one transect each 200 metres. Depth and mean water column velocity were measured every metre across the transect. This sampling intensity seems somewhat low to quantify available habitat sufficiently. A considerably more detailed habitat mapping was implemented by Hermansen and Krog (1984), but they only related total number of brown trout within each study section (approximately 100 m long) to the physical characteristics measured. Gatz et al. (1987) quantified available habitat by using transects spaced 5 m apart and measuring at 1 m intervals across the transects, or alternatively using a 1-m grid sampling. A somewhat different approach was adopted by Heggenes (1988a, b) who systematically mapped two streams in detail, and related all brown trout observations to the smaller habitat "cells" within the streams, described by the mapping. Thus available habitat and habitat actually occupied by trout were measured with equal accuracy. Heggenes and Saltveit (1989) used a stratified transect spacing methodology for habitat description, and only observed fish across the transects, which were mapped in detail.

The best way to obtain data for available habitat and habitat preference seems to be a two step procedure. The first step is to map the study section(s) systematically and in detail, and using transects as references may be the more efficient method. The next step would be to observe fish by a combination of diving and electrofishing techniques, systematically screening the study section(s) along the same reference transects (Heggenes et al. 1989).

At least two more factors may affect the rating of habitat variables. Differences in habitat use within a species between streams may not only reflect availability, but also physical factors with other spatio-temporal dimensions such as waterflow and temperature regime, and biological factors such as food supply and presence of other species (Moyle and Balz 1985, Bowlby and Roff 1986, Wesche et al. 1987a, Heggenes and Saltveit 1989). Furthermore, population data must also be taken into consideration. Habitat use may vary with population density (Moyle and Balz 1985). The relation between abundance and distribution of brown trout is poorly known (Heggenes 1988a), and more research is needed.

There have been some attempts on rating different habitat variables in a more precise, statistical way. By collecting an array of different habitat measurements from numerous streams and relating these to estimates of total standing crop by using multiple regression procedures, a so-called Habitat Quality Index was developed (Binns and Eiserman 1979). From 22 attributes characterizing fluvial habitat for trout in Wyoming (including brown, rainbow, cutthroat and brook trout) a model, rating nine habitat attributes as significantly important (late summer stream flow, annual stream flow variation, water velocity, trout cover, stream width, eroding stream banks, stream substrate, nitrate nitrogen concentration and maximum summer stream temperature), explained 96 % of the variation in trout standing crop. But the results from attempts to apply this model in other streams or areas have been less impressive. The same index only poorly predicted trout biomass in Ontario stream sites (Bowlby and Roff 1986). A Habitat Suitability Index-model developed by the US Fish and Wildlife Service (Raleigh et al. 1986) rating 18 variables as important for describing brown trout habitat, was not significantly correlated with brown trout standing stock in Wyoming streams (Wesche et al. 1987a). A simpler model including flow regime and a composite single-valued function of overhead cover, substrate and depth gave the best results. However, ranking habitat variables by their ability to predict biomass may be a dubious procedure. The underlying assumption would be that fish biomass is largely habitatlimited and that fish populations are always at carrying capacity. This may not be the case in many instances (Platts and Nelson 1988). Gatz et al. (1987) used principal component analysis to identify the more important habitat variables, and found water velocity and its correlates substrate and surface turbulence, to be most important. Two measures of cover (distance to overhead vegetation and shade) were of secondary importance, while water depth was of quite minor importance. Using the same statistical technique, Heggenes and Saltveit (1989) also reported water velocity to be most important, with depth second and substrate third. However, none of the variables explained more than one-third of the observed variation. This may type of approach may be useful, but the procedure treats each variable as independent.

Most authors reporting on studies of habitat selection by brown trout in streams, have treated each habitat variable separately. The problem of interaction between habitat variables, i.e. where two or more factors combine to produce an added effect which is not due to one of them separately, has not been addressed except in a few cases in a quantitative way (Karlström 1977, Shirvell and Dungey 1983). If interactions exist neither one habitat factor can individually show the "best" predictor to optimize the habitat (Mathur et al. 1985).

The first model of trout habitat quality (Habitat Quality Index) published by Binns and Eiserman in 1979, tried to establish a more objective basis for trout habitat evaluation. Their approach (multiple regression analysis) was basically to build a correlation model with additive effects of independent variables. However, various combinations of the attributes with correlations coefficients of <0.30 were also tried in this case. Essentially similar statistical procedures with the basic assumption of additive effects of independent variables, have also been adopted in later attempts to build models of trout habitat quality (Bowlby and Roff 1986, Wesche et al. 1987a). The Habitat Suitability Index (HSI, Raleigh et al. 1984) developed to be used in the Instream Flow Incremental Methodology (IFIM; Bovee 1982), explicitly states the assumption that fish select each habitat variable independently of the other variable(s) (Bovee 1982, Orth and Maughan 1982, Raleigh et al. 1984). The validity of this basic assumption has rarely been tested, and never for brown trout. For some warmwater fishes violation of this assumption has been demonstrated (Orth and Maughan 1982, Mathur et al. 1985). Morantz et al. (1987) found no significant interactions among nose velocity, depth and substrate for Atlantic salmon fry and parr, but this may be due to the selected study areas. They did not derive true preference curves by quantifying total available habitat. DeGraaf and Bain (1986) demonstrated a lack of independence between the effects of velocity and substrate on fish distribution for juvenile Atlantic salmon. Use and preference for nose velocity differed significantly between different habitats. For yearling brown trout in a stream aquarium Hartman (1963) observed an increase in degree of association with experimental structures, with increase in water velocity.

Based on a study of an assemblage of California stream fishes, Moyle and Balz (1985) suggested that the suitability of a physical habitat could not in general be assessed from data of depth, velocity and substrate alone. Suitability curves should use selectivity curves developed on site, as several other factors could influence habitat selection (e.g. habitat availability, population density, competitive interactions). Thus they suggested that depth, velocity and substrate could not be considered as independent, additive variables. Mathur et al. (1985) proposed that the violation of the assumption of independence may be more universal than might have been previously believed. Obviously, if interactions have to be considered, interpretation of biological data and statistical treatment will be more complicated.

Several tentative conclusions can be drawn if this proposition is correct. Firstly, it might explain some of the different ranking of different physical habitat variables in different streams. The corollary is that it might also explain the poor performance of the different models of trout habitat quality arrived at in the literature. Secondly, habitat suitability curves may not easily be transferred from one stream to another. It may be necessary to develop suitability curves on site or in nearby, comparable sites (Moyle and Balz 1985). Thirdly, it is even more important to also consider total available habitat and not habitat use data alone (Moyle and Balz 1985, DeGraaf and Bain 1986, Gatz et al. 1987, Heggenes 1988a, Heggenes and Saltveit 1989).

Another aspect of field habitat studies which contributes to the same problem, is the correlation between physical habitat variables in running waters (Mathur et al. 1985, Gatz et al. 1987, Morantz et al. 1987). Depth and velocity are correlated (Fraser 1972, Hermansen and Krog 1984), velocity may be correlated with degree of macrophyte cover (Hermansen and Krog 1984) and substrate particle size is related to water velocity (Gatz et al. 1987, Morantz et al. 1987). Consequently, it is per se also difficult to observe in the field whether the selection of one habitat variable by fish is independent of the other variable(s). Careful selection of contrasting habitat types for study in different streams is likely to be necessary, as is more experimental work on contrasting the different habitat variables (Wilzbach 1985).

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Estimating the Number of Species and Relative Abundance of Fish in Oligotrophic Swedish Lakes using Multi-Mesh Gillnets

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Abstract

Data from 133 test-fished oligotrophic, acidified and limed Swedish lakes have been used to estimate the number of gillnets needed to catch all catchable fish species and to estimate the relative abundance of dominating species. The test-fishing was depth stratified using benthic and pelagic, multi-mesh, gillnets.

1. The number of randomly set benthic gillnets required to catch all catchable fish species increased with lake area, e.g. 5 randomly set benthic gillnets were needed to catch all fish species in lakes with an area of 100 ha.
2. The CPUE (catch per unit effort) was transformed using LOG_{10} (CPUE + 1) to dissociate the variances and the means.
3. The number of nets required to attain a certain precision in the estimate of the CPUE for dominating fish species was calculated. The number of nets required increased with lake area for perch but not for other dominating species.
4. Depth stratified sampling considerably increased the precision of the whole-lake CPUE of dominating species.

Introduction

In 1983 a monitoring program was initiated to study the long-term effects of freshwater liming on fish populations in Sweden. The program's main objectives were to assess the population changes on a whole-lake basis, give estimates of the number of species present, sample length frequencies and also to estimate the relative abundance and growth of the dominating species.

Since gillnets are passive gear there are some drawbacks involved in their use. Temperature (Neuman 1974, 1979), and spawning (Neuman 1979, Nyberg and Degerman 1988), affect fish activity, while light and turbidity (Berst 1961) determine whether fish will see and avoid the nets. Net-selectivity determine what sizes, and sometimes even what species of fish that can be caught (e.g. Hamley 1975, Rudstam et al. 1984, Jensen 1986, Wulff 1986, van Densen 1987, Boy and Crivelli 1988). The length of the nets (Davis and Schupp 1987) and set time (Minns and Hurley 1988), also affect their catching ability. Nevertheless, the method is versatile and suitable for sampling lakes of different sizes and depths (Hamley 1980, Hubert 1983).

The accuracy of multi-mesh gillnet sampling has been reported in only a limited number of studies (Moyle and Lound 1960, Bagenal 1972, 1979, Craig and Fletcher 1982, Craig et al. 1986). When comparing different fish sampling gear (gillnets, trammel-nets, seines, trawls and fyke-nets) Bagenal (1979) found that gillnets had the lowest variance between individual samples and Jensen (1976) found that gillnets gave a correct estimation of the proportion of tagged fish in a perch population. The main point, however, is to make sure that the catch probability does not vary from population to population (or from time to time). As suggested by Hubert (1983) this can be avoided by standardizing the sampling with regard to the type and numbers of gillnets used, test-fishing season and technique, and fishing strategy. Using this approach, comparable estimates for analyses of trends in population dynamics (Carlander 1953, Le Cren 1987), as well as comparisons between different lakes and lake types can be obtained (Nyberg et al. 1986 a, Appelberg et al. 1989).

The present paper focusses on the sampling strategy for estimating the number of fish species present and the catch per unit effort for any given lake, i.e. number of gillnets, stratified sampling and basic statistical processing of the data. The aim is to facilitate planning of whole lake investigations of fish populations so that a fishery manager without previous studies can decide on the sampling strategy and estimate the effort needed. Reports describing the lakes studied, fish assemblages and the effects of acidification and liming is presented elsewhere (Nyberg et al. 1986 a, Nyberg 1988, Appelberg et al. 1989).

Material and methods

The studied lakes are oligotrophic, acidified lakes in the southern and middle parts of Sweden (Table 1). The majority have been limed at least once (Appelberg et al. 1989). Each year 30–40 lakes are test-fished and the lakes are revisited every third to fourth year. Up until 1988 133 unique lakes have been test-fished and 84 lakes have been test-fished twice, comprising 217 sampling occasions.

On average 5 fish species were caught per lake and the two dominating species constituted more than half the catch in numbers in all lakes sampled between 1983 and 1988. On 83 % of the sampling occasions the two dominating species made up for more than 70 % of the CPUE (catch per unit effort). Principal component analysis has shown the lakes to have four major fish assemblages; lakes dominated by littoral/benthic species such as perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), by pelagic species such as cisco (*Coregonus albula*), whitefish (*Coregonus* spp.) and smelt (*Osmerus eperlanus*), by Arctic char (*Salvelinus alpinus*) and by brown trout (*Salmo trutta*) (Appelberg et al. 1989). In this study the dominating species are regarded to be those constituting more than 30 % of the catch in CPUE in numbers.

The sampling was performed using multi-mesh monofilament nylon gillnets consisting of 14, randomly distributed, panels of various mesh sizes. The different mesh sizes used were 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60 and 75 mm and the twine diameter 0.12–0.25 mm (see Hammar and Filipsson (1985) for a detailed description of the gillnets and the relations between mesh size and catch). Each panel was 3 m long and when used as a benthic gillnet 1.5 m high, thus the total gillnet length was 42 m and the area 63 m^2.

The pelagic survey gillnets were also 42 m long but had a depth of 6 m and a total area of 252 m^2. They were horizontally divided in two by a coloured marking at the middle allowing the catch to be separated between the upper and lower 3 m of the gillnet. The catch in each benthic gillnet was considered as a single sample

Table 1. Median values and range of physical and chemical variables of the 133 lakes. Also given is the number of caught fish species.

Variable	Median value	Minimum value	Maximum value
Lake area (ha)	144	4	14,307
Altitude (m)	192	46	582
Maximum depth (m)	20	2	106
pH (mean)	6.4	5.0	7.2
Conductivity (mS/m)	4.8	2.2	10.8
Water colour (mean, mg Pt/l)	34	4	215
Number of fish species	5	1	12

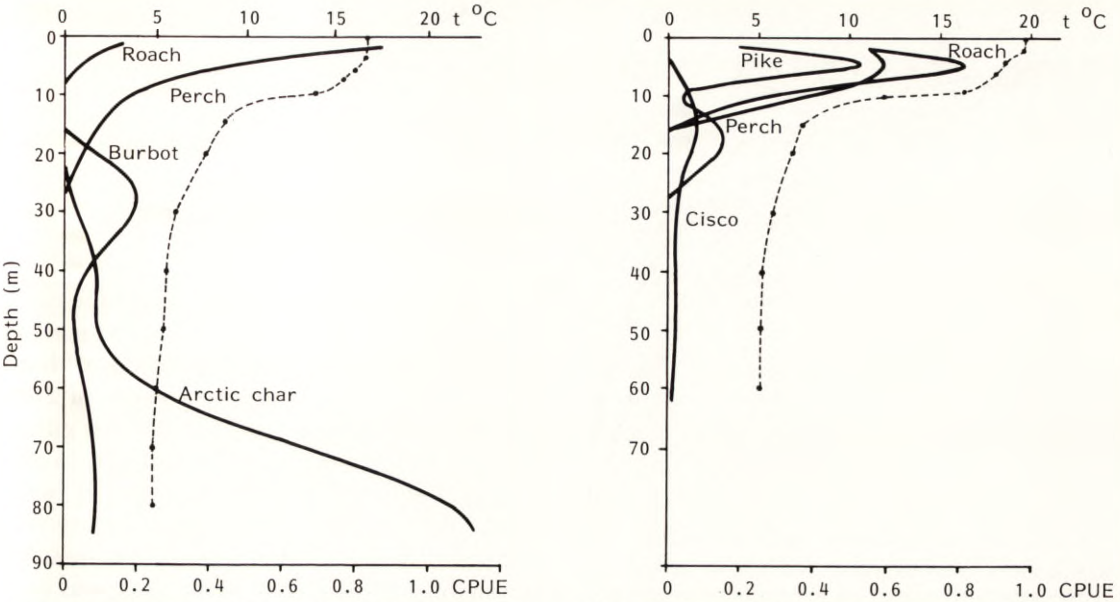

Figure 1. Catch per unit effort (CPUE) as kg/benthic gillnet and night of dominating fish species (smooth lines) along with temperature curve (°C) (dotted line) versus depth (m) in the lakes Unden and Östra Nedsjön test-fished 1983. (Data from Nyberg et al. 1986 a.)

and one gillnet fished one night (06.00 p.m. to 08.00 a.m.) was defined as one effort. Each gillnet was set randomly with regard to horizontal location in the lake and angle to the shore line.

The catch from each gillnet was identified to species, and each species was counted and weighed separately. Each fish was measured (total length) to the nearest mm. A subsample of the catch was taken for analysis of sex and individual weights.

In order to estimate the number of benthic gillnets required to catch all fish species present in the lakes sampled, the catches in the gillnets from each lake were afterwards chosen at random with regard to location and depth in the lake. The number of gillnets required to catch all catchable fish species was then defined as the lowest number of randomly chosen nets after which no additional species were caught (cf. Fig. 3).

The fishing was carried out during July–August each year when most of the investigated lakes were thermally stratified. The species distribution within the lakes depended on the water temperature, preferred habitats and species interactions, resulting in large differences in CPUE between different depth layers (Nyberg et al. 1986 a, Fig. 1). Warm water species such as roach were caught mainly above the thermocline whereas cold water species such as Arctic char were caught below the thermocline even when this species lived solitary in the lake.

To improve the precision of the CPUE, i.e to minimize the variance, the lakes were vertically stratified into fixed depth zones (0–2.9, 3–5.9, 6–11.9, 12–19.9, 20–34.5, 35–49.9, 50–74.5 and 75– m) and a CPUE was estimated for each stratum. The stratification of the upper depth zones were shallower since they represent a larger part of the total lake volume. For instance, in a lake with a maximum depth of 20 m, the depth zone of the uppermost 6 m constitute about 50–85 % of the total lake water volume (Fig. 2). For most lakes the chosen depth stratification approximately equalizes the volume of sampled water between the depth strata.

After LOG_{10}-transformation of CPUE the number of gillnets required to attain a certain

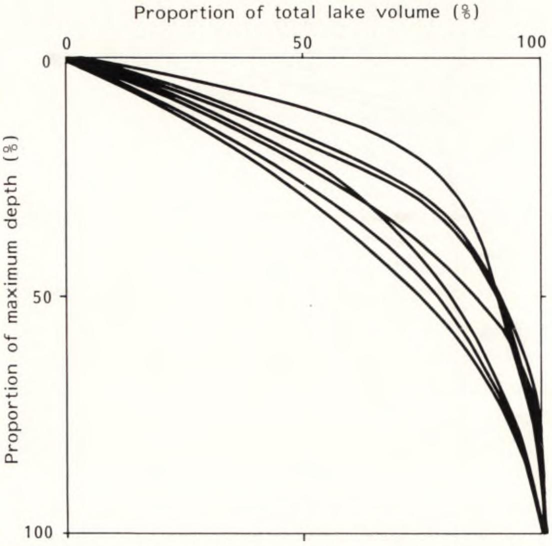

Figure 2. Proportion (%) of lake volume against proportion (%) of lake maximium depth for seven investigated lakes. (Data from Andersson et al. 1987).

precision within each depth zone was determined according to Pringle (1984);

$$\text{No of gillnets} = \frac{(SD)^2}{(CPUE)^2 * (C.V.M.)^2}$$

where SD is the standard deviation, C.V.M. is the Coefficient of Variation for the Mean. In this context C.V.M. is defined as the standard error divided by the mean CPUE. This term should be distinguished from the Coefficient of Variation (C.V) which is the standard deviation divided by the mean. The calculation was done for the depth zone where the respective species was most dominant. If C.V.M. was 0.10 it would mean that differences between two sampling occasions of 50 % in CPUE could be statistically significant at the 95 %-level, whereas a C.V.M. of 0.05 would allow changes of the CPUE of 20 % to be detected (Bohlin 1984), provided the number of samples is not to small.

Assuming that the variances of CPUE were approximately equal after LOG_{10}-transformation, the means and variances of CPUE were weighted with regard to the number of gillnets in each stratum in order to calculate pooled estimates for the entire lakes (Edmondson 1971, Box et al. 1978).

Results

The number of gillnets required to catch all catchable species

Between 1 and 43 gillnets were required to catch all the catchable fish species in the 133 investigated lakes. In Lake Linnebjörkesjön, with an area of 410 ha and a maximum depth of 2 m, four fish species were caught in the first gillnet and one additional species was caught in the eleventh gillnet. No additional species were caught in the reminding 29 gillnets.

In Lake Unden, with an area of 9,540 ha and a maximum depth of 106 m, test-fishing was performed with 72 gillnets. Four species were caught in the first gillnet but not until 40 randomly chosen gillnets were analyzed were all 12

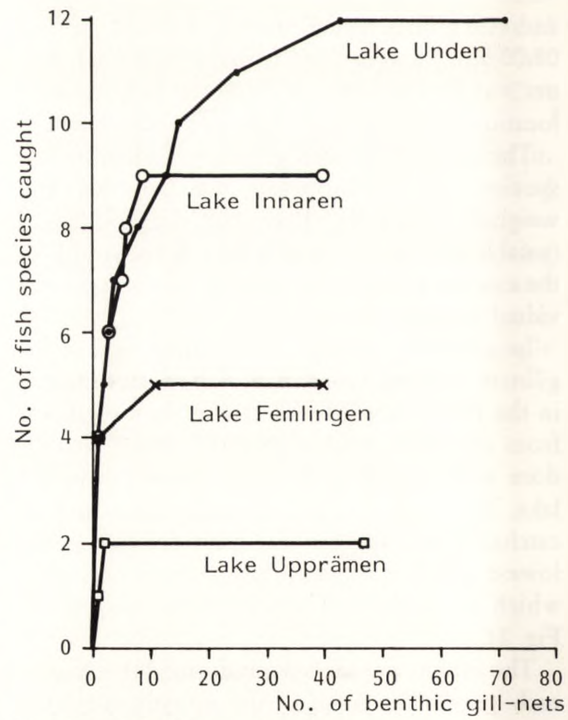

Figure 3. Cumulative number of fish species caught versus the number of benthic gillnets used for four test-fished lakes.

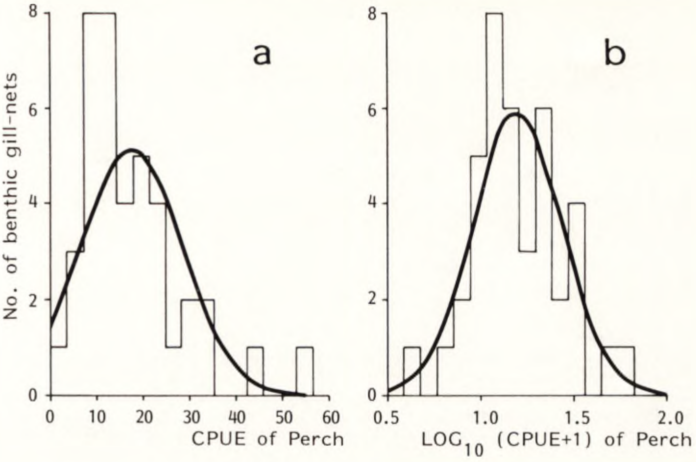

Figure 4. CPUE (numbers/gillnet and night) of perch in lake Linnebjörkesjön 1983 before (a) and after (b) transformation of the catch per benthic gillnet with LOG_{10} (CPUE+1). Normal probability curve shown for comparison.

species present in the lake caught (Fig. 3). The number of gillnets used to sample all species in the 133 unique lakes was significantly correlated with the lake area (LOG_{10} of the number of gillnets = 0.387 * LOG_{10} of lake area (ha) – 0.047, $r^2 = 0.40$, $p < 0.001$). Thus, on average 2.2 gillnets were required to sample all fish species in lakes of 10 ha, 5.3 in lakes of 100 ha, 13.0 gillnets in lakes of 1,000 ha and 31.7 gill-nets in lakes of 10,000 ha.

Although the gill-nets used do catch eels (*Anguilla anguilla*) in low numbers, only two specimens were caught for 217 sampling occasions (approx. 13,000 unit efforts). This should be compared to the known occurrence of the species in 40 % of the investigated lakes.

Normalization of the CPUE

When transforming the CPUE and estimating the number of gillnets required to achieve a certain sampling precision only the one or two most dominating species in each of the four fish assemblages were included (see above).

As the catch per unit effort (CPUE) was not normally distributed within each depth zone, the CPUE of the dominating species was transformed using LOG_{10} (CPUE + 1). This transformation resulted in a distribution of CPUE close to normal in most of the investigated lakes. However, the samples were usually too few to perform a proper testing of the distribution of the CPUE within each lake. Chi-square good-

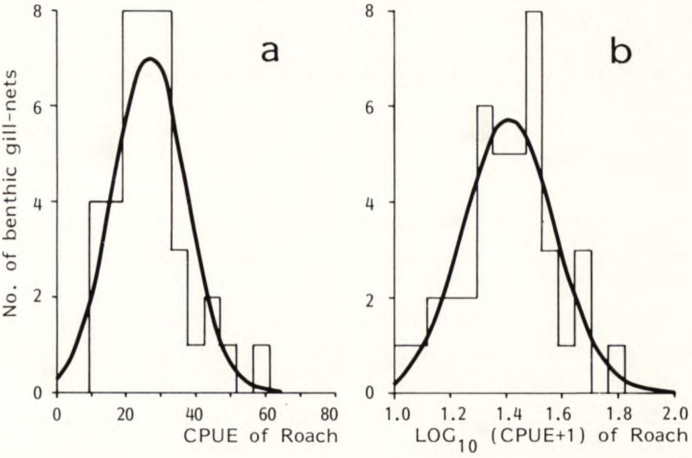

Figure 5. CPUE (numbers/gillnet and night) of roach in Lake Linnebjörkesjön 1983 before (a) and after (b) transformation of the catch per benthic gillnet with LOG_{10} (CPUE+1). Normal probability curve shown for comparison.

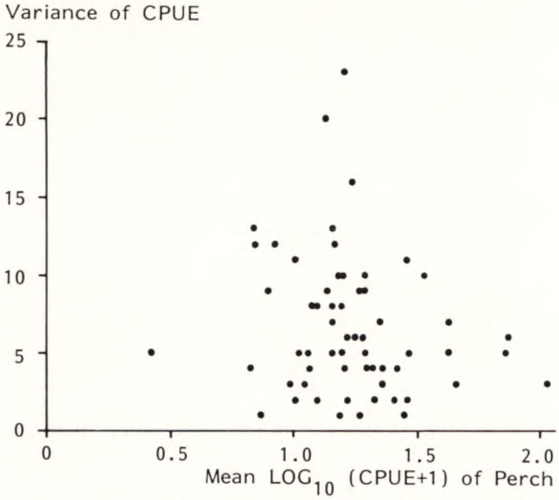

Figure 6. Variance of the mean CPUE (numbers/gillnet and night) of perch caught in depth zone 0–3 m with benthic gillnets in each lake versus the mean CPUE for perch in the same depth zone in the lake. (Catch in individual gillnets transformed using LOG_{10} (CPUE + 1).)

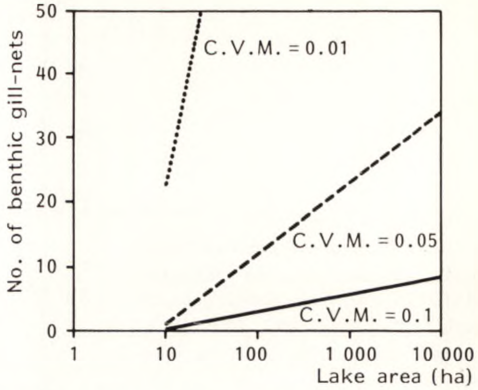

Figure 7. Estimated median numbers of benthic gillnets required to achieve a precision of C.V.M., i.e. the standard error divided by the mean, of 0.01, 0.05 and 0.10 for the CPUE (numbers) of perch in the depth zone 0–3 m in the investigated lakes.

ness-of-fit showed that the transformed CPUE did not deviate significantly from a normal distribution in the few cases that permitted testing. For Lake Linnebjörkesjön the CPUE of perch significantly differed from a normal distribution before transformation ($x^2=9.6$, d.f. $=3$, $p=0.022$), whereas it did not differ significantly after transformation ($x^2=3.7$, d.f. $=3$, $p=0.294$) (Fig. 4).

For roach from the same lake untransformed CPUE was not significantly different from a normal distribution ($x^2=3.7$, d.f. $=4$, $p=0.454$) but after transformation a closer fit was achieved as revealed by a lower x^2-value ($x^2=0.87$, d.f. $=3$, $p=0.833$, Fig. 5). After the transformation of CPUE the variance was not found to be dependent on the mean (CPUE) for the dominating species (e.g. for perch, Fig. 6).

Precision of the CPUE

A total of 96 lakes with areas from 4–14,307 ha were included in the calculations for perch. The number of gillnets required to achieve a certain precision were significantly correlated to the LOG_{10} of the lake areas (e.g. perch in depth strata 0–3 m, linear regression, $r=0.36$, $p<0.004$, $n=96$). However, the unexplained variation was large (87 %). The number of gillnets required to estimate the CPUE of perch in the depth zone 0–3 m with a C.V.M. of 0.1, i.e. a standard error of 10 % of the mean, was 2 to 3 gillnets in lakes with areas of 100 ha. In lakes ten times larger, at least 7 gillnets were required to achieve the same precision (Fig. 7).

For roach, no significant correlation was obtained between lake area and the number of gillnets required to attain a certain precision for roach, in 62 lakes with areas 4–3,270 ha where the species dominated. The median value of gillnets required to achieve a C.V.M. of 0.01 in the sampled lakes was 459 and 4.6 gillnets were required for a C.V.M. of 0.10 (Table 2).

As was the case for roach, there was no significant correlation between the number of benthic gillnets required to achieve a certain precision of the CPUE and lake area for brown trout, Arctic char or the three dominant pelagic fishes taken together either. In the 8 brown trout lakes sampled, with lake areas ranging between 4 and 260 ha, 9 was the median number of gillnets required to achieve a sample precision of C.V.M. 0.1 (Table 2). For Arctic char, 10 lakes with areas of 15 to 343 ha were investigated and 6 gillnets were required for a C.V.M. of 0.10.

Table 2. The number of gillnets required to achieve a precision in the estimate of the CPUE where the C.V.M., i.e. the standard error divided by the mean, equals 0.01, 0.05 and 0.10 for roach, brown trout, Arctic char and pelagic fishes. For the last group the listed value referres to pelagic gillnets, whereas benthic gillnets are referred to for the other species.

Species/group	Type of net	Coeff. of Variation for the Mean		
		0.01	0.05	0.10
Roach	Benthic	459	18	5
Brown trout	Benthic	866	34	9
Arctic char	Benthic	554	22	6
Pelagic fishes	Pelagic	1,555	62	16

For a comparable precision in the CPUE of pelagic fishes, 20 lakes with areas ranging from 53 to 3,270 ha, the number of pelagic gillnets needed were considerably higher than for the other groups of fish (Table 2). One pelagic gillnet consists of two sampling units (see Material and methods), but even so the number of gillnets required was high.

Random versus stratified sampling

For convenience only single depth strata have been dealt with above. However, the precision of the CPUE for a species in the entire lake was increased when the mean and variances of the CPUE for the dominating fish species within each strata were pooled for each lake. Pooling the CPUE of different depth zones resulted in smaller confidence intervals compared to those obtained by estimating CPUE from unstratified sampling with an equal number of gillnets (e.g. perch and whitefish from Lake Mien, Fig. 8). N.B. that the confidence intervals are asymetric due to the transformation and following anti-log of the data.

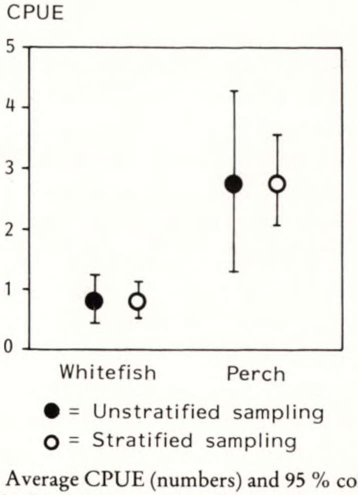

Figure 8. Average CPUE (numbers) and 95 % confidence intervals of whitefish in pelagic gillnets and perch in benthic gillnets in lake Mien 1984 when test-fishing was performed unstratified and stratified with regard to depth. (Data initially transformed using LOG_{10} (CPUE+1), then antilogged).

The C.V., Coefficient of Variation, for the whole lake CPUE with stratified sampling for the transformed data in the example above was 0.55 for perch and 0.85 for whitefish. For the depth zone 0–3 m the C.V. for perch was 0.43. For all perch lakes (n=96) the C.V. in depth zone 0–3 m was 0.07 to 0.53, with a median value of 0.19.

Discussion

The transformation of the CPUE using LOG_{10} (CPUE+1) was found suitable as it dissociated the means and the variances, i.e. the variances did not depend on the means, which has previously been found for gillnets data (Bagenal 1972, Craig et al. 1986). A negative binomial model could also have been used for the transformation (Moyle and Lound 1960), but the logarithmic transformation was regarded to be sufficient and easier to use (c.f. Bagenal 1972).

The results of the present study indicate that more gillnets were required to catch all catchable fish species in larger lakes due to higher habitat heterogeneity. However, not all fish species in our lakes could be caught. From interviews with local fishermen and information from fishery managers it was obvious that eels were seldom caught with the gillnets used.

Since the number of benthic gillnets required for a certain precision of the CPUE of perch increased with increasing lake area, this is possibly an effect of high habitat heterogeneity in large lakes. This trend was clearly demonstrated for perch where the number of lakes was high and the area interval was 4–14,307 ha, whereas the number of lakes with brown trout and Arctic char as dominating species was low and the range of the lake areas was smaller. Any existing correlation between lake area and variance was therefore harder to detect. For roach no correlation between lake area and the number of nets required was obtained although a high number of lakes with areas ranging between 4 and 3,270 ha were included in the analysis. The difference between roach and perch may be an effect of the ability of large specimens of perch to become piscivorous, an effect that increases with lake area (Nyberg et al. 1986b), and a tendency to hunt the schooling pelagic fishes. As a result of an increased tendency towards schooling the estimate of dominating pelagic species using pelagic gillnets required a considerably greater number of efforts than for the other dominating species.

Increasing habitat heterogeneity in larger lakes calls not only for a depth stratified sampling but also for horizontal stratification into different subareas of the lake. However, an adequate, horizontal stratification cannot be performed without detailed information about each specific lake.

The CPUE is considered to be directly proportional to the actual abundance of a species and a constant called the "catchability" (Hamley 1980). Although the catchability constant varies between species and season, sampling gear etc., standardized gillnetting would give an estimate of the relative abundance for each species which is comparable between lakes and years. The assumption that the CPUE obtained by gillnets is proportional to the size of the fish population has, however, been questioned (Richards and Schnute 1986, Rudstam et al. 1988) and has to be tested for each species. The effects of mesh-size selectivity is another drawback in the use of gillnets which has been widely studied (Hamley 1975). However, despite these disadvantages gillnet data can be used to assess differences between fish assemblages and changes in fish assemblages over time (Carlander 1953, Le Cren et al. 1977, Rosseland et al. 1981, Filipsson 1983, Le Cren 1987, Appelberg et al. 1989).

Davis and Schupp (1987) and Minns and Hurley (1988) showed that gillnet length effected the CPUE for some species. The cause could be saturation, i.e. that the gillnets can only catch and hold a certain amount of fish. Hamley (1980) reports that this saturation effect begins when a gillnet with a mesh-size of 19 mm has caught 0.12 kg fish/m^2 and for a mesh-size of 70 mm when 0.34 kg/m^2 is caught. With regard to the gillnets used in the present study this would mean that the saturation effect would start to appear when about 13 kg and 52 kg of fish had been caught in the benthic gillnet and the pelagic gillnet respectively. Since the average catch from 1983 to 1987 was 0.9 kg per benthic gillnet (Appelberg et al. 1989) and 0.7 kg per pelagic gillnet, the saturation effects should be negligeable in low productive lakes. However, Hammar and Filipsson (1985) have reported extreme catches of up to 19 kg for a single gillnet fished for 24 hours in an oligotrophic and unexploited Canadian Arctic char lake indicating the possible need for shorter set time in specific lakes. Enderlein and Wickström (1989) test-fishing tropical reservoirs in Sri Lanka found the catch per net and night with identical gillnets to be so high that they recommended shorter set times than an entire night.

Neuman (1974) showed that the dependence of the CPUE on temperature for perch is lowest during the summer. In 31 of our lakes test-fished during July–August of 1983 and again 1986 a high correlation was achieved for the CPUE of dominating species; perch (r = 0.84) and roach (r = 0.92). The difference in CPUE between 1983 and 1986 could not be explained by the temperature during test-fishing in the lakes (Nyberg and Degerman 1988).

The size of the gillnet used is seldom discussed, whereas the size of the gear is often considered in invertebrate sampling (Edmondson 1971, Elliott 1971, Pringle 1984). The average catch in our gillnets was 20 individuals and the number of species 1–3. This has been considered a reasonable size of catch to allow statistical processing, since few zero catches occur for dominating species. A catch of this size is also easily handled in the field. In general, the probability of taking rare fish species will be at least as great with the present size of the gillnets as with the same net-area using smaller gillnets (Edmondson 1971).

The C.V. in the example (Fig. 8) was 0.55 for the benthic perch and 0.85 for the pelagic whitefish. Craig et al. (1986) showed that data from the literature (Bagenal 1972, 1979, Craig and Fletcher 1982) and their own data, all together 14 estimates, gave an average C.V. for gillnet studies of 0.765. This value could also be compared to results for perch in depth zone 0–3 m in our lakes where the C.V. ranged between 0.07 and 0.53. Hence the variance in CPUE in our material was comparatively small for all but the pelagic species.

In conclusion gillnets are easy to use and although a high degree of standardization and a large number of sampling units are required to estimate the CPUE for the whole lake it is a versatile method for obtaining comparable estimates of fish population dynamics. With an accepted C.V.M. of 0.10 approximately 5 gillnets would have to be used per depth zone in an 100 ha lake dominated by perch and roach. With a maximum depth of 12 m the lake would be divided into 3 depth zones (see above) and a total of 15 benthic gillnets should be used. Fifteen unit efforts should also be sufficient to catch all fish species in the lake. Such an investigation, including handling of the catch in the field, could easily be carried out by two persons in two days.

Acknowledgments

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Pleistocene Age of the Spring-Spawning Cisco, *Coregonus trybomi*

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Key words: *Coregonus trybomi*, *albula*, *fera*. Younger Dryas glacier readvance. Regressive speciation. Genetic relicts.

Abstract

Spring-spawning ciscoes, *Coregonus trybomi*, live, or lived, in four Swedish and two Finnish lakes. Sympatric to all six populations is *C. albula*, the autumn-spawning cisco. In the Swedish lakes, the large sparsely-rakered whitefish *C. fera* is sympatric as well. In Sweden *C. trybomi* is restricted to three river systems, one draining to the Baltic and two to the Kattegat.

The transition from Pleistocene to Holocene in Fennoscandia is marked by the drainage of a huge glacial lake, the Baltic Ice Lake. Recent Quaternary geology research has revealed that the drainage of the lake took place in two steps, separated by glacier readvances in Younger Dryas (11,000–10,000 years BP). The readvancing glacier filled the Vättern basin, which had then been populated by fauna elements from the Baltic Ice Lake, including the three *Coregonus* species. The drainage of the Baltic Ice Lake, and the Öxnehaga glacier of southern Vättern, probably brought the *Coregonus* stocks to their present localities in south Sweden, 11,200–10,400 BP.

Morphological as well as electrophoretic studies of enzyme loci suggest a slight gene flow between the sympatric cisco species. In spite of that, neither the ciscoes nor the whitefish – in ten thousand years of isolation – have lost their main specific characters, i.e. the different spawning periods and the low number of gillrakers. These facts strengthen the hypothesis of regressive speciation of *Coregonus* in postglacial times (Svärdson 1979). This further implies a postglacial invasion of genetically distinct stocks, evolved in glacial or preglacial isolation, and subsequent introgression during the postglacial period, the outcome of which depends on the lake topography and number of invading stocks. To lump all stocks into two formal species, instead of recognizing two cisco and six whitefish species, merely serves to destimulate the study of this particular type of incomplete species evolution.

Introduction

Filip Trybom, the prominent Swedish fisheries biologist, was taken by surprise when he, on April 11, 1903, got three almost ripe cisco from Lake St. Hålsjön, southwest Sweden. He learnt that local fishermen caught large numbers of spawners in late April and May. The spawning depth was 15–20 metres (Trybom 1903).

Later the same year, Trybom got another sample of ordinary autumn-spawning cisco from the lake. Trybom was very puzzled by the sympatric forms. He referred to some marine fish, known to spawn at different seasons, but he knew of no freshwater case. He discussed the tendency in some fish for younger individuals to spawn somewhat earlier, and was familiar with the fact that deep-living subpopulations may spawn later (Trybom, op. cit.)

Trybom was reluctant to call the two cisco populations different races. Specific rank in his view was out of the question, since their morphology was inseparable.

Ekman (1909) reported on two sympatric cisco populations, one of them May-spawning, from Lake Ören, close to Lake Vättern. He did not penetrate the situation further in any of his later writings.

Runnström (1941) actually found some small morphological differences between the two cisco populations of Lake St. Hålsjön, as far as the number of vertebrae and fin rays was concerned. He was also informed by Elis Skoglund, the fisheries officer of the district, that spring-spawning cisco also lived in Lake Åsunden, Ätran river.

Svärdson (1949) pointed out that the sympatric cisco populations were two biological species and that the spring-spawners could not have evolved in their present small lakes. Runnström and Svärdson (1956) summarized the evidence available and asked for more local search. It was then reported, and confirmed, that spring-spawning cisco also lived in Lake Fegen, Ätran river (Svärdson 1960).

The spring spawners of Lake St. Hålsjön were transplanted to Lake Oklången, Viskan river, in the 1930s by Skoglund and the Ören stock to Lake St. Jougdan, Faxälven river, in 1956, by Svärdson. Unfortunately, none of the transplanted fry were later recaptured.

The spring spawners in their home lakes have recently been reduced by industrial pollution, by agricultural as well as communal eutrophication and also by acid rain. Their actual status is poorly known. Some populations may have vanished.

Airaksinen (1968) described spring-spawning cisco from two lakes in that small part of southeast Finland which was free from ice when the Baltic Ice Lake drained. He also recorded winter-spawning stocks (February). So far it is not proven that these winter spawners are anything else than subpopulations spawning deeper and therefore later. Fabricius (1950) described spawning activities, related to local cooling, of one whitefish stock, in Lake Vojmsjön, from the last days of September to the midst of January. This well-known phenomenon should be kept separate from real spring spawning in late April or May. The regulating photoperiod must be different in the latter case.

Svärdson (1979) formally described the four Swedish populations of spring-spawning cisco as belonging to a new species, *Coregonus trybomi.* All six populations known are geographically associated with the Baltic Ice Lake. The detailed Swedish distribution is rather enigmatic. Three rivers are involved, two of which run to the Kattegat, where the salinity is ten times higher than that which cisco are known to tolerate. Cisco are also regarded as poor climbers of rivers.

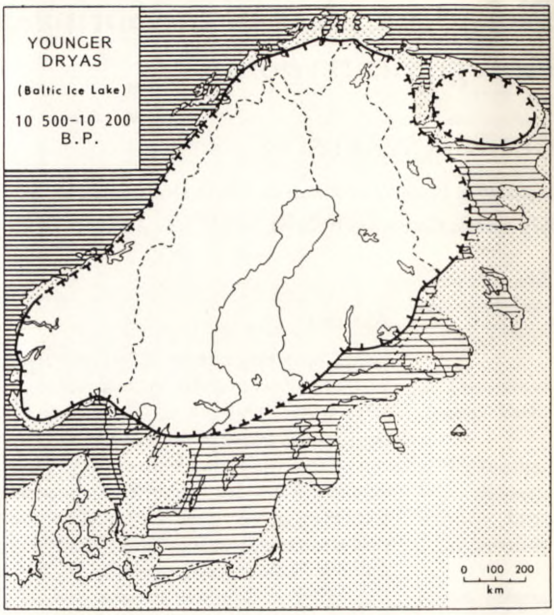

Fig. 1. The Baltic Ice Lake (BIL) before drainage. Modified from Hyvärinen (1975).

Recent progress in Quaternary geology has now spread some new light on how some fish colonization of the Småland highlands might have occurred.

The Younger Dryas glacier readvance

The Pleistocene epoch ended, and the Holocene began, when the Scandinavian inland ice sheet withdrew from mount Billingen, 250–275 masl. (Fig. 1). The Baltic Ice Lake was then drained, westwards, and lowered, by some 25 metres. The western sea, filling part of the Vänern basin at the time, was now in contact with the Baltic and this stage is called the Yoldia Sea. This stage of the Baltic persisted for some 1,000 years, or less. However, brackish water could only enter the Baltic during a 100 years long period at about 10,000 B.P. (Björck pers.comm.).

There is still a gap between the classical varve dating (De Geer 1940) and the modern ^{14}C dates. Strömberg (1985 a) suggests the ^{14}C dates under-

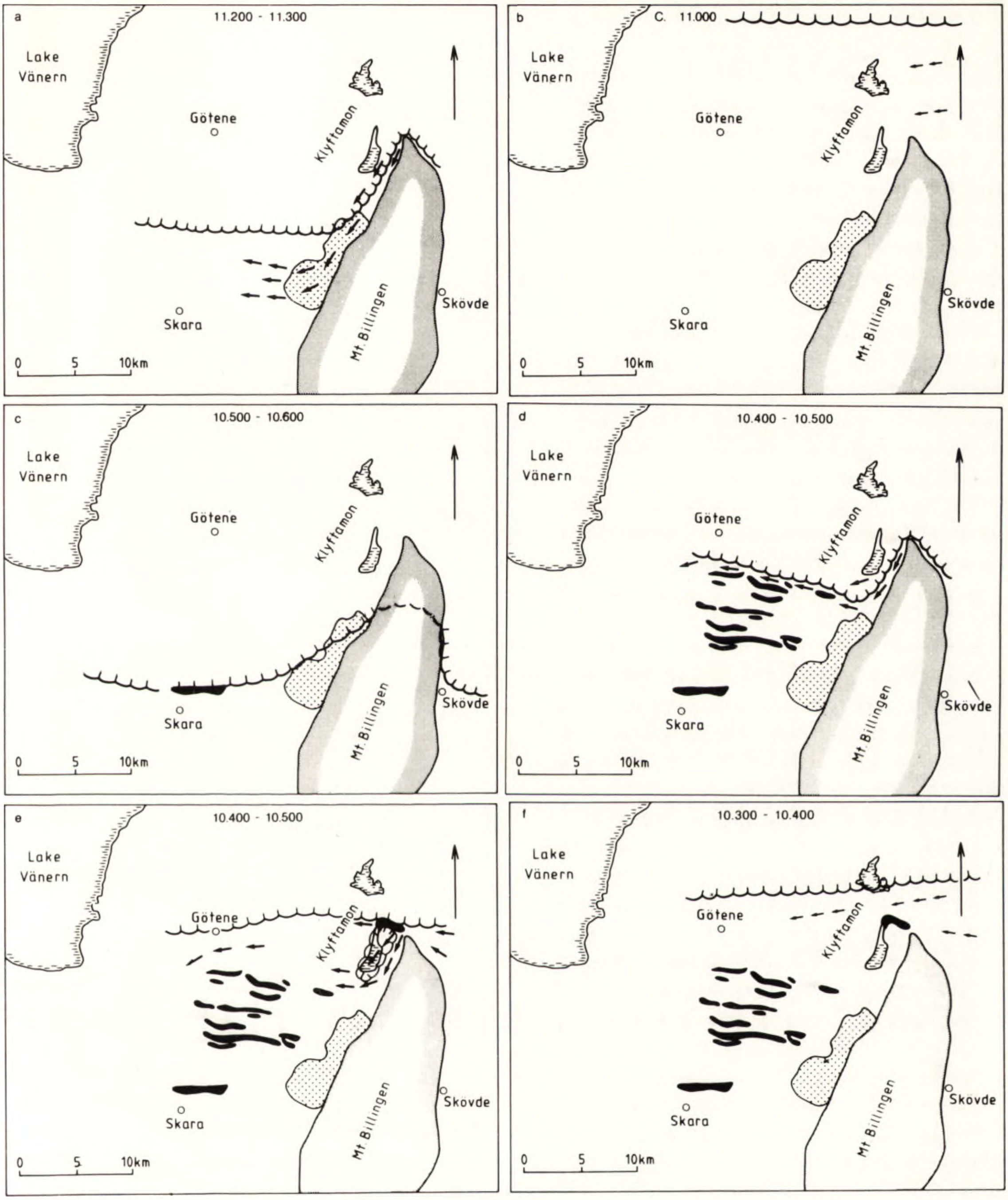

Fig. 2. The two drainages of the Baltic Ice Lake. From Björck and Digerfeldt (1986).

estimate the real age by some 200–400 years for the Younger Dryas chronozone. Björck et al. (1987) found that the difference between the time scales increases between 11,000 and 10,300 B.P. from 400 years to some 500–600 years. Björck et al. (1988) summarized the results obtained in eastern and western Sweden by different methods (varves do not occur in the sea). The relatively small time difference between authors, and methods, is of little consequence to zoologists.

Much more important is the recent discovery, that the Baltic Ice Lake (BIL) was actually drained twice, at c. 11,200 and 10,400 B.P., respectively. The first drainage was by some ten metres (Björck 1979, Björck and Möller 1987, Björck and Digerfeldt 1986) (Fig. 2.). The ice-sheet readvanced at 11,000 B.P., again damming up the BIL. According to the lithostratigraphy in the Middle Swedish end-moraine zone there were several glacier oscillations during the first part of the Younger Dryas chronozone.

The oscillations were small in the Skövde area west of Lake Vättern and east of Mt. Billingen (Strömberg 1985b) and at Ödeshög–Mjölby–Linköping east of the lake (Johansson 1979, Svantesson 1981). SE of Vättern, in the Lake Sommen area, the evidence of glacier readvance is scanty (Agrell 1974, Kristiansson 1986), but the varves are disturbed and the annual ice recession was very small.

In the Vättern basin, however, the glacier probably surged, possibly because of low friction. The readvances were actually two, called the Rosenlund and the Öxnehaga glaciers (Fig. 3) in the Jönköping area (Waldemarson 1986). The last readvancing glacier split up into three local tongues, into the Landsjön, the Tenhult and the Taberg valleys. Waldemarson correlates the Öxnehaga glacier to the interval between the two drainages at Billingen, i.e. the beginning of the Younger Dryas chronozone. Björck et al. (1988) warn, however, that it is not dated and the time correlation therefore may be spurious.

Waldemarson found glacial deposits, indicating proglacial lakes, at 220–230 masl altitude at the front of the local tongues. He says the lakes probably filled the valleys up to the thresholds or pass points to other water systems. The theoretical prerequisite for a faunal transfer, according to the principle of Högbom (1917) was thus formed, if fauna elements from the BIL had penetrated into Lake Vättern in the interval between the two BIL drainages.

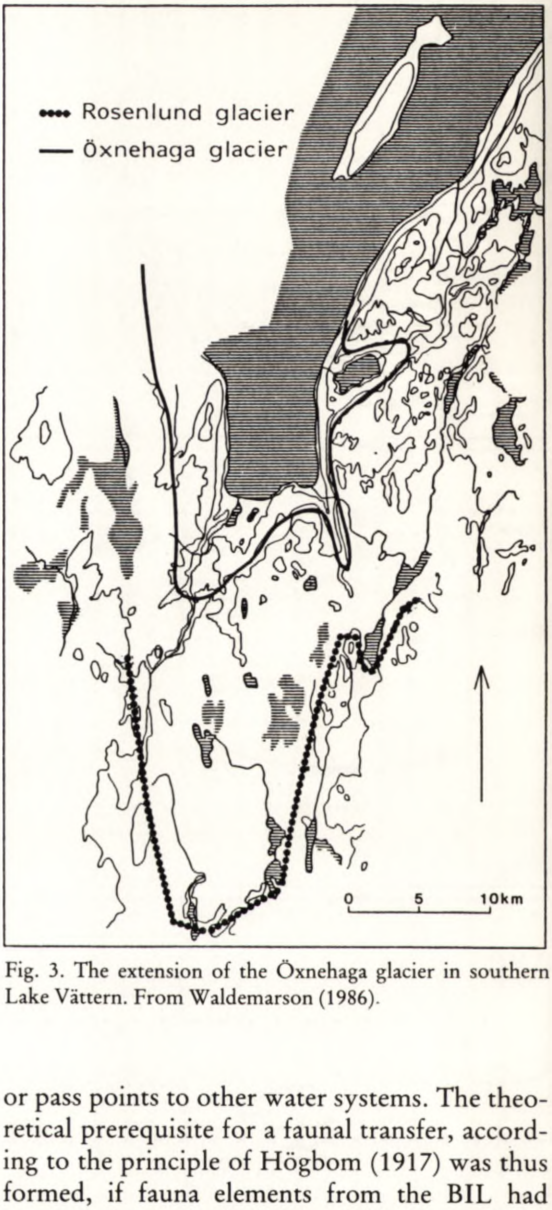

Fig. 3. The extension of the Öxnehaga glacier in southern Lake Vättern. From Waldemarson (1986).

Lake St. Hålsjön, Viskan river

The altitude of Lake St. Hålsjön is 79 masl. It means that the lake was close to the highest sea level in the area (Fig. 4). It has a smelt population. The smelt (*Osmerus eperlanus*) is nowhere in Scandinavia known to have climbed to lakes higher than the MG (marine limit) or HK (highest shore) on the west and east coast. The MG at the mouth of river Viskan was reached about 12,000 B.P., at the local deglaciation, when the smelt must have colonized the lake. Later, at the time of the BIL drainage, the isostatic change had lowered the sea shore to 25–30 masl (Björck pers.comm.).

Beside the two cisco populations there is/was a population of the large sparsely-rakered whitefish, *Coregonus fera*, in the lake (Svärdson 1957, 1979). This species tends to be the whitefish best capable of living sympatrically with the cisco in smaller lakes. It lives in freshwater, and belonged to the BIL fauna. Very probably it colonized the lake at the same time as the ciscoes.

Both drainages at Billingen of the huge BIL brought a mighty flood of fresh water westwards into the Vänern basin, which was then filled by brackish or sea water. The flush should have brought BIL fauna elements into an environment that became more and more hostile, the longer the drift continued into the western sea. It was suggested (Svärdson 1976) that *Coregonus albula* and *C. fera* (and the glacial relict *Pontoporeia affinis*) were then flushed along the land-ice margin, in a layer of fresh water, all the way to southwest Norway.

The common cisco cannot permanently stand a higher salinity than 2–3 per mille (Järvi 1950). The species is also known to be very easily flushed into the outlet by high waters in lakes (Trybom 1899, Järvi 1920, Ekman 1924). Thus, ciscoes were probably among the fauna elements flushed out by the drainage of BIL and, not tolerating the salinity, they should have 'panicked' into any fresh water outlet from rivers or lakes close to the shore.

If the three *Coregonus* species by the drainage were brought along the eastern shore of the Vänern basin, southward to the mouth of river Viskan, they obviously had to climb some 50 metres in altitude to Lake St. Hålsjön. The whitefish, *C. fera*, has climbed the northern Swedish rivers up to headwaters in the mountains, but the common cisco is a poor climber and the spring-spawning cisco, which lives deeper, would even more rarely enter running water.

In northern Sweden, the common cisco was reported from 71 lakes by Svärdson (1966). He found 4 localities above an altitude of 300 metres, three of which were known introductions by man. Most of the lakes were below the HK, and the maximum climb above that limit was 30–40 metres, which is the highest known in Europe, except in the lakes of the Småland province. Large and slow-running rivers should be more easily penetrated by the pelagic, schooling cisco than smaller streams, with rapids or water falls.

Upstream Lake St. Hålsjön in river Viskan, the common cisco is also known from Lake Ärtingen (151 masl). If colonized from the rivers' mouth, the cisco would have had to climb 120 metres in altitude and a long horizontal distance to reach this lake. An alternative scenario, with colonization from Lake Vättern, will be discussed below.

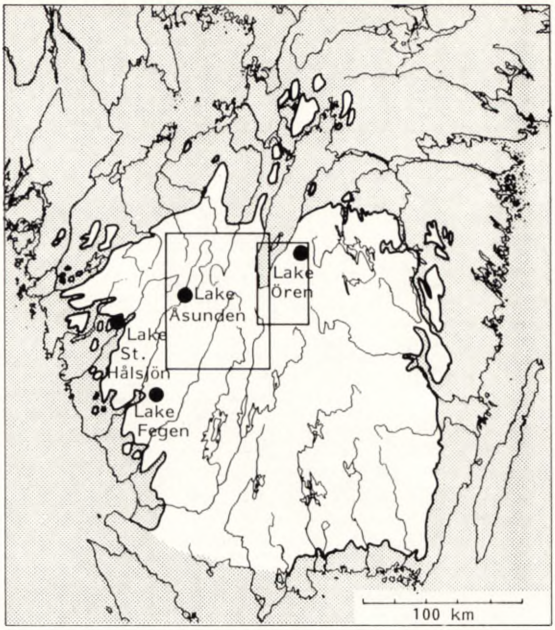

Fig. 4. The four Swedish lakes inhabited by *Coregonus trybomi* are situated in an area never covered by sea or the Baltic.

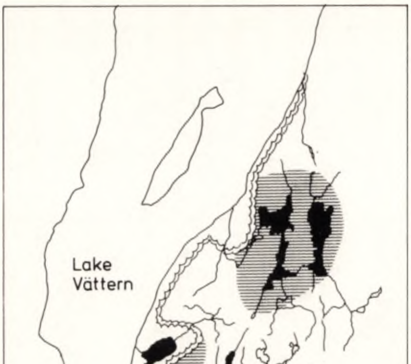

Fig. 5. Three Öxnehaga glacier tongues in southern Lake Vättern and their proglacial lakes, the extension of which is uncertain. Black means lakes inhabited by *Coregonus albula*.

Lake Ören, Motala Ström river

Lakes Ören and Bunn are connected by a short stream. They have the same altitude, 196 masl. The lakes are drained by the Röttleå stream, in a steep valley down to Lake Vättern, at 88 masl (Fig. 5).

The common cisco and the fera whitefish live in both lakes. The spring-spawning cisco and arctic char live only in Ören, which is deeper (39 m). The char (*Salvelinus salvelinus*) is documented from about 1760 (Svärdson and Rundberg 1973) and is therefore considered spontaneous. The smelt, however, which now lives in Lake Ören, was probably introduced in 1902–04 (Trybom 1896, 1897 and files of the Freshwater Institute).

Clearly, the ciscoes as well as the other fish species, must have colonized the lakes via Vättern. The recent more than 100 m altitude difference could hardly have been overcome by pelagic ciscoes, which are not known ever to climb small streams. The narrow Röttleå stream has some rapids and small falls and a length of 6,000 metres.

The Öxnehaga glacier readvance in Lake Vättern, during the Younger Dryas chronozone, provides a mechanism for fish dispersal. Waldemarson (1986) did not deal with the Röttleå valley, only with three more southern valleys, all of which had their own glacier tongues. Very likely also the Röttleå valley was filled by a glacier tongue at the same time. First, the Vättern basin is narrowing there in front of a southerly proceeding glacier. Secondly, the Röttleå valley opens first to the southeast. Both factors could contribute to the development of a glacier tongue.

The water level of southern Lake Vättern should have been some 100 masl when the lake was again isolated from BIL during the ice readvance. The south-proceeding glacier was from now on blocking all the southern inlets of Vättern. With high shores on both sides, the Lake Vättern should have got a progressively higher water level. Its fauna (from BIL) was forced to the south and laterally into the proglacial lakes that developed between the Öxnehaga glacier and the steep shore.

There are shore-lines around Lakes Bunn and Ören at an altitude of some 220 masl. The interpretation of the local shore-lines in this area has been disputed by Quaternary geologists for a long time. But the idea of a late ice-dammed lake, during the Younger Dryas, is new, and has not, so far, been investigated by the geologists. By analogy with the ice-dammed lakes studied by Waldemarson some 20–30 km to the south, an Ören glacial lake, lifted to about 220 masl, seems very reasonable.

This, of course, should have given the two cisco populations, the *fera* whitefish as well as the char, excellent possibilities to colonize the ice-dammed lake, and later, during the final deglaciation, to be left behind in a smaller lake, a progenitor to the present Lakes Bunn and Ören.

According to this scenario, the colonization of Ören by *C. trybomi* should have taken place midway between the two drainages, i.e. some 10,800 B.P.

Lakes Åsunden and Fegen, Ätran river

The two remaining lakes, known to have been colonized by the spring-spawning cisco, belong to the Ätran river system (Fig. 4). Lake Åsunden has an altitude of 164 masl and Lake Fegen 132 masl. Both lakes have documented populations of the fera whitefish, as well as the common cisco, *C. albula*, spawning in late autumn. Both lakes were found to lack crustacean glacial relicts in 1960 (Fürst 1966), but the copepod *Eurytemora lacustris* is reported from Lake Fegen (Ekman 1907).

The marine limit at the mouth of the Ätran river is at about 70 masl. But when the BIL drainages occurred, the land had risen and the sea was at 10–20 masl. (Björck, pers. comm.). That means that both species of cisco would have had to climb some 115 metres to Lake Fegen and some 150 metres to Lake Åsunden. To reach the latter lake, the two ciscoes also should have covered a distance of more than 100 km. This scenario is not very probable, especially as far as the pelagic, deep-living, spring-spawning cisco is concerned.

But there is an alternative (Fig. 6). Waldemarson describes the glacier tongue filling the Taberg valley, damming ice-lakes up to water system divides, at a level of 220–230 metres. If fauna elements were living in the ice-dammed lake, they could have been spilled over the divide at Olsbo (Waldemarson, op. cit.) from a former Lake Dumme Mosse, at 225–230 masl. They would then have spread downstream the Nissan river. A Nissan headwater lake, Mulserydssjön, at 194 masl, is still inhabited by common cisco and (formerly) a whitefish, very likely the fera species to judge from its described size.

Olsbo outlets from the Taberg Ice Lake could also reach the headwater Lake Stråken of the Tidan river (flowing to Lake Vänern). Stråken and some lakes further upstream (Fig. 6) are inhabited by common cisco, at altitudes 239–207 masl.

Between inlets to Lake Brängen, 239 masl, which is inhabited by cisco and belongs to the Tidan river and Lake Lönern, 241 masl, headwater of the Ätran river (nowadays with no cisco) there is only 1,100 metres. Ten thousands years ago, there was probably a connection so outlets from the Taberg Ice Lake could flow into River Ätran as well. Waldemarson (op.cit.) pointed out that the Olsbo outlet ran independently of the present topography, westwards.

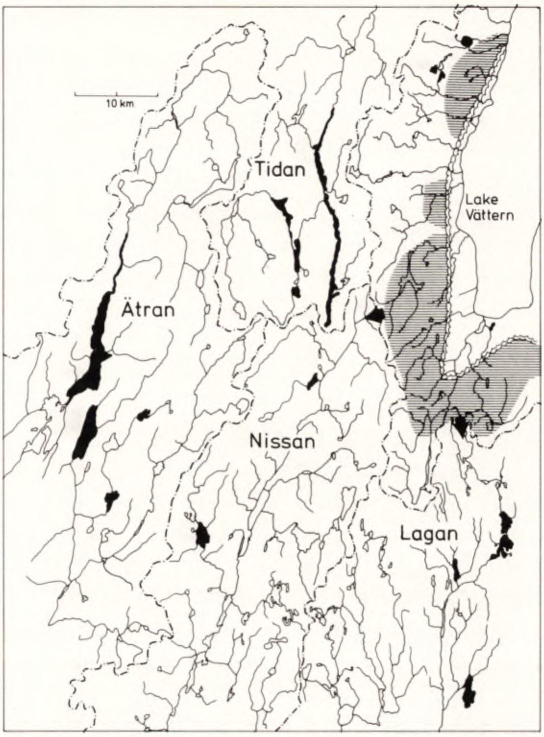

Fig. 6. From proglacial lakes associated with the glacier of the Taberg valley, fauna elements could spread to headwaters of Rivers Tidan, Ätran, Nissan and Lagan. Lakes inhabited by *Coregonus albula* are in black.

Two alternatives emerge to explain the colonization of the Ätran lakes by ciscoes and the fera whitefish. Either, they all climbed the Ätran river from its mouth – then arriving there by freshwater outflow from the BIL drainage – or, alternatively, they were flushed out of the Taberg Ice Lake – ultimately coming from Lake Vättern – into the headwaters of three rivers: Nissan, Tidan and Ätran (Figs. 4 and 6).

By comparison, the second alternative seems to be more conforming to what is known about cisco ecology. According to this scenario, the three species should have spread, principally downstream, from the ice-dammed lakes created laterally by the Younger Dryas glacier within the Taberg valley. This should have happened at the same time as the colonization of Lake Ören took place, i.e. about 10,800 BP.

Ten kilometers north of Lake Åsunden, at Timmele-Dalum, the headwaters of River Viskan are only some few km westwards from River Ätran. It is possible that the Viskan lakes also were populated via the Taberg Ice Lake.

General aspects of the Dryas glacier dispersal

The conventional hypothesis, until now, has been that fish (and some other elements of the limnic fauna) have climbed the rivers in order to arrive to the Småland highland lakes. This means that they could have started from the Lake Vättern basin (to the north), the Baltic coast (east, southeast, south) or the western Kattegat coast (southwest, west, northwest). Lakes of these highlands are situated at 150–280 masl, the highest just south of Lake Vättern.

The new results of Quaternary geology studies (Björck and Digerfeldt 1986, Waldemarson 1986), if true, imply that the distributional facts have to be reconsidered in light of the possibility that some lakes have been colonized via the Vättern basin (ultimately the BIL) while the rivers now run directly to the Baltic or the Kattegat.

The most important zoological support for the influence (and existence) of the Dryas glacier probably comes from Lake Sommen, southeast of Lake Vättern. Lake Sommen is drained by the northrunning River Svartån, a tributary to the Motala Ström river.

Lake Sommen is inhabited by the glacial crustacean relicts *Pontoporeia affinis*, *Pallasea quadrispinosa* and *Limnocalanus macrurus* (Ekman 1940). The smelt in the lake is also a relict. The arctic char, the *fera* whitefish and the common cisco add to the pronounced cold-water fauna of the lake.

The altitude of Lake Sommen is 146 masl. The geologists and zoologists of an older generation agreed that the BIL had covered the lake and thereby explained the existence of the relicts. However, Agrell (1974, 1976), and others, have demonstrated that Lake Sommen was never a bay of the BIL, which reached only about 136 metres in the area. How, then, could the relict crustaceans, and the smelt colonize the lake? Somehow, they must have been lifted at least ten metres, and probably more, above the HK created by the waves of BIL.

Svantesson (1981) described glacial clay, at 145 masl, south of the end-moraine zone at Ödeshög-Sättra, on the eastern shore of Lake Vättern. It was deposited in a glacial lake, dammed between an ice-sheet in the Lake Vättern basin and the highlands of Hålaveden. This lake should have been connected, through the Lillån valley, with the northernmost bay of Lake Sommen. When the northflowing River Svartån was blocked by the glacier at the end-moraine wall, the glacial Lake Sommen should also have had a higher water level. Thus, the Öxnehaga glacier of the Vättern basin, in Younger Dryas, could spill over glacial relicts, and fish, from Lake Vättern to the northern bay of Lake Sommen.

On the western Vättern shore, at the town of Hjo, Lake Mullsjön is also inhabited by the three relicts *Pontoporeia affinis*, *Pallasea quadrispinosa* and *Limnocalanus macrurus* (Ekman 1940). The altitude of the lake, 133 masl, is below that of the local BIL shoreline (138 m) within the Vättern basin. The lake is shallow and has not provided a habitat for the survival of cisco, smelt or arctic char, which probably once lived there.

Further south on the eastern shore of Vättern in the Landsjön valley, a glacier tongue climbed and produced a proglacial lake with a water level of "at least +225 m" (Waldemarson 1986). According to Svantesson (1985), the HK of BIL in this part of Lake Vättern is at 106–110 masl. The recent Lake Landsjön, a remnant of the glacial lake, is at 145.5 masl. It is inhabited by common cisco and the relict *Pallasea*.

The amphipod *Pallasea quadrispinosa* is the most littoral of the benthic glacial relicts (Svärdson et al. 1988) and has been suggested to be able, exceptionally, to spread upstream a river.

Ekman (1940) and Nybelin and Oldevig (1944) reported the only known and recently discovered *Pallasea* populations above the HK in lakes of the Ljungan River. But the evidence of a natural invasion is very slight, because the lakes concerned have been objects of intensive fish culture operations by the Kälarne fisheries research station for a long time. *Pallasea* can be entangled in fish nets or be included in fish transports, i.e. spread by man. The spontaneous occurrence of *Pallasea* in Lake Landsjön thus add credibility to the lifting effects of the Öxnehaga glacier in Lake Vättern.

Is there any evidence of Öxnehaga transfer of glacial relicts to other river systems? Well, Lake Ören, discussed above, may be a case. When the glacial Lake Ören was at its maximum, with an altitude of 220 metres or more, it could have spilled fauna elements to the upper part of the (recent) Svartå river, and via the Eksjö region, to headwaters of the Emå river. Cisco now live at 229 masl in Lake Älmhultasjön (upper Svartå river) and in a cluster of lakes at 219–195 masl in the upper Emån river (above waterfalls). The *fera* whitefish lives in Lake Nömmen (219 masl) and arctic char in Lake Mycklaflon (Trybom 1899, Almer et al. 1976). The copepod *Eurytemora lacustris*, which may be a glacial relict, is recorded from Lake Ören (Freidenfelt 1912), Lake Valen in River Svartån (Trybom 1895) and Lakes Nömmen (Trybom 1899) and Mycklaflon (Almer et al. 1976) of the Emå river. And finally, *Limnocalanus macrurus*, a true relict copepod, was found by Trybom in Lake Nömmen (Trybom 1899). Recent search for the relict in the lake was negative (Fürst pers. comm.).

The best marker of glacial dispersal, however, seems to be the common cisco. On the western shore of Lake Vättern, Norrman (1963) described a local ice-dammed lake within the Hökensås ridge, at an altitude of 225–230 masl. At present, cisco live in Lakes Bredsjön (239.9 masl) and Nordvattnet (238 masl) and probably in Lake Alvasjön, at 229 masl, as well (Sandberg pers. comm.). The occurrence of cisco in these small, highly elevated lakes, close to Lake Vättern, has been enigmatic up till now.

The Tenhult valley opens in the SE of the Vättern basin. It was filled by a glacier tongue and in the upper part a glacial lake deposited silt and clay at levels above +210 m (Svantesson 1985, Waldemarson 1986). Nowadays, the common cisco inhabits the small Lakes Tenhultsjön at 214 masl and Ramsjön, at 221 masl. This is about the level at which the glacier lifting could have brought them. Higher upstream in the valley and still within the Huskvarnaån stream, cisco are missing in the relatively large lakes Ylen and Nätaren (251 masl), Ryssbysjön (263 masl), Hästsjön (272 masl) and others. Higher upstream still, an introduced population of cisco thrive in the small Lake Skärsjön, at 277 masl (Hamrin, pers. comm.). The evidence from the Huskvarnaån stream supports the idea that the cisco is a poor climber, and that most of them inhabit lakes of the area to which they could have come by glacier uplifting or spreading downstream.

Discussion. The specific status of *Coregonus trybomi*

For Trybom (1903) as well as for some later Swedish zoologists, the morphological evidence was decisive. Since the sympatric cisco populations were not possible to separate morphologically, the spring-spawning cisco simply could not be an independant species.

Apart from being theoretically irrelevant (Svärdson 1949), the argument is not true in detail, since slight differences do occur, namely in the form of number of vertebrae, fin rays and striae on the first summer growth zone of the scales. These differences are probably caused by the late spring or early summer hatching of *trybomi* fry. Allopatric populations of autumn-spawning cisco may have gillrakers varying from 39.9 to 47.8 (Svärdson 1957) while the spring-spawners have 42.0 to 44.0 (Svärdson 1979). The number of gillrakers tend to be similar in the sympatric populations of cisco and suggest some slight gene flow between the species.

Recently, evidence from gene-frequency studies have accumulated. Ryman (pers. comm.) could find no significant genetic difference between the two Ören populations. He got the samples in the 1970s and studied only a few loci. Later Vuorinen (1988) found very slight differences between the two Ören stocks in the 32 loci studied. Vuorinen and Lankinen (1978) found some evidence for differentiation at the α-Gpdh-l locus between the two sympatric ciscoes in Lake Kajoonjärvi, Finland. Vuorinen et al. (1981) found the locus α-Gpdh-3^{96} strikingly different between the two spring-spawning stocks of Lakes Kajoonjärvi and Sokojärvi. The two sympatric stocks of Lake Sokojärvi had a short genetic distance (Nei's $D=-0.014$), which was, however, about one order of magnitude greater than usually observed between allopatric stocks (Vuorinen 1985). Finally, Vuorinen (1988) summarized 35 samples of ciscoes (including three spring-spawning stocks) in a dendrogram, where the spring-spawners did not stand out as a separate entity.

The conclusion, drawn by Vuorinen from the enzyme studies is that the spring-spawning cisco are polyphyletic and do not form a species of their own. Essentially, then, the evidence from gene-frequency studies conforms to the morphological studies.

The zoogeographical evidence, as presented in this paper, however, strongly suggests that all known six populations of *trybomi* are relicts from the Baltic Ice Lake. More specifically, the four Swedish populations reached their present lakes during a very short period of time, associated with the two drainages of the BIL or the intermediate readvance of the Younger Dryas glacier, called the Öxnehaga glacier in the southern part of the Lake Vättern basin. This means that all populations of spring-spawners are monophyletic. In spite of local environmental selection and some gene flow from the sympatric *Coregonus albula* during more than 10,000 years, the six populations still display the crucial ecological character: the genuine *trybomi* spawning period almost half-a-year apart from *C. albula*. The fact that the period of spawning is maintained when *Coregonus* stocks are transplanted to new environments has earlier been observed (Svärdson 1951, Svärdson 1979) and supports the view that this character has a genetic basis.

The zoogeographical evidence supports the interpretation given by Svärdson (1949, 1979) that the whitefishes, as well as the ciscoes, consist of a number of different species colonizing Fennoscandia in late glacial or early postglacial time. In sympatry they often develop a gene flow, which may be strong and sometimes swamp two or more species into one hybrid swarm. The ecological characters are the main isolating mechanisms and are therefore under strong natural selection for persistence. The final outcome is dependent on the original ecological difference between the invading stocks, as well as the available niches in larger lakes. When the gene flow is not too strong, the ecological identity of the sympatric stocks remains intact, while more neutral characters (like gillrakers and enzyme alleles) tend to converge. The whole process is a speciation in regress, in contrast to that of *Salmo*, where postglacial diversification of Scandinavian *trutta* and *salar* stocks is a progressive speciation (not yet reaching the level of species).

Admittedly, the term species as conventionally used, does not fit the postglacial sympatric whitefish or cisco populations. But the term subspecies is even more inappropriate, since it should be used for geographical (allopatric) populations of the same species.

The taxonomic term may be ambiguous. More important is the understanding of the phenomenon of regressive speciation, a process which has not been completed during a period of 10,000 years or more. It tends to stress the stability of a *Coregonus* population along the time axis, provided there is not a sympatric population with which it may exchange genes. Within a shorter time span, the process is well illustrated by the genetic change in 50 years of the Lake Kallsjön whitefish, transplanted to Lake Landösjön. The allopatric Kallsjön population is stable, while sympatric native species in Lake Landösjön, by gene flow, modified the transplanted stock (Svärdson 1979, p. 17).

Vuorinen (1988) pointed out that the clearly genetically differentiated stocks of whitefish (and ciscoes) should not be neglected in management practice. For a better understanding of the speciation process, however, the various *Coregonus* species suggested within the *lavaretus* and *albula* groups should be upheld. Thereby a continued study of their origin, age, dispersal and destiny in allo- and sympatry and in various lake basins, could be stimulated. The present genetic differences of sympatric *Coregonus* stocks have not evolved in postglacial times but are genetic relicts of an incomplete speciation during glacial or preglacial periods.

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Depth Distribution, Habitat Segregation and Feeding of the Crayfish *Astacus astacus* in Lake Steinsfjorden, S.E. Norway

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Abstract

Depth distribution, habitat segregation and food choice were examined in the crayfish (*Astacus astacus*) in Lake Steinsfjorden, S.E. Norway, by trapping and SCUBA diving. Temperature was the main determining factor regulating depth distribution, while feeding and oxygen conditions seemed to be of minor importance. A significant difference was found between the size distribution on shallow soft- and hard-bottom substrates, but not between shallow and deep soft-bottom substrates. Food items did not differ between the habitats. The preference by smaller individuals for hard-bottom habitat was probably caused by substrate diversity, and consequently, the degree of shelter offered by the hard-bottom substrate.

Introduction

In Norway, the noble crayfish (*Astacus astacus*) reaches its northern limit of distribution. Most present-day crayfish localities were stocked during the last century (Huitfeldt-Kaas 1918, Lund 1969). In the 1880's, the noble crayfish was introduced to Lake Steinsfjorden, and at present this lake supports a dense population of crayfish. Exploitation has been heavy since the turn of the century (Lund 1944), and during 1979–83, yields ranged from 2.5–4.1 kg/ha, corresponding to an annual removal of 75–90 % of legal-sized crayfish (Qvenild and Skurdal 1986, Skurdal and Qvenild 1988).

Crayfish production is strongly influenced by factors such as temperature, lake productivity, water chemistry and substrate composition (Abrahamsson 1966, 1971, 1983, Abrahamsson and Goldman 1970, Flint and Goldman 1977, Niemi 1977, Momot 1984, Ridderstolpe 1987). Substrate, providing shelter, is essential to the survival of small crayfish subjected to cannibalism and fish predation (Bovbjerg 1970, Goldman 1973, Stein and Magnuson 1976, Goldman and Rundquïst 1977, Dehli 1981). The aim of this paper is to record the depth distribution of crayfish from trap catches in relation to environmental factors in Lake Steinsfjorden. Further, we tested whether substrate composition or depth are main determinants for length and sex distribution, and determined how feeding is influenced by habitat and the overlap in food between various habitats.

Study area

Shallow, mesotrophic Lake Steinsfjorden, S.E. Norway, has a surface area of 13.9 km^2, a maximum depth of 24 m, and a mean depth of 10.2 m (Fig. 1). The lake is situated 63 m.a.s.l., and is connected to the larger Lake Tyrifjorden (121 km^2) through a narrow and shallow sound. The climate is semicontinental, characterized by cold winters and relatively warm summers. The ice-

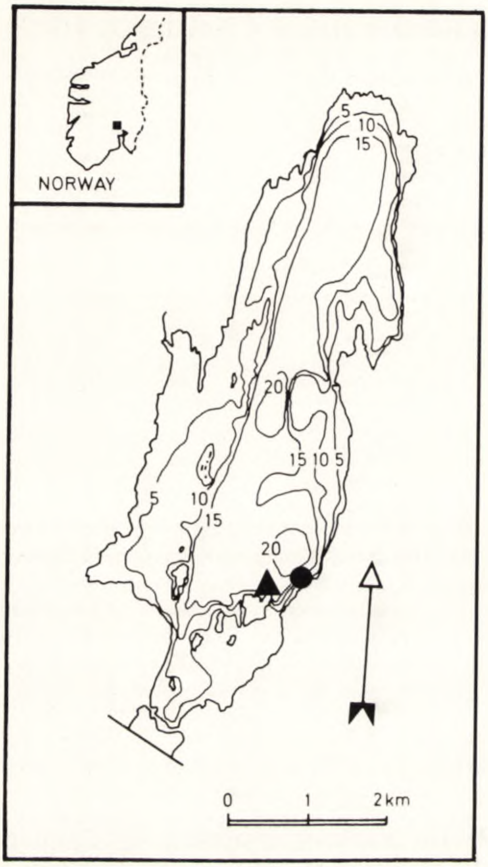

Fig. 1. Lake Steinsfjorden, S.E. Norway, with sampling locatities (● trapping, ▲ SCUBA diving).

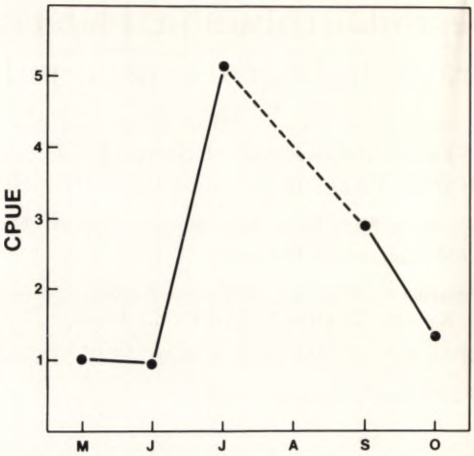

Fig. 2. Seasonal depth distribution of the crayfish *Astacus astacus* in Lake Steinsfjorden, S.E. Norway, with temperature °C (solid line) and oxygen saturation in per cent (stippled line) (temperature and oxygen data from D. Berge, Norwegian Institute of Water Research).

free season extends from late April–early May to late December.

During spring the temperature of the epilimnion increases rapidly to a maximum of 20–25°C. The temperature of the epilimnion is above 12°C from June until turn-over occurs in October (Fig. 2). Mean secchi-depth during summer is approximately 4.5 m, pH ranges between 6.9–9.0 and conductivity 86–92 μS cm^{-1} (20°C). The lake is surrounded by calcareous deposit rocks, giving a high calcium concentration to sediments, and a content of 12–13 μg Ca l^{-1} in the lake water (Skogheim and Rognerud 1978, Berge 1983).

Due to increased nutrient loading, a transition from oligotrophic to mesotrophic conditions has occurred in the last decades. Current mean primary production (May 1–December 15) is about 70 g C m^{-2} year^{-1} (Berge 1983), resulting in high O_2-concentrations in epilimnion during summer. During late summer, however, hypolimnetic O_2-concentrations may be less than 25 % saturation (below 15 m) (Fig. 2).

The bottom substrate consists mainly of rocks, stones and gravel together with patches of soft mud and vegetation. In 1977, Canadian waterweed (*Elodea canadensis*) invaded the lake, and by 1981, this plant was established in 76 % of the shallow areas (<6 m) (Rørslett et al. 1986).

Material and methods

The depth distribution was investigated in 1981 by placing 4 traps once a month (May 7, June 17, July 22, September 2 and October 21) at 9 depths (1, 3, 5, –, 17 m). The commercial crayfish trapping season starts on August 6. Due to the interference from the intensive trapping (cf. Qvenild and Skurdal 1986) we did not investigate the catch distribution in August. The traps (mesh size: 10 mm) had one funnel entrance at the top, were baited with fresh fish and emptied after 24 hours. In total, 408 crayfish were caught. Catch per unit effort (CPUE) was expressed as ind./trap 24 hrs^{-1}. The catchability of crayfish varies with temperature (Capelli and Magnuson 1975, Abrahamsson 1983), however, the relative depth distribution may be interpreted from the trap catches.

Habitat segregation and feeding were investigated in 1984 (July 5, September 18 and October 10) by SCUBA diving. In total, 268 crayfish were collected from three different habitats:

(A) Shallow hard-bottom (0–3 m) with stony substrate and sparse vegetation (N = 145).
(B) Shallow soft-bottom (0–3 m) with muddy substrate and more dense vegetation (N = 100).
(C) Deep hard-bottom (3–6 m) with muddy substrate and some vegetation (N = 23).

Sex and total length (from rostrum to end of telson) were recorded for all specimens. Immediately following capture, a 10 % formalin solution was injected into the stomachs, then the crayfish were stored frozen.

The stomach contents from 158 individuals were analyzed using a magnifying glass. Stomach fullness (those with empty stomachs were excluded) was subjectively evaluated; 1≤ 25 %, 2≤50 %, 3≤75 % and 4≤100 %. For each individual the volume (%) of each food group was estimated. From this, mean volume (%) was estimated for each habitat.

Food overlap was estimated from Schoener's (1968) index:

$$D=1-1/2\overset{n}{\underset{i=1}{}}\ \mathrm{I}\ p_{ij}-p_{ik}\ \mathrm{I}$$

were p_{ij} and p_{ik} are the fractions of the food resource $\underline{i}$ in the habitats $\underline{j}$ and $\underline{k}$, respectively. D varies between 0 and 1, and high values indicate a high food overlap. We used detritus, vegetation, benthic animals and carapaces as resource categories.

Results

Catch variation with season and depth

In May, trap catches were high in the shallow littoral zone, contrary to the summer situation (June–September), when the highest trap catches were in the zone 5–11 m (Fig. 2). The fall-turnover in Lake Steinsfjorden was initiated in early October at 12°C, and in late October the crayfish catches were evenly distributed down to at least 17 m.

During summer and early autumn (June, July and September) no significant differences were found in depth distribution. In both May and October, however, the depth distribution was

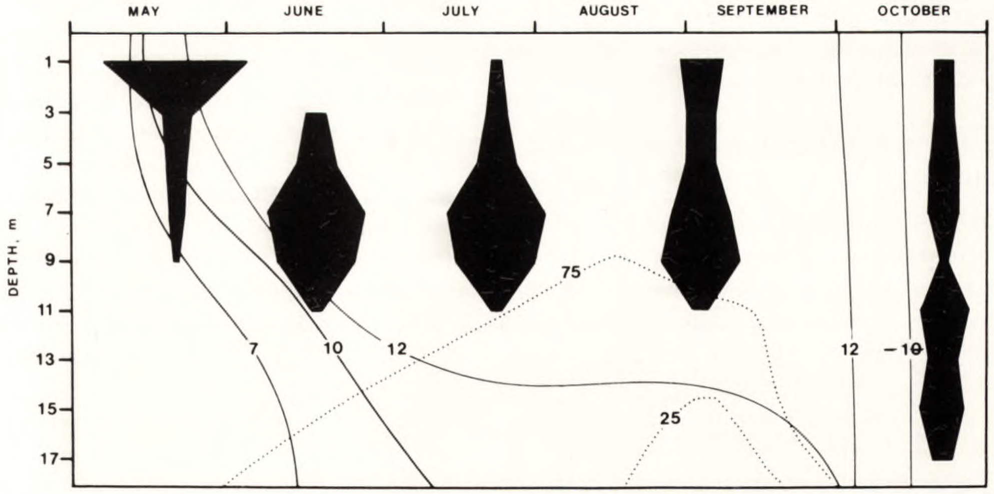

Fig. 3. Seasonal variation in trap catches of the crayfish *Astacus astacus* in Lake Steinsfjorden, S.E. Norway.

significantly different from the summer depth distribution (Kolmogorov–Smirnov tests; Sokal and Rohlf 1981). Catch per unit effort (CPUE) varied during the season (Fig. 3). In spring and late autumn, CPUE was low compared to July and September.

The sex ratio in the trap catches varied according to season. In July, there was a significant numerical dominance of males ($\chi^2=56.8$, $P<0.001$), whereas females dominated in October ($\chi^2=5.71$, $P<0.05$). At the other sampling periods, the sex ratio did not differ significantly from 1 (χ^2-tests, $P>0.05$).

Size and habitat distribution

In the shallow (0–3 m) littoral, hard-bottom habitat (loc. A), all length groups of crayfish were present (Fig. 4). In the soft-bottom habitats, individuals smaller than 50 mm were not observed in the shallow areas (loc. B), whereas only individuals larger than 72 mm were caught in the deeper (3–6 m) soft-bottom habitat (loc. C).

Statistically significant differences in length distribution (Kolmogorov–Smirnov-tests) were found between; a) shallow soft-bottom and shallow hard-bottom habitats, and b) deep soft-bottom and shallow hard-bottom habitats, while no significant differences were found between the two soft-bottom habitats (despite the shape of the graph in Fig. 4).

In neither habitat, the sex ratio was significantly different from 1 (χ^2-tests, $P\geqslant0.05$).

Feeding

Detritus, benthic macrophytes and epiphytic algae were the most important food items for the crayfish in all habitats (Table 1). In July, detritus and vegetation constituted about equal amounts of stomach contents, together with a large fraction of carapaces. Carapace fragments were found only in post-moulted individuals indicating that these fragments were own exuviae.

In September, vegetation increased in relative importance and constituted between 65–85 volume per cent of stomach content in all habitats. In the deep, soft-bottom habitat, crayfish were sampled on a layer of decaying Canadian waterweed, in which they consumed large numbers of the amphipod *Gammarus lacustris*, responsible for the large share of zoobenthos in the stomachs (33 %) expressed in Table 1. In October detritus made up 1/3 and vegetation almost 2/3 of stomach contents. At this date, four individuals less than 30 mm in size were examined, all exclusively with benthic zooplankton in their stomachs (*Eurycercus lamellatus* and *Megacyclops gigas*).

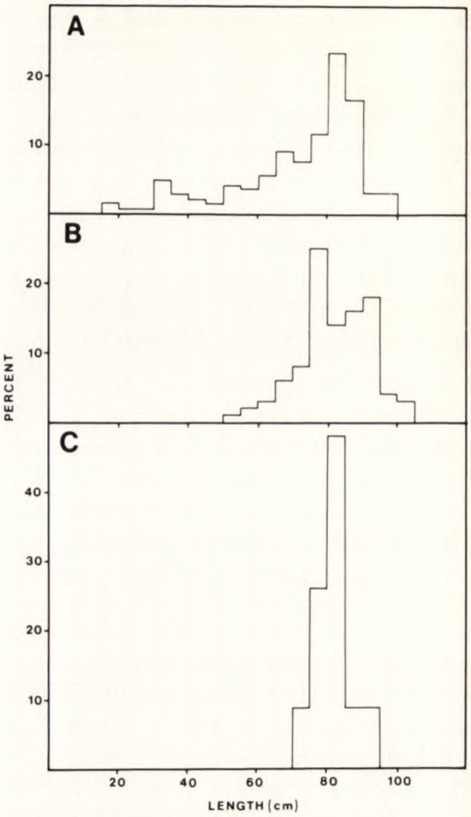

Fig. 4. Length distribution of the crayfish *Astacus astacus* on different habitats: (A) shallow hard-bottom (0–3 m), (B) shallow soft-bottom (0–3 m) and (C) deep soft-bottom (3–6 m).

The food overlap was high between shallow soft- and hard-bottom habitat, whereas the food overlap was lower between either of the shallow habitat and the deep habitat (Table 2).

Table 1. Percent volume of different food items in stomachs of the crayfish (*Astacus astacus*) in Lake Steinsfjorden, S.E. Norway.

K: Frequency of individuals with stomach contents.
n: Number of individuals with stomach contents.
f: Mean relative stomach fulness (1–4).
A: Hard bottom, 0–3 m. B: Soft bottom, 0–3 m. C: Soft bottom, 3–6 m.

				Food items (%)			
Date Habitat	K %	n	f	Detritus	Vegetation	Zoobenthos	Carapaces
05.07 A	66	29	1.1	42.2	44.5	1.2	12.1
05.07 B	46	13	1.4	48.8	24.2	7.5	19.2
18.09 A	68	23	2.3	23.4	77.6	+	—
18.09 B	73	24	2.5	12.5	85.6	1.9	—
18.09 C	52	12	1.9	1.7	65.0	33.0	—
10.10 A	58	31	1.4	32.9	56.5	10.6	—
10.10 B	87	26	1.2	30.2	56.8	9.3	3.8

From 54–13% of the individuals had empty stomachs. This was, however, not correlated to substrate, date or depth. The highest proportion with high stomach fullness was found in September.

Discussion

Temperature influences the activity, and thus, the trappability of crayfish (Abrahamsson 1983, Capelli and Magnuson 1975). Trappability is also influenced by moulting and reproductive cycle. However, when temperature exceeds 12°C, it probably has only a minor influence on trappability. In the areas deeper than approximately 10 m, temperatures was roughly 12°C from June to October. Crayfish were caught in traps when temperatures were below 12°C both in May and October. Thus, in this study the relative depth distribution may probably be interpreted from the trap catches.

The depth distribution of the crayfish *Astacus astacus* in Lake Steinsfjorden seemed strongly dependent upon temperature. The crayfish were restricted to the more shallow areas above the thermocline throughout the summer, a phenomenon well established among other crayfish species (Abrahamsson 1971, Fast and Momot 1973, Capelli and Magnuson 1975, Magnuson et al. 1975).

Reproduction requires temperatures above 15°C (Abrahamsson 1972) and moulting is restrained in cold water. This probably is an important factor regulating depth distribution. During autumn, as the temperature is lowered, lake turnover is initiated at about 12°C. After fall turnover, crayfish trap catches become

Table 2. Food overlap, as estimated from Schoener's (1968) index, for the crayfish (*Astacus astacus*) on different habitats in Lake Steinsfjorden, S.E. Norway.

Date of sampling	Shallow hard bottom vs. shallow soft bottom	Shallow hard bottom vs. deep soft bottom	Shallow soft bottom vs. deep soft bottom
05.07.85	0.80	—	—
18.09.85	0.90	0.66	0.69
10.10.85	0.98	—	—

evenly distributed to a depth of at least 17 m. Such autumnal downward migrations have also been observed in other crayfish species (Aiken 1969, Abrahamsson 1971, Capelli and Magnuson 1975), and is also consistent with earlier observations from Lake Steinsfjorden (Hessen and Skurdal 1986). This migration may be due to interspecific competition, predator avoidance, reproduction (i.e. reduced day length) or food search. Stomach fullness was high in September, and both decaying Canadian waterweed and the amphipod *Gammarus lacustris* were important food items in the deep soft-bottom habitat.

As indicated in Fig. 2, oxygen is probably not yet a limiting factor in depth distribution of the crayfish in Lake Steinsfjorden, although the need for well aerated water is clearly documented (Lindroth 1949, Ridderstolpe 1987). In the dense stands of decaying *Elodea*, oxygen may be reduced below levels acceptable to crayfish (i.e. <2 mg O_2/l; Buschemi 1958, Ridderstolpe 1987). In the near future, this may limit both depth distribution and overall production of crayfish in parts of Lake Steinsfjorden. *Elodea* is now established on 76 % of the shallow areas of Lake Steinsfjorden. Although year-to-year variation in biomass is recorded (Rørslett et al. 1987), the dense cover of *Elodea* accelerates eutrophication and initiates internal phosphorus loading. This will further increase oxygen depletion in the hypolimnion and become a serious threat to the dense crayfish population during periods of decaying.

The seasonal variation in trap catches resulting in reduced autumn catches is mainly due to heavy exploitation. The crayfish trapping season extends from August 6 to September 14 in Lake Steinsfjorden. During 1979–83 approximately 75–91 % of legal sized crayfish were harvested annually. Reduced feeding activity (cf. Hessen and Skurdal 1986) or reduced activity due to low temperature, mating or pleopodal eggs in females may also contribute to lower catches in spring and autumn.

Numbers of male crayfish are usually greater in trap catches, due to their larger size and dominating aggressive behaviour. In Lake Steinsfjorden, the sex ratio was close to 1, except for July and October. The dominance of males in July is probably due to a time-lag in the moulting cycle of females. Males are more susceptible to trapping and as a result females dominate in the late autumn catches after the intense exploitation during the trapping season.

As choice of food did not differ within the habitats, the observed difference in length distribution between hard- and soft-bottom habitats is probably due to other reasons. Food-choice does not depend on sex or size for crayfish larger than 35 mm (cf. Hessen and Skurdal 1986), however, among the earliest stages there is a preference for zooplankton. Furthermore, in July, when size differences at the various habitats were recorded, food was in excess as indicated by high values of relative stomach fullness. Thus, the horizontal and vertical distribution was not due to food choice or availability.

Probably, shelter is more essential in regulating size distribution. Crayfish are aggressive, with larger individuals dominating smaller ones (Abrahamsson 1966, 1972, 1983). Predation risk is also important, as smaller crayfish moult frequently and are subject to fish predation (Momot et al. 1978, Dehli 1981). Thus, small crayfish are confined to areas providing sufficient shelter (which also means a high diversity of substratum) because of the predation risk from conspecific individuals and predacious fish in open soft-bottom areas. Preference for hard-bottom and avoidance of soft-bottom habitat may also be involved in the observed size distribution.

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