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Contents

Egg Characteristics and Hatchery Survival in a Baltic Salmon, *Salmo salar* L., Population

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ABSTRACT

Egg characteristics and survival was studied in a Baltic salmon population at the Norrfors hatchery on River Ume (63°50′N, 20°25′E), Northern Sweden. Large females produce more and larger eggs. A weak correlation during the egg stage between egg colour and death rate was found. However, drastical death rates occur only among the pale and medium coloured eggs. Long impoundment and late stripping were found to increase mortality and to yield more coloured eggs, suggesting an optimal time for stripping. Future research areas are discussed.

I. INTRODUCTION

In salmon hatcheries the death rate during the early stages has with improved techniques and knowledge decreased to a very low level. But, it is still very important to gain some further understanding of the factors influencing the survival of *Salmo salar* L., both for ecological theory construction and for efficient hatchery operations. It is a well-established fact that large females produce more and larger eggs in salmonid species (MILLENBACH 1950, DONALDSON and OLSON 1957 and GALL 1974 for *Salmo gairdneri* and POPE 1961, AULSTAD and GJEDREM 1973 and LARSSON and PICKOVA 1978 for *Salmo salar*).

There is also a reverse relationship between fecundity and egg size, relatively more eggs mean smaller eggs (POPE 1961). The influence of egg size on survival and fry size of different *Salmo* species has been studied by several authors. The results do not give any clear indication of a relationship between egg size and survival during the existing conditions. From theoretical standpoints SVÄRDSON (1949) suggested that large eggs generally have a higher survival rate to compensate for their smaller number. In accordance a higher survival during the egg and fry stages was found among larger eggs of *Salmo salar* compared to small eggs (YANDOVSKAYA 1976). In contrast to this, FOWLER (1972) found that larger eggs in Chinook salmon were subject to higher mortality during the egg and fry stages than smaller eggs.

However, it should be stressed that SVÄRDSON was referring to the natural situation while the tests were done in the laboratory.

The egg colour varies between females. Pale eggs are looked upon as being inferior to red eggs by fish culturists (pers. comm. H. JOHANSSON). The pigments *e.g.* the carotenoids are important during reproduction, especially during stringent environmental conditions; for a review see MIKULIN and SOIN (1975). It is known that rainbow trout fed on carotenoids (*e.g.* cantaxanthin) produce eggs with a higher colour intensity leading to a higher survival than parent fish fed without carotenoids (DEUFEL 1965).

This paper deals with an empirically based analysis of factors influencing the death rate of *Salmo salar* during its egg stage. Consideration is given to the covariation between parent fish and egg qualities.

II. MATERIAL AND METHODS

Salmon are caught during their spawning run from July to early September. The migrating fishes consist of wild and crosses of wild and cultivated salmon. The stripping starts by mid October and ends at the beginning of November. The eggs are fertilized, allowed to swell and rinse. One male is used to fertilized on average three females. As a standard procedure a number of variables is recorded on the spawning salmon

used for rearing at Norrfors Hatchery, Umeälven (Ume river 63°50'N, 20°25'E). The following data, from the years 1977—81, were used in this study:

— Origin: Wild or reared. All smolts reared in the hatchery have their adipose fin removed. The wild salmon has its origin in the Vindel-älven (Vindeln river) while the cultivated salmon originates from the rivers of Ume and Vindeln.
— Number of days the females are stocked until stripping.
— Days of stripping, recorded as the number of days from the beginning of the year.
— The weight of females and males before stripping, recorded to the nearest $5 \cdot 10^{-1}$ kg during 1977—79 and to the nearest 10^{-1} kg from 1980.

— The length of females and males from the tip of the snout to the fork of the tail, measured to the nearest 10^{-3} m.
— The number of eggs per female is estimated by the method described by BROFELD (1935).
— The egg diameter is estimated from the number of swollen eggs per 25 cm.
— The egg colour is estimated visually using a commercial colour scale, ranging from 121 (light yellow) to 165 (dark orange).
— The death rate is calculated as the per cent dead when the eggs are eyed.

Due to lack of space in the hatchery, eggs from some of the females were mixed. Such data are excluded from the present analysis. Scales from the females were collected but information of female age is not available at present.

Table 1. *Means (median for the death rate) and standard deviations for variables classified by colour and origin.*

Variable	Colour			Total (n=302)
	Pale (=87)	Medium (n=123)	Red (n=92)	
Per cent death	7.60	9.80	8.65	9.15
	(17.65)	(13.11)	(8.42)	(13.50)
— Wild	7.2	9.45	8.30	8.30
	(18.48)	(13.30)	(8.28)	(14.29)
— Cultivated	8.55	10.80	9.40	9.65
	(16.40)	(12.97)	(8.61)	(12.52)
Egg size	.58	.59	.59	.59
	(.03)	(.03)	(.02)	(.03)
— Wild	.57	.59	.58	.58
	(.03)	(.03)	(.03)	(.03)
— Cultivated	.59	.60	.60	.60
	(.04)	(.02)	(.02)	(.03)
Weight females (g)	5057.47	5619.51	5578.26	5545.03
	(1469.19)	(1362.29)	(1471.66)	(1443.94)
— Wild	5110.00	5442.86	5436.59	5327.71
	(1464.39)	(1338.02)	(1401.10)	(1419.63)
— Cultivated	4984.38	5852.83	5692.16	5588.24
	(1497.98)	(1371.50)	(1460.59)	(1465.58)
Length females (cm)	85.49	90.07	89.20	88.49
	(8.49)	(8.03)	(8.79)	(8.29)
— Wild	86.30	87.89	88.51	88.37
	(8.82)	(8.76)	(7.96)	(8.67)
— Cultivated	84.13	90.32	89.76	88.64
	(8.78)	(9.04)	(7.68)	(7.82)
Number of eggs	7285	8543	8570	8189
	(2228)	(2259)	(2188)	(2295)
— Wild	7580	8548	8635	8246
	(2382)	(2147)	(2297)	(2299)
— Cultivated	6720	8537	8520	8117
	(1865)	(2420)	(2120)	(2296)

III. RESULTS

The material, classified by egg colour and origin, is presented in terms of means (medians) and standard deviations in Table 1. The death rate is given as a median due to its skewed distribution (Fig. 1). The whole material is based on the offspring from 302 females fertilized by 122 males. The average number of days in impoundment is 44; ranging from 33 to 157 days. The average stripping day is 306; ranging from 290 to 334. No consideration is given to the number of days that males were stocked nor to the day they were stripped. No significant differences between the death rates of the colour groups are found. However, from Fig. 1 an increase in variance is noticed for pale eggs and in particular the number of extreme death rates (more than 50 %) is highest among the pale eggs. There is no significant difference in egg size between the colour groups. The cultivated females have fewer and larger eggs, presumably due to different genetic background. They also seem to be slightly longer but not heavier than non-cultivated females. The mean female weight in the whole material is 5445.03 g and the number of eggs per female is 8188, which gives a mean number of 1525 eggs produced per kilogram female. According to TVENNING (1980) the mean number of eggs produced per kilogram female is 1200.

Correlations for colour and origin groups are presented in Table 2. Female length has been found to represent size rather than weight according to POPE (1961). The table reveals that egg size is positively correlated with female length, which agrees with earlier results (*e.g.* AULSTAD and GJEDREM 1973). The day of stripping is negatively correlated with egg size and female length. This is largely due to the hatchery operations, as smaller females with smaller eggs tend to be saved for later stripping. Further, for all eggs, there is throughout a negative correlation between egg size and death rate (though not generally significant). This is in agreement with SVÄRDSON (1949) and YANDOVSKAYA (1976). The death rate is generally not correlated with male size. The number of days that females are kept in impoundment is positively correlated with the death rate. The day of stripping is also correlated with the death
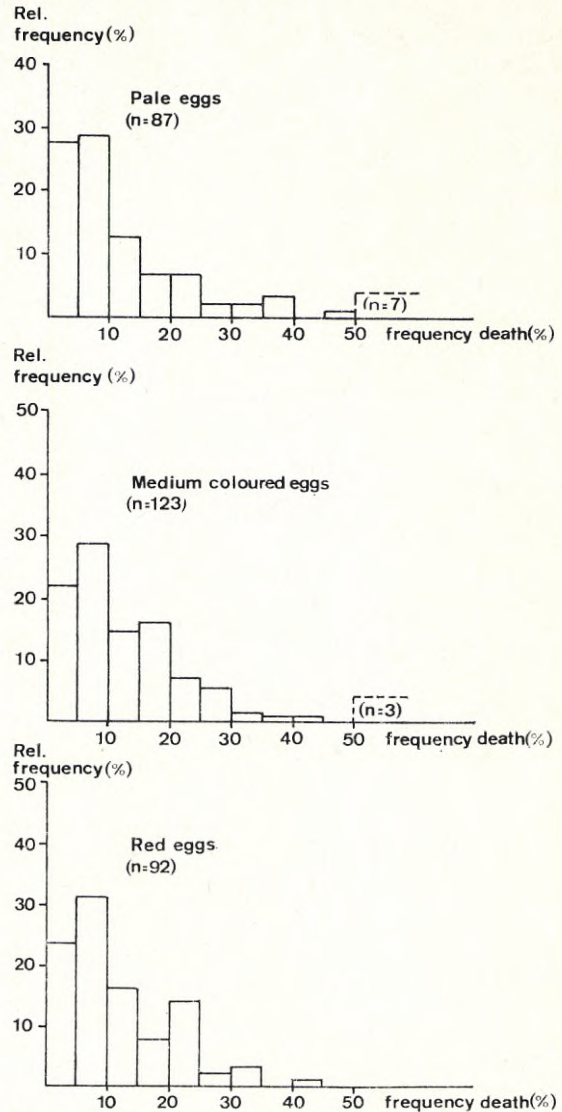
Fig. 1. Death rates classified by colour.

rate; for the wild group a later stripping date indicates a decreased survival of the eggs. A feature of the material is that the day of stripping and impoundment is not correlated with the above variables among red eggs.

Egg colour is correlated with the number of impoundment days, the day of stripping, female length, egg size and death rate (Table 3). The first two variables are strongly correlated with egg colour, while there is no significant correlation

Table 2. Correlations between variables classified by colour and origin.

Variables	Colour												Colour		
	Pale [1]			Medium [2]			Red [3]			All colours					
	Wild	Cultivated	Total	Wild	Cultivated	Total	Wild	Cultivated	Total	Wild	Cultivated	Total			
Egg size/ Female length	.69***	.72***	.63***	.67***	.50***	.61***	.71***	.76***	.71***	.70***	.67***	.66***			
Number of eggs/ Female length	.72***	.33*	.62***	.83***	.80***	.81***	.73***	.72***	.72***	.70***	.77***	.74***			
Egg size/ Day of stripping	−.39***	−.53***	−.45***	−.07	−.25*	−.16*	−.07	−.06	.10	−.17*	−.24**	−.15**			
Egg size/ In % death	−.07	−.03	−.02	−.03	−.19	−.07	−.18	−.26*	−.22	−.05	−.16*	−.08			
Female length/ In % death	−.19	.04	−.13	−.19	−.23*	−.20*	−.18	−.16	−.17	−.17*	−.14*	−.16*			
Day of stripping/ In % death	.52***	.23	.41***	.48***	.16	.34***	.30*	.00	.10	.45***	.06	.27***			
Days of impoundment/ In % death	.40**	.27	.35***	.16	.46***	.26**	.15	.23	.20*	.25***	.33***	.26***			
Female length/ Day of stripping	−.39**	−.39***	−.39***	−.23**	−.26**	−.24**	.09	.04	.09	−.20**	−.13	−.16**			

[1] The number of observations is approximately 55, 32, and 87, respectively
[2] The number of observations is approximately 70, 53, and 123, respectively
[3] The number of observations is approximately 41, 51, and 91, respectively

Table 3. *Correlations of colour with time variables, female length, egg size and death rate.*

Correlation of colour with				
Day of impoundment	Day of stripping	Female length	Egg size	ln per cent death
.23*** (n=236)	.21*** (n=301)	.07 (n=299)	.09 (n=301)	—.07 (n=302)

Table 4. *Estimated regression coefficients (standard errors within parenthesis).*

Explanatory variables	Response variables			
	Number of eggs	Egg size	ln death rate	Egg colour
Egg colour	— —	— —	.019 (.007)	— —
Stripping day	— —	—.0003 (.0001)	.021 (.005)	.153 (.038)
Impoundment day	— —	— —	.012 (.003)	— —
Female length	204.171 (11.003)	.002 (.001)	— —	— —
Egg size	— —	— —	— —	29.845 (13.180)
Origin	— —	.017 (.002)	— —	— —
Constant	9869.848 (977.292)	.461 (.041)	2.896 (1.636)	63.600 (14.922)
R^2	.54	.52	.13	.06

with the other variables. When the stripping days are divided into three groups ($\leq$ 305, n=150; 305—320, n=103; > 320, n=27) and the egg colour is correlated with death rate no significant correlation appears. The same procedure is made with the number of impoundment days ($\leq$ 70, n=46; 70—100, n=191; > 100, n=43) where a significant correlation appears in the medium group (p=0.048).

The above results are in terms of single or paired variables. However, the causal structure among the variables is much more complex and other analytical tools are required. The causal analysis carried out here is based on regression models.

The results of the regression analyses are given in Table 4. The egg size is determined by female length, the day of stripping and the origin of the female. If the female is 0.1 m longer the egg size will increase by 0.02 cm. Further, one postponed day of stripping decreases the egg size with 0.0003 cm. Cultivated females have 0.017 cm larger eggs.

For the number of eggs an increase of female length by 0.01 m causes an average increase by 204 eggs. In the colour relationship an increase in egg size by 0.01 cm increases the colour intensity by 0.3 units. A ten days later stripping increases the egg colour with about 1.5 units. The number of days in impoundment did not fit into the model, but showed a strong correlation with egg colour (Table 3).
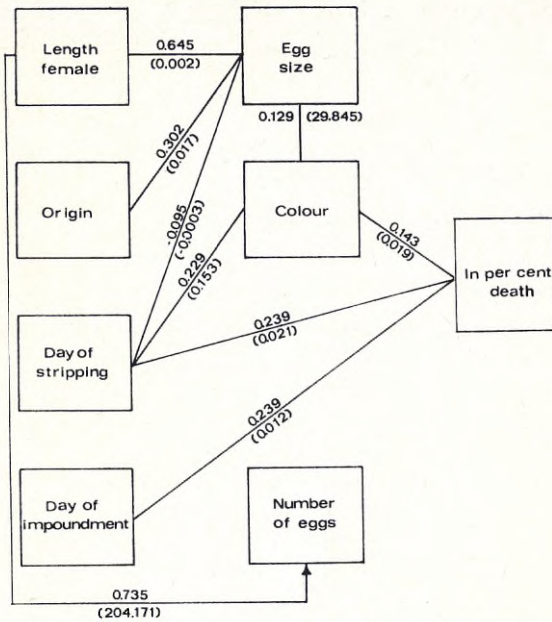
Fig. 2. Schematic description of relationships. (Upper figures are beta-coefficients and lower ones regression coefficients).

IV. DISCUSSION

Large females produce more and larger eggs than small females according to the high correlations and the estimates in the regression model. Further, the egg size is negatively affected by the day of stripping, and cultivated females give larger eggs. The longer the females are kept in the river and the later the stripping is made the more coloured are the eggs. The influence of the day impoundment of the egg colour is nonsignificant in the regression context. From the model, the female size has an indirect influence on the egg colour through the egg size. No direct influence could be found.

The model shows that the time has the strongest effect on the death rate. A later stripping day and a longer impoundment of the females increases the death rate. The stripping day seems to be of particular importance as it also affects the death rate weakly and indirectly through colour, while no direct relationship exists.

The importance of the egg colour, *e.g.* the carotenoids, for survival during the egg stage is not clearly established in this material. A tendency is, however, to be seen, as very high death rates occur only among the pale and medium coloured eggs. The colour of the eggs increases with time and so does the death rate. There is possibly an optimal time for the females to be stripped. The higher death rates could be a result of overripeness. Complicating the matter further is the lack of correlations for the red eggs for most of the factors described above. The stripping date is negatively correlated with death rate only in the wild population. The sexually mature salmon, that originates from the River Vindeln, returns earlier in the summer. When females are chosen for stripping, it is suggested that special attention should be given to the origin. The place for keeping the females might also be important. They are kept in the river until the stripping starts, but are moved to the hatchery at the end of this period.

For the death rate a log-linear relationship is employed. An earlier attempt to include female length was unsuccessful. The model implies that an increase in colour will decrease the death rate with 0.019 in logarithmic units. The death rate increases with a later stripping day and the number of days in impoundment. When using mean values for the explanatory variables a later stripping of ten days increases the death rate by 23.43 per cent. The corresponding value for the number of days the females are kept in impoundment is 12.8 per cent.

The pattern between variables is illustrated in Fig. 2. The figures in parentheses correspond directly to the estimated coefficients in the equations. The standardized estimates (beta-coefficients) are also given in the figure. The variables are standardized in order to make estimates comparable. According to Table 4, the female size strongly affects the size and number of eggs. The egg size affects the death rate through egg colour, while the number of eggs provides no significant explanation.

In order to find out the most important factors for high survival and high quality of the fishes, controlled experiments should be made with a few variables at a time. The low R^2 when explaining death rate suggests that there might be one or

several factors missing, like for instance age of the females.

Two of the functions that have been ascribed to carotenoids are protection against photodynamic action (KRINSKY 1971 and HAIRSTON 1978) and resistance against bacteriomycotic disease (JARZOMBEK 1970). These effects cause no real problem in the hatchery, as the eggs are kept covered and treated with chemicals to prevent the growth of fungi. The effect of egg colour on survival during the egg- and fry stages should be studied under natural conditions, *i.e.* in darkness but without any chemical treatment.

V. ACKNOWLEDGMENTS

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Ecological Testfishing with the Lundgren Gillnets of Multiple Mesh Size: the Drottningholm Technique Modified for Newfoundland Arctic Char Populations

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ABSTRACT

An ecological standardized testfishing programme was carried out in insular Newfoundland and Labrador, in order to collect information on the population ecology and genetics of the Arctic char (*Salvelinus alpinus*) species complex. Two types of the Lundgren experimental gillnets of multiple mesh size, 6.25—75 mm and 10—75 mm, knot to knot, were used in both benthic and pelagic habitats in 20 water bodies. These systems contained Arctic char, brook trout, lake trout, Atlantic salmon, rainbow smelt, white sucker, three-spined stickleback and American eel. The testfishing design, equipment and techniques used are described. The use of gillnets of multiple mesh size is also discussed in terms of size and species selective characters, and the characteristics of the Lundgren experimental gillnets are pointed out. A complete model of a testfishing programme designed for northern freshwaters is recommended for future surveys in eastern Canada.

I. INTRODUCTION

Only minor parts of the "inaccessible" freshwaters of interior Labrador and insular Newfoundland have been explored in terms of their fish fauna. In fact it was not until 1949 that the presence of Arctic char on the island became known to the public (SCOTT and CROSSMAN 1964). This relict species is still today considered by many to be restricted to a few large and deep lakes. As a consequence of the increasing exploitation and development on lakes and rivers in the province, there is major concern about the loss of information on the original and virgin ecosystems.

A standardized testfishing programme was carried out in 20 water bodies in insular Newfoundland and Labrador (Fig. 1) during the summer and autumn of 1984. This study was conducted in order to collect information on the ecology and the systematics of the Arctic char (*Salvelinus alpinus* LINNÉ 1758) species complex, and levels of heavy metals in the fish.

A set of the Lundgren survey type gillnets of multiple mesh size was used in both benthic and pelagic habitats. The equipment and the techniques used are described. The species and the size selectivity of the gillnets are presented and discussed, in the shadow of general criticism of the use of gillnets, as well as in the light of the experience of several years of their use in Swedish lakes.

This paper emphasizes the significance of the testfishing design and describes gear for a biological, qualitative and semi-quantitative sampling programme rather than a solely quantitative approach to testfishing.

The paper addresses administrators, researchers as well as personel in the fields.

It is the authors' hope that the present study can be used as a model for future testfishing programmes performed by the D.F.O. and consultant groups in eastern Canada to evaluate the impact of environmental changes, salmonid enhancement and stocking programmes as well as to gain a basic understanding of freshwater fish biology.

The testfishing programme in Red Indian Lake has been chosen as a representative example of the recommended sampling technique.

II. BACKGROUND

The need for longterm, comparable information about the structure of different fish populations in natural lakes and lake reservoirs in Sweden, in order to understand the effects of impoundment and compensatory management during the 1940's, produced a series of standard gillnet gangs with different combinations of mesh sizes. The surveys which were conducted in large reservoirs with low densities of benthic and pelagic fish populations, required large-sized gear. A system of 9 different gillnets, 270 metres long and representing 7 different mesh sizes ranging from 16.5 to 50 mm knot to knot, where 30 and 33 mm occurred twice, was most frequently used. It was commonly called a biological test gang.

These first gillnets were made of cotton, but at the end of the 1940's nylon gillnets were fabricated (in pink of course, since the fibre originated from a corset factory) and later on introduced to testfishing. At the beginning of the 1960's the multifilament gillnets were replaced successively by transparent monofilament nets. It became increasingly common to use two additional sections with mesh sizes of 10 and 12.5 mm, instead of the extra 30 and 33 mm sections. The latter combination was used permanently in the pelagic testfishing programmes. However, the catch area of this gear was four times larger than that of the benthic gangs.

The different mesh sizes used were thus 10, 12.5, 16.5, 22, 25, 30, 33, 38 and 50 mm. As an alternative to the 12.5 mm mesh 13 mm was sometimes chosen. These were basically the standard mesh sizes available to any commercial and non-commercial fisherman in Sweden, providing a practical solution in terms of both economy and management directives.

Typical biological test fishing gear would thus consist of a few doubled benthic sets, each consisting of 9 gillnets per night, used at different depths and in different habitats. A pelagic set would be anchored in the deeper central part of the lake and used repeatedly for periods of 12 or 24 hours at different depths by lowering the nets successively from the surface down towards the bottom.
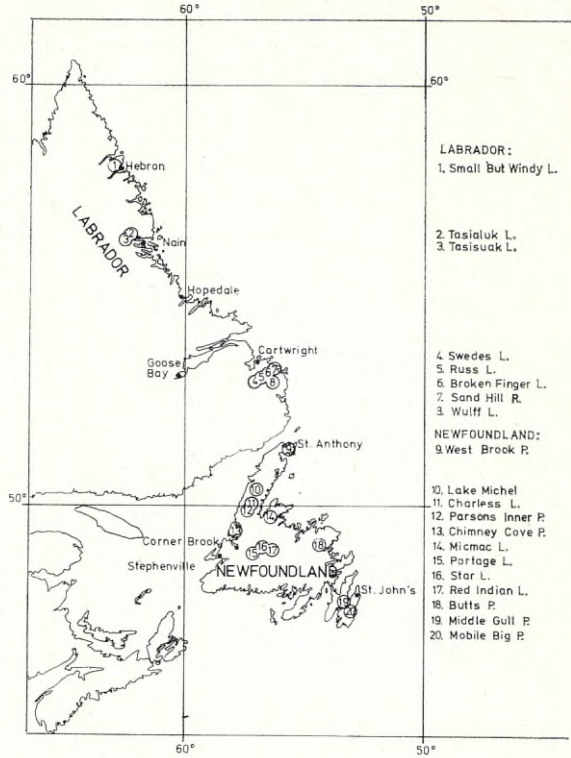
Fig. 1. Map of the Province of Newfoundland showing the location of the lakes where testfishing took place during 1984.

This was the successful technique which lay behind the large ecological programmes concerning the effects of water level regulation, the biology of sibling species complexes, and inter- and intraspecific competition and segregation between fishes conducted by G. SVÄRDSON, T. LINDSTRÖM and N.A. NILSSON at the Institute of Freshwater Research, Drottningholm in the following decades.

Altough this technique worked well in large lakes the biological standard gang was unpractical in small lakes; too large to use on spawning grounds and for small and valuable fish populations, and too coarse for detailed studies of the depth distribution of species close to the shores. On the other hand, in lakes with dense fish populations the catch was sometimes too large to handle and it was furthermore very difficult to vary the number of efforts gradually.

In cooperation with Lundgren's of Stockholm, the first small bottom net of survey type with multiple mesh sizes was constructed and used in 1968. The traditional mesh sizes previously used were supplemented with some additional larger mesh sizes.

This type of gillnet now dominates in the test-fishing programmes performed by the Drottning-holm staff, and has been used in scientific studies of fish populations in different parts of the world, from Svalbard, Greenland and Iceland in the North to South Africa and Sri Lanka in the South. The gear and the methods are described by FILIPS-SON (1972).

The idea of catching a substantial amount of fish of different species and sizes at a specific depth in gillnets set parallel to the shore was put forward at the end of the 1960's by the visiting research scientist T. NORTHCOTE from the University of British Columbia, Canada (*e.g.* NORTHCOTE 1974).

In 1984, a joint research programme arranged by the Institute of Freshwater Research, Drott-ningholm, Sweden, and the Fisheries Research Branch, Department of Fisheries and Oceans, St. John's, Newfoundland, initiated an intense study of the population ecology and genetics of Arctic char (*Salvelinus alpinus* L.) in Newfoundland and Labrador.

The Arctic char is an important resource in the Northern region and as such heavily exploited by Man (JOHNSON 1980). The management of this sensitive and mosaic species complex is comp-licated by an immense variety in ecology, mor-phology and ethology (FILIPSSON and SVÄRDSON 1976, NYMAN 1984). Studies of population ecology and genetics combined with the knowledge of the group's circumpolar distribution, the preglacial isolation refuges and possible successive postglacial invasions might be one way of coming closer to the unravelling of this taxonomic problem.

The testfishing and the collection of Arctic char and coexisting species were performed using the Lundgren small experimental gillnets of multi-ple mesh size and the techniques regularly used at Drottningholm today.

A detailed description of two versions of the

Table 1. *The order, mesh sizes and material of 12 dif-ferent panels of the Lundgren type S gillnet of multiple mesh size.* (Two bars=one mesh.)

Order	Bar mesh size (mm)	Stretched mesh size (inch)	Twine diameter (mm)
1	10	3/4	0.12
2	60	4 3/4	0.25
3	30	2 3/8	0.15
4	43	3 3/8	0.20
5	22	1 3/4	0.15
6	50	4	0.20
7	33	2 1/2	0.18
8	12.5	1	0.12
9	25	2	0.15
10	38	3	0.18
11	75	6	0.25
12	16.5	1 1/4	0.15

gillnets of multiple mesh size, its practical use and the sampling procedures are presented in "Material and Methods". Elementary instructions for pelagic gillnetting and a check list of equipment is given in an appendix. The species- and size-selectivity of the gillnets are discussed in "Results and Dis-cussion".

III. MATERIAL AND METHODS

Description of the Lundgren gillnets of multiple mesh size

During the survey of populations of Arctic char in Newfoundland and Labrador two types of benthic gillnets and one type of pelagic gillnet were used exclusively.

The Lundgren benthic survey gillnet of type S is a transparent monofilament nylon gillnet, 1.5 metres (5 ft.) deep, with a 36.6 metres (120 ft.) long headline and a 45.7 metres (150 ft.) long sinkline. It is composed of twelve 3.0 m (10 ft.) panels of different mesh sizes (Table 1). The order of the panels is such that the larger mesh sizes are surrounded by smaller ones.

In the revised type S gillnet another two panels with finer mesh sizes have been included, resulting in a 42.7 metres (140 ft.) long gillnet with 14 panels in the reverse order (Table 2).

The two pelagic types of gillnet consist of the same mesh sizes and material as the benthic nets

Table 2. *The order and the mesh sizes of different panels of the Lundgren revised type S gillnet of multiple mesh size.*

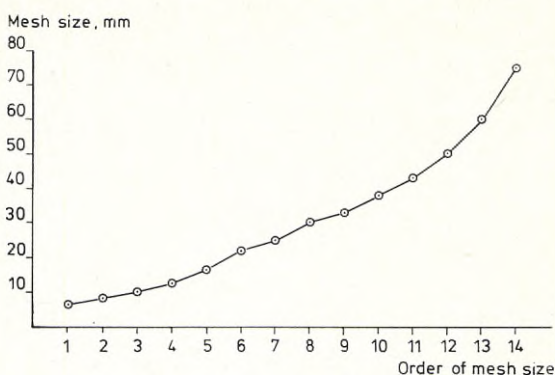| Order	Bar mesh size (mm)	Stretched mesh size (inch)	Twine diameter (mm)
1	6.25	1/2	0.10
2	8	5/16	0.10
3	16.5	1 1/4	0.15
4	75	6	0.25
5	38	3	0.18
6	25	2	0.15
7	12.5	1	0.12
8	33	2 1/2	0.18
9	50	4	0.20
10	22	1 3/4	0.15
11	43	3 3/8	0.20
12	30	2 3/8	0.15
13	60	4 3/4	0.25
14	10	3/4	0.12

Fig. 2. Graphical illustration of the series of 14 different mesh sizes in the Lundgren experimental gillnet of multiple mesh size. The actual order of mesh sizes in the gillnet is different. For further information see text.

although the former are 6 metres (20 ft.) deep with each panel being 6 metres (20 ft.) long. The different panels are arranged in order of increasing mesh size. In order to facilitate the practical handling of such large gear, the gillnet is divided into two sections.

A gillnet of multiple mesh size for experimental use in running water close to inlets and outlets is also marketed by Lundgren's. This so called stream gillnet is mainly a net of multiple mesh size with doubled headlines and sinklines. The series of increasing mesh size would thus be the following: 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60 and 75 mm. The series is shown graphically in Fig. 2. It must be pointed out again that the present range of mesh sizes in the Lundgren experimental gillnet is based on mesh sizes used previously in the larger biological test gang mentioned earlier, and is by no means the result of an adjustment to a specific geometrical series.

We do not know the degree of variation in the size of a specific mesh in a new net, nor the changes that occur during a season's use. These are probably comparable with the variation in any standard gillnet.

Description of the lakes

The survey carried out comprises oligotrophic water bodies ranging in size from small and shallow ponds (less than 25 ha) in alpine regions to deep river canyons and lakes (larger than 18.000 ha) in insular Newfoundland and Labrador (Fig. 1).

Description of the fishing technique

The main aim was to collect samples and ecological information from all of the major habitats and different depth zones, both benthic and pelagic. In order to gain a representative view of the population structure, habitat use and depth distribution of the Arctic char and all coexisting fish species, every mesh size had to be exposed in every habitat and depth zone (Fig. 3).

Benthic gillnetting

In each lake a regular and even shoreline with a gentle depth gradient was chosen for the placing of successive series of gillnets of multiple mesh size at different depths. Since the size of the catch usually decreases with increasing depth, the number of gillnets used in each set was simultaneously increased with depth.

The individual gillnets were attached to each other end-to-end by the existing loops and plastic net handles. By connecting several gillnets together the risk of having the entire equipment tangled by a very large fish is minimized.

With the help of a simple echo-sounder the depth profiles were easily located. The gillnets were set on the bottom parallel to the shore, with a small buoy at each end of the gang. These buoys
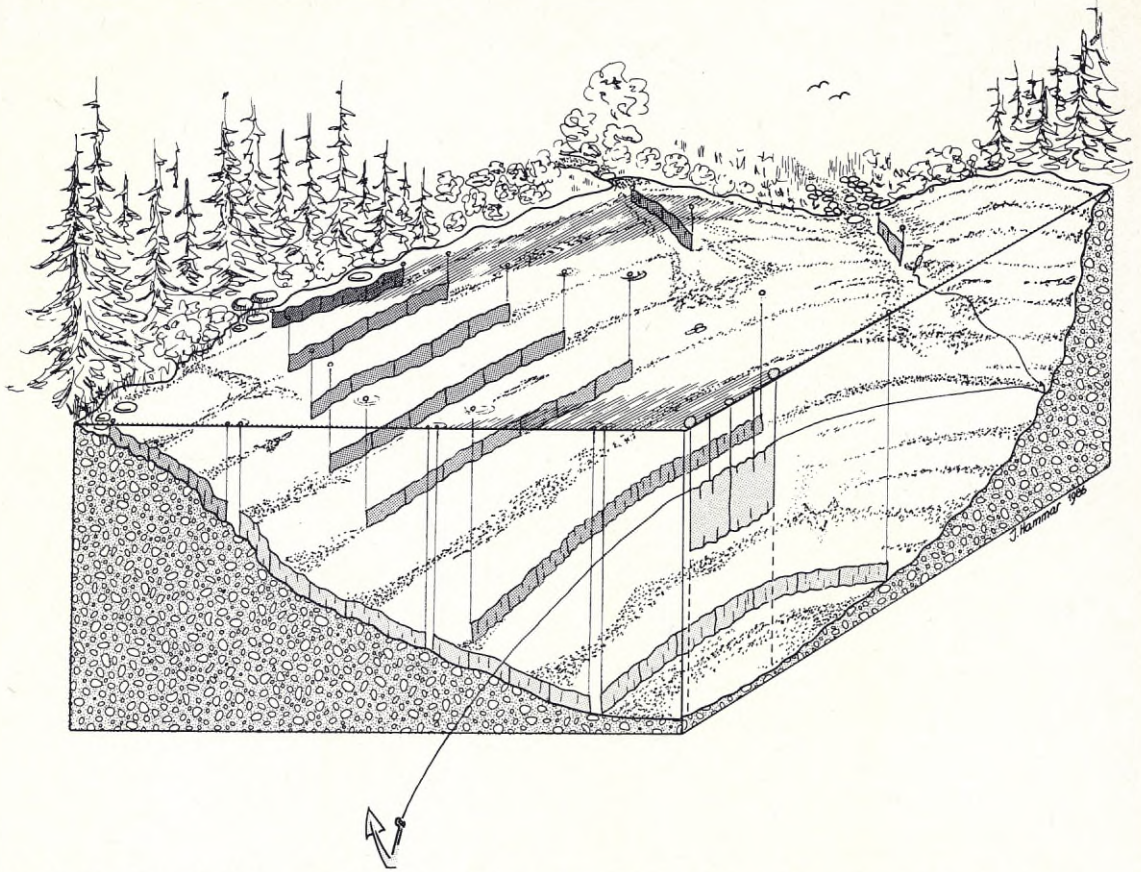
Fig. 3. The Drottningholm technique for ecological sampling of a lake with pelagic and benthic gillnets of multiple mesh size. (Drawing J. Hammar.)

were prepared in advance, with different lengths of line attached and carefully marked. The buoy lines were made of thin cord and with several metres of excess line in order not to disturb the gillnet during rough weather.

The sinkline is heavy enough to keep the small gillnet in place, and there was no need for anchors. The gillnets were hung loose. This is the old fisherman's trick to catch more fish, and according to RIEDEL (1963) loosely-hung gillnets tangle more fish and also fish of a much wider size range than a straight gillnet.

Depth zones were chosen at 5 or 10 metre intervals from close to shore at 1 to 2 metres depth all the way down to the maximum depth. As a further check of the depth distribution of different fish species a gang of many gillnets of multiple mesh size may be set at a right angle from the shore down to the required depth. Heavier experimental gillnets of stream-type may be used close to the major inlets and the outlet (Fig. 3).

The benthic gillnets were set in late afternoon and examined in the morning.

Pelagic gillnetting

The huge pelagic gillnet requires special handling in order to provide comparable results. The set has to be suspended by buoys and properly straightened with long ropes attached to heavy anchors (Fig. 4).

The buoy lines for the pelagic gillnet were carefully prepared in advance. Since the depth of this gillnet is 6 metres and the gear was lowered 6 metres every 24 hours, the lines were twined around the buoys and tied carefully with two
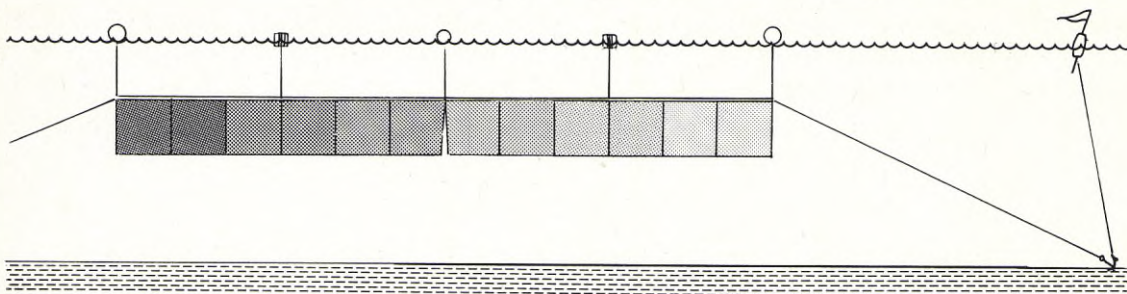
Fig. 4. A model of a correctly floated pelagic gillnet of multiple mesh size.

reversed half hitches at every sixth metre. This knot will lock the line to the buoy at each depth interval and when untied properly it does not form any irritating knots on the cord.

The two sections of the pelagic gillnet were connected to each other end-to-end. Two large and clearly visible red buoys were attached at both headline ends of the whole set. When fishing in the uppermost depth interval these buoys were tied to the gillnet itself. Because of the tension in this part of the gear heavier buoy lines are required, and a number of 6 metre long ropes were tied between the buoys and the headline end of the gillnet in each set.

The rest of the buoys were made of rectangular and protectively painted pieces of plastic foam, around which the line was wrapped symmetrically. Two buoys were attached to each section of the gillnet and one larger buoy was tied inbetween.

Two strong braided ropes of a floating synthetic material were used to anchor the gear from the headline ends. The length of each rope should be three times the water depth. At the other "end" of the heavy anchor, another rope slightly longer than the water depth was connected to a large flag buoy. This was done in order to haul up the anchors from the opposite direction, in the case of a change in wind direction.

The pelagic gear was usually located over the deepest part of the lake, and was set and checked in the morning every 24 hours.

Elementary step by step instructions for setting the pelagic gear are given in an appendix (page 30).

Other procedures connected with testfishing

The survey carried out with gillnets was accompanied by the recording of the following data, in order to broaden the scope of the study.

(1) Exact depth of both ends of each gillnet in metres.
(2) Date and time for setting and checking the nets.
(3) Surface water temperature in centigrade.
(4) Air temperature in centigrade.
(5) Wind strength in metres per second, and the major wind direction.
(6) Cloud cover in per cent and general weather comments.
(7) Comments regarding any factors that could affect the catch statistics such as brown humus slime, sticks and branches in the gillnet, or factors that might be of value for the food analyses, such as mass occurrences of flying ants, sprucebud butterflies and so on.

While the boat was connected to an anchored line it was very convenient to:

(1) Sample zooplankton qualitatively by means of vertical hauls of a plankton net between the bottom and the surface. A standardized mesh is important and in this study 60 μm was used. The plankton sample was preserved in well-buffered 5 % formalin.
(2) Measure the water temperature cline from the surface down to the bottom with a thermistor or a water sampler.
(3) Record the water transparency by using a Secchi-disc. (It is important to standardize the

time of the day for this measurement. Also the side of the boat, *i.e.* shade, and the use of a viewer (to be really correct).)

Sampling techniques

The benthic gillnets were brought back in large baskets to a suitable place, where they were hung up in the shade to be examined and cleaned. The fish from each gillnet were treated as a unit and kept separate in a cold place for further sampling, which was carried out as soon as possible.

The sampling procedure for individual fish depends of course on the objectives of the study. In the present study the Arctic char were of particular interest, although the entire catch was sampled. (It should be a principle in research to measure as many parameters as possible on every fish killed.)

Each fish was given an individual number. This and the number of the gillnet were recorded on a scale envelope. The species, the gillnet number and the date could then be traced to the testfishing form.

The usual standard procedure included:

(1) Measurement of fork length to the nearest mm. (In Sweden the total length is measured as a standard.)
(2) Measurement of the total weight to the nearest gram.
(3) Sampling of otoliths for ageing. The otoliths were cleaned in water before being put into the scale envelope.
(4) Sampling of scales as an additional means of ageing salmon, brown trout, whitefish, rainbow smelt and other large scaled species. (Avoid putting the scales and the otoliths in the same corner of the envelope.)
(5) Recording of sex and degree of sexual maturation.

There are several systems, but generally a description in words of the appearance of gonads is preferable in order to avoid later misinterpretation. In the present study two systems were used parallel:

At the Drottningholm Institute a system combined after DAHL (1917), and SØMME (1941) is

generally used. The system was later examined and compared with histological observations (FLUMÉ 1978).

The thickness of the male gonads was described according to six stages of maturity (LINDSTRÖM 1962) including ripe and spent males. The females were described in terms of the size of the eggs combined with the proportion of the gonads in relation to the body cavity (LINDSTRÖM 1962). Ripe and spent females were noted as well as the presence of new eggs.

The system modified after VLADYKOV (1956) generally used by the Freshwater & Anadromous Program, DFO, St. John's, is as follows:

Immature	1
Maturing	2
Mature	3
Ripe	4
Spent	5
Spent last, mature present	6
Spent last, mature next	7

(6) The meat color (white, light pink, pink or red), visible external and internal parasites, and morphological characteristics were also noted on the envelope.
(7) For heavy metal analyses some specimens were sampled with acid-washed glass knives on a clean table covered by plastic sheeting. Samples of muscle, liver and kidney were put in separate acid-washed tubes and frozen. (It is of utmost importance to avoid contamination by metal instruments.)
(8) For electrophoretic studies samples of muscle and liver, and whole eyes were taken with a clean scalpel, and kept in numbered test tubes in a freezer.
(9) The gut was preserved in formalin for further stomach and parasite analyses. (Studies of internal parasites of the stomach region are facilitated by digesting gut tissue in acidic Pepsin. This technique is described by MEYER and VIK (1961). An illustrated key to the metazoan parasites of salmonids of insular Newfoundland is given by PIPPY (1970).)
(10) Some specimens were frozen or preserved whole in formalin after sampling, for morphometric measurements and meristic counts.

IV. RESULTS AND DISCUSSION

Standardized testfishing

The repeated standardized use of defined gear, at certain stations and at certain times of the day and the year constitutes the traditional method used in fish biology to collect information about the status, the relative population size and the changes in various fish populations in a system. Information is sought on different ecological characters such as food habits, growth patterns, length and age structures and competitive rank orders.

Testfishing may be directed to a wide range of species or restricted to only one or few species, by using knowledge about the size and/or species selective characters of the gear.

There are several methods of collecting fish; *i.e.* the passive use of gillnets, fences or fyke traps and the active use of trawls, beach seines, electricity or rotenone. They all show important limitations and/or various degrees of selectivity. Most of them are best suited for studies in streams and smaller bodies of water and provide very limited and narrow information about the ecology of lacustrine fish populations. The common use of fyke traps in Newfoundland freshwater surveys has been shown to be valid for littoral populations of brook trout, whereas the catches of Atlantic salmon showed excessive seasonal differences (RYAN 1984).

The best way to collect samples of and ecological information about fast-swimming salmonids inhabiting lakes and larger bodies of water would at present thus seem to be by gillnetting.

Gillnets are easy to handle and are considered to be very efficient. However, comparative studies based on material sampled by gillnets have been thoroughly criticized by several authors due to the selective nature of the method (HAMLEY 1975). Various mathematical approaches are exemplified in McCOMBIE and FRY (1960), McCOMBIE and BERST (1969), HAMLEY (1975) and HAMRIN (1979). Different experimental combinations of multiple mesh sizes have been tried in order to reduce the size-selective restrictions of the gear (MOYLE 1950, WILDE and ROMEO 1951, BERST 1961, HORAK and TANNER 1964, HOUSER and GHENT 1964, GRINSTEAD 1969, TAKAGI and ISHIDA 1971). Other models of gillnets of multiple mesh size from Lundgren's have been used by JOHNSON (1983) in his comprehensive study of Arctic fish populations and by the GREENLAND FISHERIES AND ENVIRONMENTAL RESEARCH INSTITUTE (*e.g.* 1985). Due to concern about the different efficiencies of the various mesh sizes these gillnets are still questioned.

Another major reason for concern is insufficiently designed testfishing programmes where even larger errors and lack of information are due to ecologically incomplete sampling in habitats other than the littoral zone. In order to gain information on the fish species of a lake and their depth distributions, as well as an ecological description of the habitat of each of the species, standardized gillnetting with multiple mesh sizes has to cover various depths and biotopes.

In spite of this there are so far no practical alternatives, and the use of gillnets of multiple mesh size is still important in biological research. Providing that the selectivity of the gillnet and its value for different species can be determined, and that it is used in a standardized way, a Lundgren experimental gillnet of multiple mesh size provides a very practical and highly valid testfishing tool in northern lakes.

Significance of the number of efforts

In a practical attempt to facilitate the comparison of catch data from different lakes MOYLE (1950), assuming a normal distribution, concluded that catch means at probability levels greater than 80 per cent do not appear to be practically feasible. In order to minimize the variation of the standard error to less than 30 % of the catch at a specific depth at least 4 efforts with Lundgren gillnets of multiple mesh size are recommended in Swedish programmes (P. NYBERG and E. DEGERMAN in prep.). In the present study, repeated efforts in depth zones with dense fish populations gave only minor differences in the numbers of specimens belonging to different taxa. This was exemplified in Red Indian Lake. In order to compare the catch data quantitatively between different depths or different lakes we recommend 4—8 efforts with Lundgren gillnets per depth zone.

Saturation and limits of the Lundgren gillnet of multiple mesh size

The small gillnets of multiple mesh size have been subjected to speculations concerning the saturation

Number
of efforts

Catch per effort, weight (kg)

Number of efforts : 139

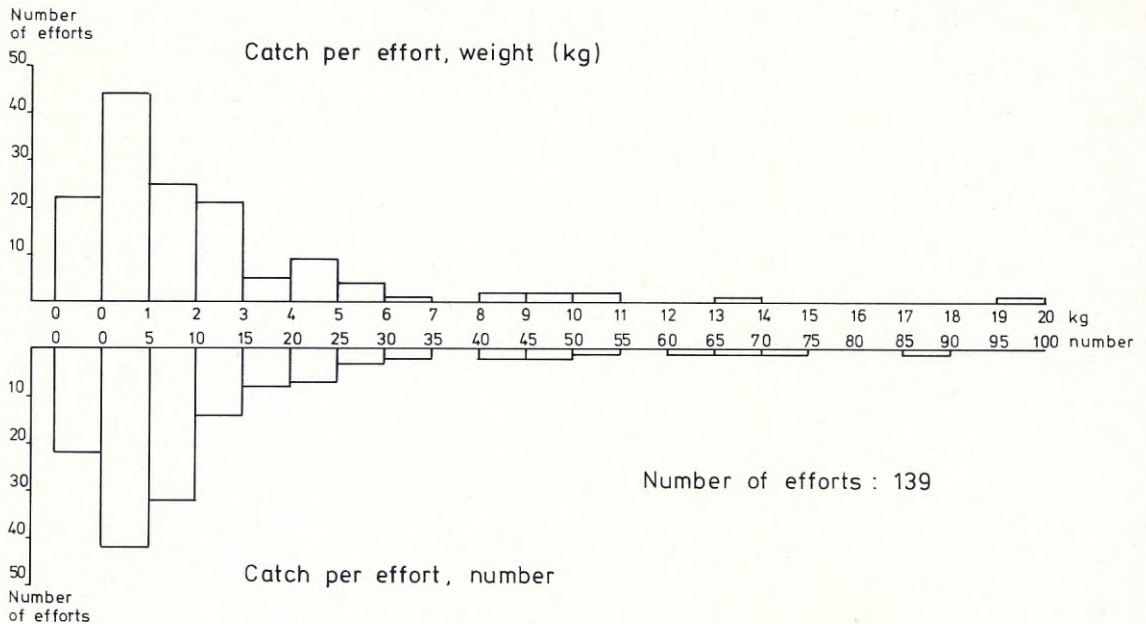Catch per effort, number

Number
of efforts

Fig. 5. Saturation of gillnets shown as weight and numbers of fish caught in individual gillnets of multiple mesh size (10—75 mm) for the entire study.

limit and a possible low limit to the number of fish caught, or the total weight of the catch in a single gillnet per night. However, the catches given by the use of this gear in lakes in the High Arctic (less than 5 kg, Hammar unpubl.), in southern Sweden (less than 6 kg, FILIPSSON unpubl.) and in tropical areas (less than 10 kg in Sri Lanka, ENDERLEIN and WICKSTRÖM pers. comm.) are far greater than the amounts usually caught in exploited alpine lakes of northern Sweden (less than 0.5 kg, FILIPSSON unpubl.). In this study testfishing in unexploited alpine lakes of Labrador gave even larger catches (Fig. 5.). In lakes with white suckers and anadromous Arctic char in the Sand Hill River region, the catch varied between 5 and 13 kg per 24 hour effort. The catch of 18 large Arctic char taken in a single deepwater gillnet weighed more than 19 kg.

Species selectivity

Lundgren gillnets of multiple mesh size have been used in 20 lakes with different ecological and physical characteristics in Newfoundland and Labrador. The gillnets have shown to be efficient for catching Arctic char, brook trout, lake trout,

Atlantic salmon, rainbow smelt and white sucker. In addition three-spined stickleback was represented, and specimens of brown trout (*Salmo trutta* LINNÉ), mottled sculpin (*Cottus bairdi* GIRARD) and winter flounder (*Pseudopleuronectes americanus* (WALBAUM)) were occasionally caught.

In a large number of lakes the catch and the gillnets showed considerable damage caused by eels, and several smaller specimens of salmonids had been partly eaten by the eels. Only one specimen of the American eel (*Anguilla rostrata* (LE SUEUR)) was caught, however, revealing an important restriction of the gear, the problem of quantifying this particular species and coexisting small salmonids.

The gillnet is a passive gear depending to a very large extent on, and perhaps providing a measure of, the activity of the fish. Different species may show different periods of activity in terms of the time of the day as well as the time of the year. The damage caused by the eels might be lessened if the gillnets are checked as early as at dawn. The standardization of the fishing period is consequently selective for certain species.

Since different species have different swimming

BENTHIC GILLNETS
Frequency, %

ARCTIC CHAR
Northern Sweden
1966 – 1985
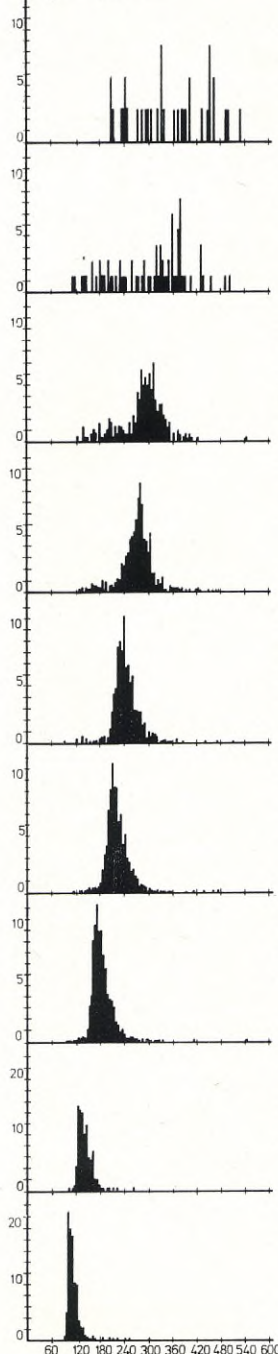
50 mm mesh
n=35
mean length=350
sd=93.1   se=15.7
skewness=0.06

min-max: 205-525

38 mm mesh
n=72
mean length=305
sd=93.4   se=11.0
skewness = -0.25
mode: 382.5
min-max: 114 – 502

PELAGIC GILLNETS
Frequency, %

33 mm mesh
n=298
mean length=284
sd=55.8   se=3.23
skewness = -0.31
mode: 312.5
min-max: 122-540
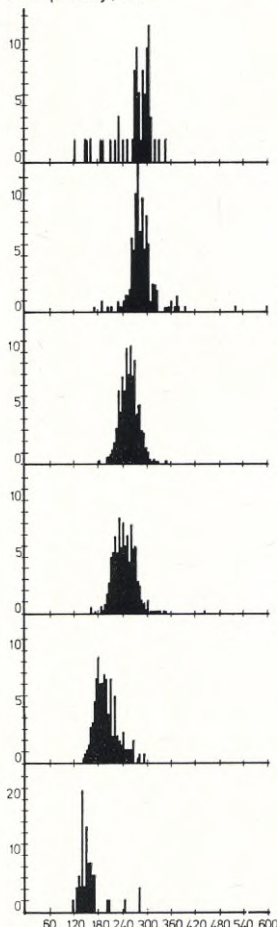
33 mm mesh
n=49
mean length=269
sd=49.8   se=7.12
skewness = -1.34
mode: 307.5
min-max: 120 -345

30 mm mesh
n=544
mean length=270
sd= 44.2   se=1.89
skewness = 0.39
mode: 277.5
min-max: 125 –470

30 mm mesh
n=196
mean length=290
sd=40.8   se=2.91
skewness = 3.05
mode: 282.5
min-max: 170 - 595

25 mm mesh
n=856
mean length=246
sd=34.0   se=1.16
skewness = 1.14
mode: 242.5
min-max: 90 – 510

25 mm mesh
n=473
mean length=256
sd=21.6   se=0.99
skewness = 0.19
mode: 262.5
min-max: 180 –345

22 mm mesh
n=1395
mean length=222
sd = 29.7   se=0.80
skewness = 1. 82
mode: 212.5
min-max : 114 – 470

22 mm mesh
n=518
mean length=243
sd = 27.5   se=1.21
skewness = 1. 03
mode: 232.5
min-max : 160-443

16.5 mm mesh
n=1995
mean length=182
sd = 27.0   se=0.60
skewness = 2. 87
mode: 172.5
min-max: 95 – 540

16.5 mm mesh
n=254
mean length=200
sd=28.8   se=1.81
skewness = 0.79
mode: 182.5
min-max: 141 – 294

12.5 mm mesh
n=185
mean length=143
sd=19.4   se=1.42
skewness = 2.06
mode: 127.5
min-max: 100 – 260

12.5 mm mesh
n=46
mean length=158
sd=34.4   se=5.08
skewness = 2.33
mode: 142.5
min-max:117-281

Total length
class, mm

10 mm mesh
n=530
mean length=112
sd=18.6   se=0.81
skewness = 4. 81
mode: 102.5
min-max: 90 – 300

60   120 180 240 300 360 420 480 540 600

Total length
class, mm

Fig. 6. Length distributions for benthic and pelagic Arctic char caught in gillnets of different single mesh sizes in a pooled sample combining several lakes and years in Sweden.

Mesh size, mm
50 BENTHIC
38
33
30
25
22
16.5
12.5
10

y = 4.78 E.007 X
r = 0.9996
n = 10
p < 0.001

Total length

10   20   30   40   cm

Mesh size, mm
50 PELAGIC
38
33
30
25
22
16.5
12.5
10

y = 3.86 E.007 X
r = 0.972
n = 6
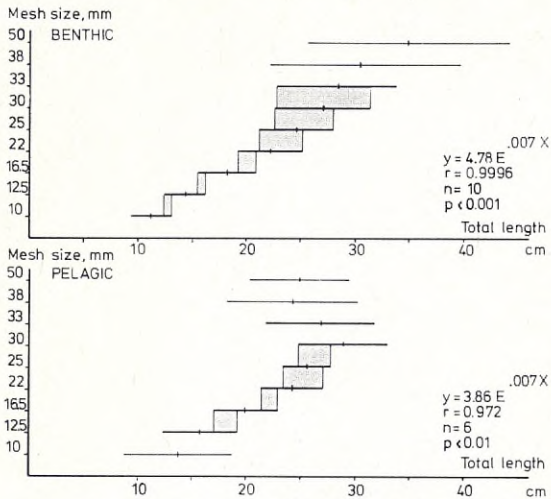p < 0.01

Total length

10   20   30   40   cm

Fig. 7. Graphic relationships of mesh size and mean length with overlapping standard deviations for benthic and pelagic Arctic char as a hypothetical illustration of size selectivity in panels of the Lundgren gillnets of multiple mesh size.

speeds, faster species should encounter a passive gear more frequently than slower species. RUD-STAM, MAGNUSON and TONN (1984) discuss this as a possible explanation for the fact that larger fish are caught more efficiently.

Another major reason for concern is the preference of fish for specific habitats and their movements to and from these habitats. A testfishing programme must therefore consider the division of the different biotopes of the lake between different species. The littoral gillnet is unlikely to catch a pelagic fish or vice versa.

By setting gillnets at an angle to the shoreline there is always a risk of catching unproportionally large numbers of fish species which perform migrations parallel to the shore and unproportionally low numbers of species which migrate between deeper bottoms and the littoral zone. This may be a general fact for migrating anadromous fish and may apply to resident Atlantic salmon and brown trout. In some lakes in this study benthic gillnets were set both parallel to and at a right angle to the shore. Comparisons between single gillnets may show large differences as in Russ' Lake, but when the catches from differently placed gillnets in Butt's Pond were pooled and tested by means of a chi-square test, the species composition showed

no significant difference between parallel and perpendicular nets. Neither was there any difference in the CPUE (catch per unit effort) of single species in the differently placed gillnets in Butt's Pond (Mann Whitney U-test).

As will be shown later on, the inclusion of the 6.25 and 8.0 mm mesh expands the length and age structure of the catch considerably, but it also adds a new species to the catch in shallow water — the sticklebacks. In deeper water and in the pelagic habitat the revised types of gillnet seems to have en important effect on yields and length frequencies of smelt.

Size selection and modal lengths

A comprehensive review with a basic statistical description of various analyses of gillnet selectivity is provided by HAMLEY (1975). Unimodal and accidental bimodal selection curves of different shapes are shown for different species.

However, longterm studies of Arctic populations of the Arctic char have exposed mono-, bi- and trimodal allopatric population structures that are thought to represent a stage of ecological climax (JOHNSON 1980, 1981, 1983). These structures differ from the normally distributed catches characterized as bell-shaped and monomodal, which have been the object of thorough analyses of gillnet selectivity (HAMLEY 1975).

The selectivity of nine of the panels used in the Lundgren gillnets of multiple mesh size were studied in Swedish sampling programmes for Arctic char using standard gillnet gangs. Arctic char caught in the pelagic zone have been treated separately because of their monomorphic and planktivorous character (HAMMAR 1984). The examples (Fig. 6) consist of pooled values from several lakes and years of sampling, and only mesh sizes for which there are a large number of samples are shown. There is a general tendency to obtain a positively skewed sample in the smaller mesh sizes and a negatively skewed sample in the large mesh sizes. This seems to be more pronounced in the benthic samples, probably due to the presence of benthic dwarfs which tangle in the nets by their teeth or fasten due to their rotund form.

KIPLING (1957) showed that a good estimate of the structure of a population can be made by

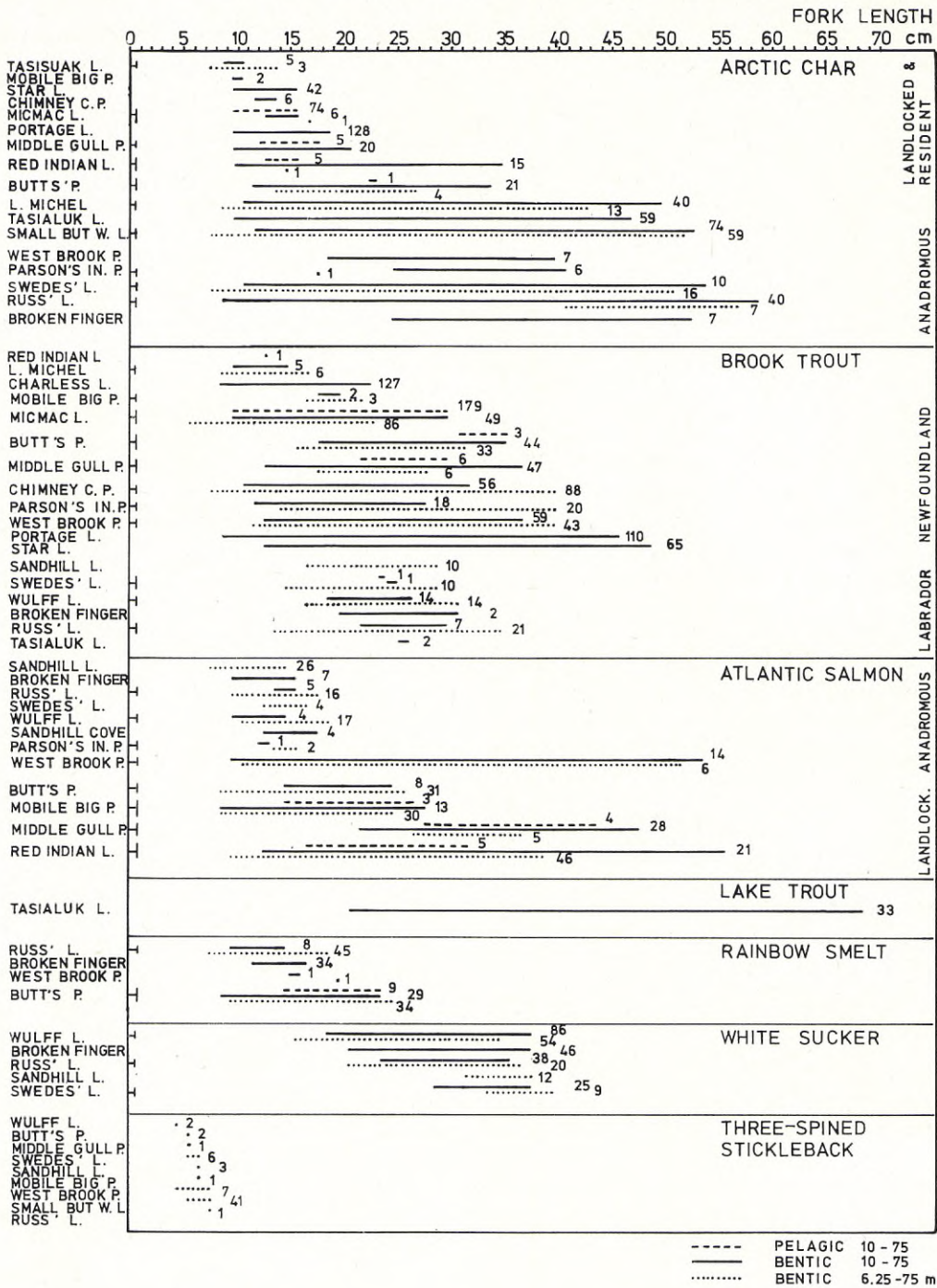Fig. 8. The size range of different species caught in three different types of Lundgren gillnets of multiple mesh size in Newfoundland and Labrador 1984. Number of specimens in the catch is given for Arctic char, brook trout, Atlantic salmon, lake trout, rainbow smelt, white sucker and three-spined stickleback. Dashed lines= pelagic gillnet, 10—75 mm. Solid lines=benthic gillnet, 10—75 mm. Dotted lines=benthic gillnet, 6.25—75 mm.

using multiple mesh sizes where the length frequency distribution of the catch of each mesh overlaps that of its neighbours.

The mean length and the standard deviation for Arctic char in benthic and pelagic catches in a hypothetical gillnet of multiple mesh size are shown graphically (Fig. 7) in order to illustrate the lack of gaps in efficiency between adjacent meshes. The graphs also clearly demonstrate the general increase in the size distribution of benthic Arctic char with increasing mesh size. This may be specific for diverse benthic populations and to a lesser extent the case for unimodal pelagic populations. However, similar studies based on catches of pelagic cisco (*Coregonus albula* LINNÉ) in the Baltic sea showed the sample distribution in single meshes to be very much affected by the presence of strong year classes (O. ENDERLEIN pers. comm.).

By choosing adjacent mesh sizes so that both ascending and descending arms of the selective curve intersect at 60 per cent, a geometrical series with the constant 1.203 is derived (JENSEN 1984). Upon this basis JENSEN (1984) recommends the following combination of multiple mesh sizes for Arctic char in the size range 160—440 mm: 15.0, 18.0, 21.5, 25.9, 31.3, 37.7, 45.7 and 50.3 mm knot to knot.

Although the Lundgren multiple series of 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60 and 75 mm is not strictly geometrical, with a constant of $1.212 \pm .074$, it greatly resembles the corresponding part of the series recommended by JENSEN (1984).

HAMLEY (1975) also emphasizes the risk of an effect on the size-selection range due to early saturation of the specific mesh that in a specific case becomes the optimal one. This is probably an important source of error for gillnets of multiple mesh size, particularly in dense populations where the testfishing period may be too long.

No doubt the gillnet can be improved to fit the structure of a certain fish population in a certain lake. A statistically-constructed gillnet of multiple mesh size to be used for different species in different lakes is, however, more interesting. It is therefore of the utmost importance for geographical and ecological surveys to develop a gear which can be used in a standardized way in many different lakes, as opposed to a gear that

only fits a single, simple population structure. Testfishing in unexploited systems may still reveal unexpected species compositions and size frequencies. The gear used must therefore be as general as possible with regard to size and species selectivity as well as statistically repeatable.

The size selectivity of the 12 or 14 mesh sizes represented in the Lundgren gillnet (Fig. 7) should also be compared with that of the standard gillnet gangs commonly used in Newfoundland. The mesh sizes were 19, 25, 38, 51 and 64 mm in the comprehensive Lower Churchill River Programme (RYAN 1980) and the Red Indian Lake survey (MORRY and COLE 1977). This combination reveals both gaps and very little overlap. A more promising gear with 7 panels ranging from 12.5 to 51 mm was used in Lake Michel (ShawMont Nfld. Ltd. 1982), but in this case all the gangs were set near the surface, with the small mesh sizes near shore.

The size distributions of the catch of different species in different lakes in Newfoundland and Labrador are demonstrated for three different gillnets of multiple mesh size based on the same geometrical series (Fig. 8). The total range includes three-spined sticklebacks as small as 45 mm in the revised gillnet, and lake trout of 685 mm in the ordinary benthic gillnet. The figure exposes the wide size range of the Lundgren gillnets and also reveals biologically different population structures. The latter are not due to the size selectivity of the gillnets, but rather to species interactions and the specific ecological characteristics of the ecosystem.

Arctic char, *Salvelinus alpinus* (LINNÉ)

As pointed out earlier, the Arctic char has a unique ecology due to the existence of allopatric populations with intraspecific complicated structures (JOHNSON 1980, 1983, HINDAR and JONSSON 1982, JONSSON and HINDAR 1982, NORDENG 1983), displaying thermodynamic responses to the environment (JOHNSON 1981, In press). There are even more complex situations in which two or three sympatric populations are known to coexist (ANDERSSON *et al.* 1971, NILSSON and FILIPSSON 1971, NYMAN 1972, 1984, NYMAN and FILIPSSON 1972, KLEMETSEN and GROTNES 1975, 1980, HENRICSON and NYMAN 1976, GYDEMO 1984, HAMMAR
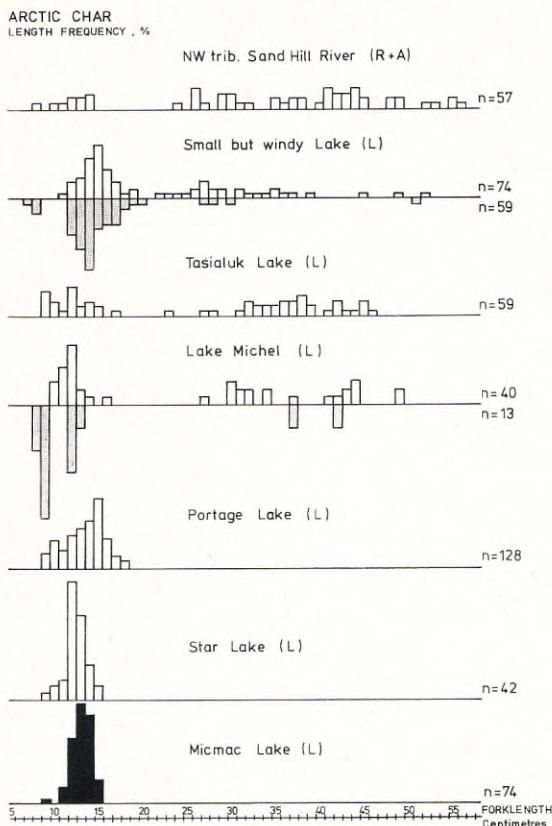
ARCTIC CHAR
LENGTH FREQUENCY , %

NW trib. Sand Hill River (R+A)

n=57

Small but windy Lake (L)

n=74
n=59

Tasialuk Lake (L)

n=59

Lake Michel (L)

n=40
n=13

Portage Lake (L)

n=128

Star Lake (L)

n=42

Micmac Lake (L)

n=74

5   10   15   20   25   30   35   40   45   50   55   FORKLENGTH
Centimetres

BROOK TROUT
LENGTH FREQUENCY , %

Star Lake (L)

n=65

Portage Lake (L)

n=110

Chimney Cove Pond (A?)

n=56
n=88

West Brook Pond (A?)

n=59
n=43

Middle Gull Pond (L)

n=47

Butt's Pond (L)

n=44
n=33

Micmac Lake (L)

n=179

n=49
n=86

Charless Lake (L)

n=127

5   10   15   20   25   30   35   40   45   50   FORKLENGTH
Centimetres

Fig. 9. Size distribution of populations of Arctic char sampled with Lundgren gillnets, 6.25—75 mm benthic (gray), 10—75 mm benthic (white) and 10—75 mm pelagic (black). (R=Resident, A=Anadromous, L= Landlocked.)
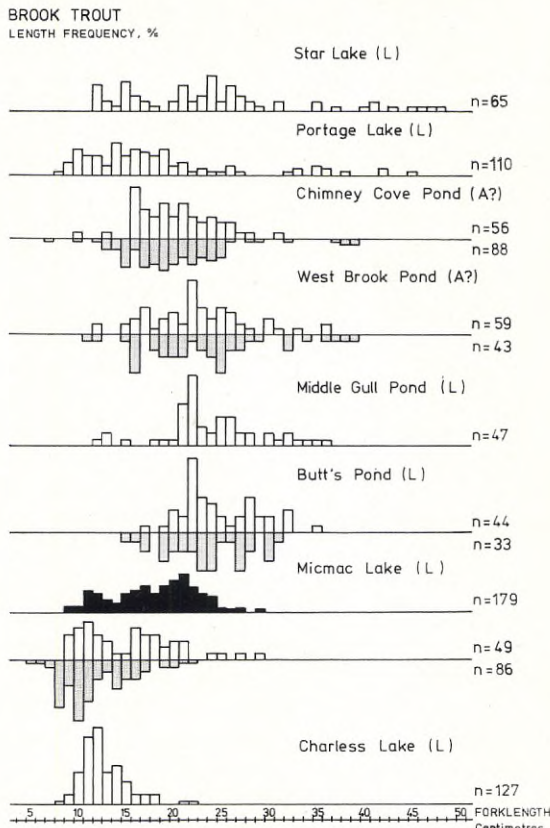
Fig. 10. Size distribution of populations of brook trout sampled with Lundgren gillnets, 6.25—75 mm benthic (gray), 10—75 mm benthic (white) and 10—75 mm pelagic (black). (L=Landlocked, A=Anadromous.)

1984 and KLEMETSEN 1984). Such populations are regarded as sibling species in a number of Scandinavian lakes (SVÄRDSON 1958, 1961, NYMAN *et al.* 1981). The Arctic char is furthermore very sensitive to gillnetting, competition and predation and displays population structures clearly affected by these factors (FILIPSSON and SVÄRDSON 1976).

The wide range of modal lengths and the number of varied population structures is strikingly apparent in some Newfoundland and Labrador lakes (Fig. 8 and 9).

The Arctic char turned out to be more common than expected, and it is probably the dominating species in several lakes in insular Newfoundland. In fact, in this study, the Arctic char was found in all lakes except one, which was of course named Charless Lake.

The Arctic char in "Small but Windy Lake" and Lake Michel may be regarded as allopatric (HAMMAR *et al.* in prep.). In Tasialuk Lake Arctic char coexists with piscivorous lake trout. In Portage and Star Lakes Arctic char is preyed upon by piscivorous brook trout, and in Micmac Lake the Arctic char is considered to be pelagic (HAMMAR in prep.).

The smallest specimen caught in the 6.25—75 mm gillnet was 75 mm and the smallest char in the 10—75 mm gillnet was 81 mm. The largest char caught measured 586 mm. The length range in the pelagic 10—75 mm gillnet was 95—223 mm.

Brook trout, *Salvelinus fontinalis* (MITCHILL)

This species has a broad geographical and ecological distribution in the province (SCOTT and
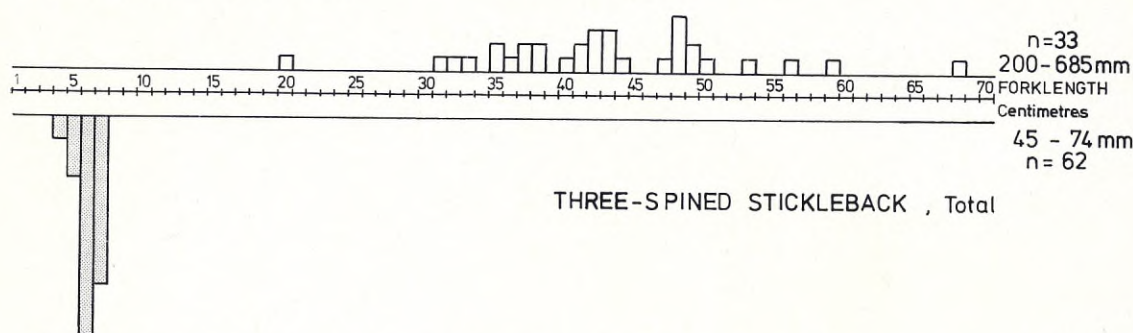
LAKE TROUT, Tasialuk Lake

Fig. 11. Size distribution of populations of lake trout and three-spined stickleback sampled with Lundgren gill-nets, 6.25—75 mm benthic (gray) and 10—75 mm benthic (white).

CROSSMAN 1964). It resembles the Arctic char in terms of morphology and ecology. The variety in length frequencies is illustrated by anadromous populations, the piscivorous populations of large brook trout in Portage and Star Lakes, and by populations in ecosystems where there are more or less complicated interactions with other species (HAMMAR in prep., Fig. 8 and 10).

The smallest specimens caught were 50 mm in the 6.25 mm mesh, 83 mm in the 10 mm mesh, and the largest specimen was 486 mm. In Micmac Lake which has a dense population (HAMMAR in prep.), the length of brook trout in the large pelagic catch ranged between 97 and 295 mm.

Lake trout, *Salvelinus namaycush* (WALBAUM)

Lake trout were caught only in Tasialuk Lake, Labrador, together with large Arctic char (HAMMAR and SKÖLD in prep.). The total length range in the 10—75 mm gillnet was 200 to 685 mm, and almost all specimens were longer than 300 mm (Fig. 11). The maximum catch in a single gillnet was 5 specimens and 5.6 kg. On one occasion a large lake trout was found to have been almost totally eaten by something, in a gang of three gillnets containing another 16 large specimens of both species. Could this be an example of lake trout cannibalism or did we in fact miss the wonderful sight of a happy otter?

Atlantic salmon, *Salmo salar* LINNÉ

Atlantic salmon were caught in littoral regions as well as in the pelagic zone close to the surface.

In Sand Hill River only smolt and parr were caught, and the size range resembles that of the smolt caught by flyfishing (Fig. 12). The figure also displays the structural differences between the anadromous and the landlocked salmon (Ouananiche) in the other bodies of water. The smallest specimens caught were 76 mm in the 6.25 mm mesh and 85 mm in the 10 mm mesh. The largest specimen caught was a 556 mm long ouananiche in Red Indian Lake.

Rainbow smelt, *Osmerus mordax* (MITCHILL)

The use of very small mesh sizes seems to be crucial for the size of the catch and the length frequency of smelt (Fig. 13), due to the inclusion of younger age groups. Large numbers were caught in the Northwest Tributary to Sand Hill River where anadromous migration is documented (ANDERSON 1985). A spectacular difference may be noted between Russ' and Broken Finger Lakes. A pulse of 5+ fish constitutes nearly 80 per cent of the catch in the second lake (HAMMAR unpubl.). Most of these specimens were severely damaged in the nets by eels and are thus underrepresented in the figure.

The 6.25 mm mesh seems to be efficient for 90 mm smelt, *i.e.* 1+ fish, but it caught specimens as small as 74 mm. The 10 mm mesh caught specimens down to 88 mm and seems to be efficient for 100—110 mm smelt. Larger and older specimens are often caught by their conspicuous teeth. The largest smelt caught in Butt's Pond was 245 mm in length.
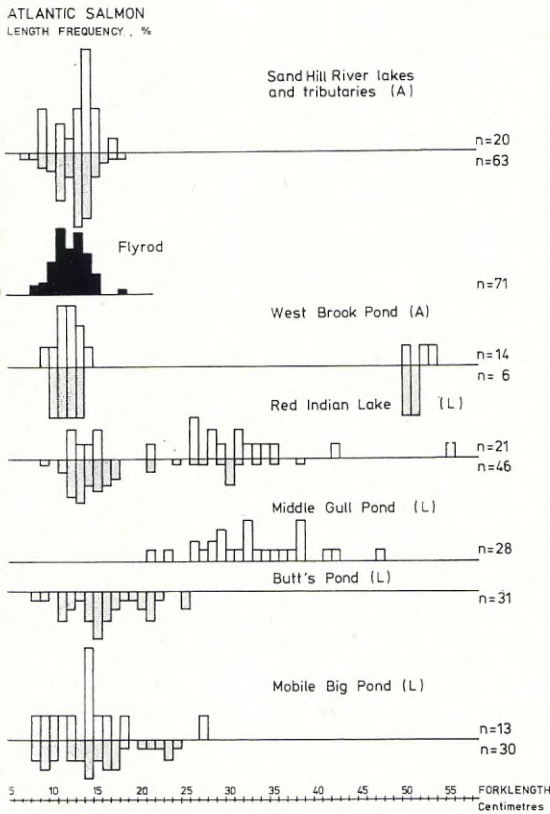
RAINBOW SMELT
LENGTH FREQUENCY, %

ATLANTIC SALMON
LENGTH FREQUENCY, %

Fig. 12. Size distribution of populations of Atlantic salmon sampled with Lundgren gillnets, 6.25—75 mm benthic (gray) and 10—75 mm benthic (white). (A = Anadromous, L = Landlocked.)

Fig. 13. Size distribution of populations of rainbow smelt sampled with Lundgren gillnets, 6.25—75 mm benthic (gray), 10—75 mm benthic (white) and 10—75 mm pelagic (black). (R = Resident, A = Anadromous, L = Landlocked.)

White sucker, *Catostomus commersoni* (LACÉPÈDE)

Surprisingly large numbers of white sucker were caught in Sand Hill River, Labrador. The total length range is 159 to 391 mm (Fig. 14). The figure exposes both similarities and differences in the length structures. The interesting pattern in Swedes' Lake is due to the different depths at which the gillnets were set. The ordinary gillnets were located on deeper bottoms (5—11 m), whereas the revised gillnets were used in the littoral zone (1 m). Since the sucker spawns in running waters and spends parts of its life cycle in different habitats, the differences in modal lengths may be an effect of size or age segregation within the river system (HAMMAR et al. in prep.).

Three-spined stickleback, *Gasterosteus aculeatus* LINNÉ

Armed with both dorsal and ventral spines, the sticklebacks became tangled in the smallest mesh size in the revised gillnets. In "Small but Windy Lake" the catch was considerable after some rough weather. The distribution shows a negatively skewed pattern (Fig. 11) with the fork length ranging from 45 to 74 mm.

WHITE SUCKER
LENGTH FREQUENCY, %

Swedes' L.

n=9
335-391 mm
280-378 mm
n=25

Broken Finger &
Russ' L.

n=20
208-369 mm
201-372 mm
n=84

Sand Hill L.

n=12
317-374 mm

Wulff L.

n=54
159-342 mm
185-379 mm
n=86

16 18 20 22 24 26 28 30 32 34 36 38 40   FORKLENGTH
Centimetres
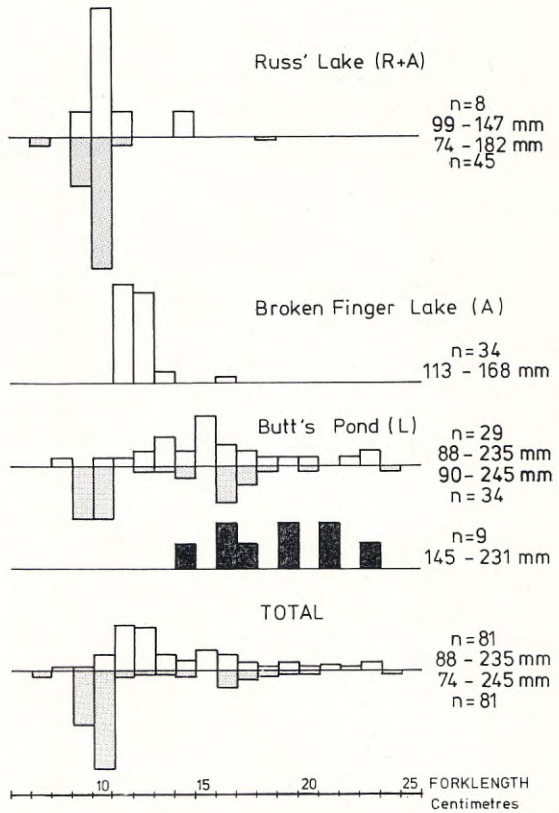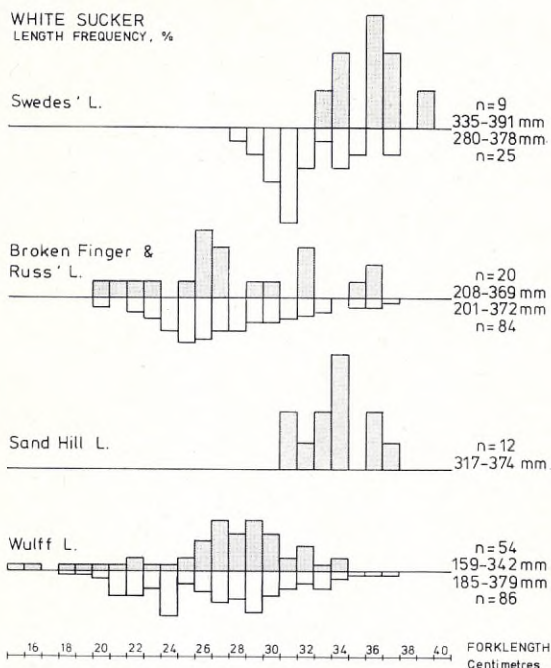
Fig. 14. Size distribution of populations of white sucker sampled with Lundgren gillnets, 6.25—75 mm benthic (gray) and 10—75 mm benthic (white).

V. EXAMPLE OF A TESTFISHING PROGRAMME IN RED INDIAN LAKE

Red Indian Lake

Red Indian Lake is located in the upper part of Exploits River in central Newfoundland. It has by far the largest watershed in insular Newfoundland. It is surrounded by coniferous woods, vast boglands and the Annieopsquotch Mountains. Red Indian Lake is the second largest lake (18.121 ha) on the island, and is impounded for hydroelectric and logging purposes. Major tributaries are Lloyds River, Victoria River and Shanadithit Brook. The lake is very deep (maximum depth 146 m, mean depth 24.7 m) and is inhabited by only four species of fish — landlocked Atlantic salmon (Ouananiche), brook trout, three-spined stickleback and, in deep waters, relict Arctic char (MORRY and COLE 1977).

Material and methods

From July 4—11, 1984, gillnets of multiple mesh size were used in the upper part of the lake to investigate the depth distributions of the different
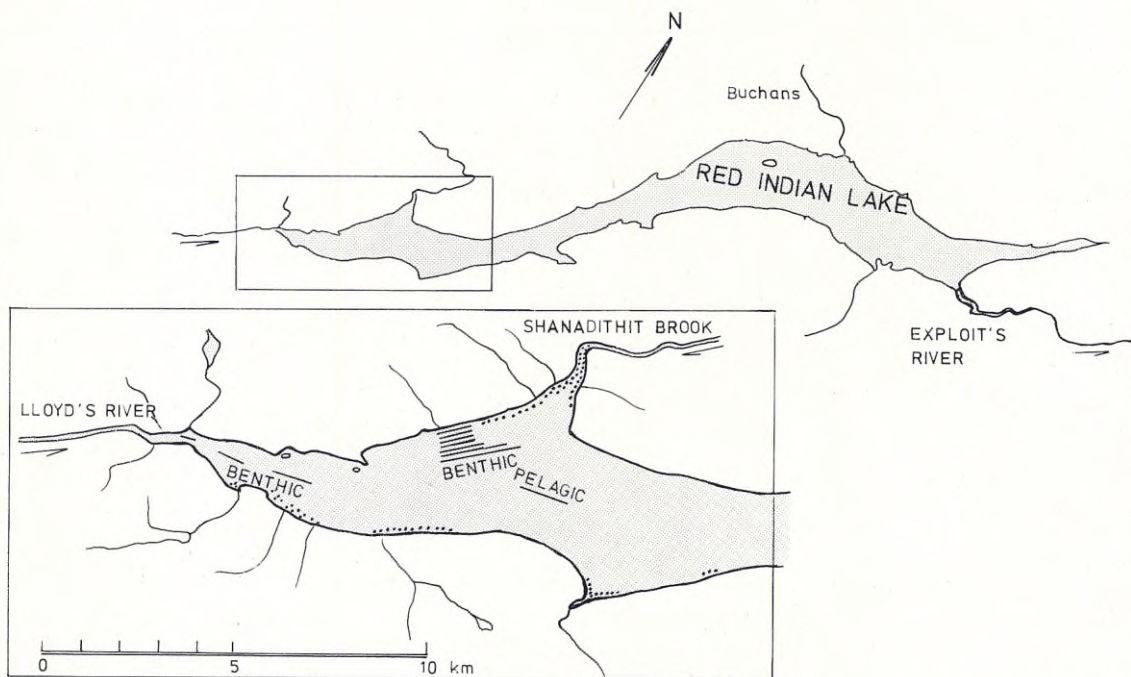
Fig. 15. Red Indian Lake with location of the benthic and pelagic testfishing stations sampled as an example of the technique described in the paper.

Table 3. *Catch data for Red Indian Lake. CPUE is expressed as numbers and grams per gillnet and 24 hours.*

| Depth | Atlantic salmon | | | | | | Brook trout | | Arctic char | |
| | Adults | | Smolt | | Parr | | | | | |
	n	g	n	g	n	g	n	g	n	g
Parallel to shore:										
2— 2 m	10.0	2165	7.2	256	24.4	542	1.4	26	0	
2— 2 m	10.0	2887	2.9	133	11.5	301	0		1.4	30
5— 5 m	1.4	218	0		4.3	79	0		0	
5— 5 m	2.9	777	0		1.4	37	0		0	
10—10 m	2.9	3023	0		0		0		1.4	33
10—10 m	1.4	142	0		0		0		1.4	26
19—19 m	1.3	302	0		1.3	43	0		1.3	24
19—19 m	0		0		0		0		2.6	34
19—19 m	0		0		0		0		2.6	21
19—19 m	0		0		0		0		1.3	24
20—20 m	0		0		0		0		0	
20—20 m	1.4	282	0		0		0		1.4	13
30—30 m	0		0		0		0		0	
30—30 m	0		0		0		0		0	
30—30 m	0		0		0		0		0	
30—30 m	0		0		0		0		0	
31—31 m	0		0		0		0		1.3	752
31—31 m	0		0		0		0		0	
31—31 m	0		0		0		0		0	
31—31 m	0		0		0		0		0	
42—45 m	0		0		0		0		1.4	20
45—45 m	0		0		0		0		0	
45—45 m	0		0		0		0		0	
45—48 m	0		0		0		0		0	
47—47 m	0		0		0		0		0	
At an angle to the shore:										
4— 4 m	3.9	1243	0		1.3	45	0		0	
5— 5 m	0		0		0		0		3.3	41
5— 5 m	5.0	1889	0		0		0		1.7	25
9—10 m	0		0		0		0		0	
10—10 m	1.7	642	0		0		0		0	
10—11 m	0		0		0		0		0	
In the pelagic zone:										
0— 6 m	2	424	0		1	32	0		4	104
0— 6 m	2	367	0		0		0		0	
12—18 m	0		0		0		0		1	16
24—30 m	0		0		0		0		0	
24—30 m	0		0		0		0		0	
54—60 m	0		0		0		0		0	

fish species in the littoral, profundal and pelagic zones (Fig. 15).

Benthic gillnets were set at 2, 5, 10, 18—20, 30—31 and 42—48 metres depth parallel to the northern shore, and at 4—11 metres at an angle from the inlet of Lloyds River. The pelagic gang was anchored over 70 metres and set at 0—6, 12—18, 24—30 and 54—60 metres depth.

The surface temperature varied between 7.0 and 11.5 °C and a weak thermocline was found at about 50 metres depth. The transparency was between 5.1 and 6.1 metres.

Results

The results of the catch per unit effort (CPUE) is expressed as numbers and weights in grams per gillnet and 24 hours (Table 3).

The testfishing programme was carried out in

an exposed part of the lake. No sticklebacks were found, and only one brook trout was caught. Salmon were found down to depths around 20 metres but dominated in the littoral zone. Salmon were also caught in the upper layer of the pelagic zone. Arctic char were caught between 2 and 45 metres and also in the pelagic zone down to 18 metres depth. This is the only species found below 20 metres depth along the bottom.

For further comparative analyses the catch has to be pooled for larger depth zones *e.g.* 0—10, 10—20 m and deeper. There were no apparant differences between gillnets set parallel to or at an angle to the shore.

All specimens were sampled. The results of analyses of the age structure, food habits and genetic variation in the Arctic char caught will be presented elsewhere (HAMMAR in prep.).

Discussion

The catch figures are small compared to the results from other lakes (HAMMAR in prep.), indicating a low density of fish. This rhymes well with earlier conclusions (MORRY and COLE 1977). These authors, who collected their fish in standard gillnets in shallow water, discussed the scarcity of the Arctic char, but speculated that char might be more common in deeper water.

It would now seem that ouananiche and Arctic char are both dominant and segregate in the lake. In fact Arctic char was discovered to be the dominant species in Portage and Star Lakes, two headwaters of Red Indian Lake (HAMMAR unpubl.). Arctic char is furthermore found in Victoria Lake (PIPPY 1966) and Lloyd's Lake (DEMPSON 1985). Electrophoretic studies showed that dwarfed Arctic char were also resident in Lloyd's River, the major tributary (HAMMAR unpubl.).

VI. RECOMMENDATIONS

Large areas of the Province of Newfoundland and Labrador which are covered by numerous lakes and streams are still unexplored in terms of their fish fauna. These areas of grand natural resources are invaluable not just to Man but as an integral part of the nature of Newfoundland.

Insular Newfoundland and Labrador have also been subjected to very large environmental changes in terms of the impoundment and redirection of salmon rivers. Today, large water systems are still being continuously subjected to exploitation and irreversible ecological injury. In addition, the expanding compensatory salmonid enhancement programme includes massive stocking of anadromous salmon in lakes above the salmon region, leading to increased competition with and predation on natural populations of Arctic char and brook trout.

With the above-mentioned facts as a background to the present sombre perspective, we would like to emphasize the importance of continued general biological surveys and monitoring in the freshwaters of interior Newfoundland and Labrador.

We would furthermore like to recommend the Federal and Provincial Fishery authorities in Eastern Canada to consider using the testfishing programme design, the described techniques and the Lundgren modern gillnets of multiple mesh size in future surveys, and to demand that consultant groups commissioned to do biological investigations also use these methods.

VII. APPENDIX — INSTRUCTIONS FOR PELAGIC GILLNETTING

When the buoys, the lines and the two sections of gillnet are prepared and ready to be used, the gear should be set at a time of the day which is convenient for the checking and lowering of the nets during the next few days.

(1) The first heavy anchor is connected to two ropes, one at each "end". The first one slightly longer than the water depth is tied to the "arms" and connected to the flag buoy. The other rope is tied to the "eye". The anchor is thrown overboard while the boat is slowly drifting with the wind and the second rope, which is three times the water depth, is played out. Make sure the anchor has dug into the bottom.

(2) The other end of the second rope is connected to the headline of the first section, preferably the one with coarser meshes, and a larger buoy is tied to the same end.

(3) While setting the first section of the gillnet, two smaller floats are connected to the headline at distances 1/3 and 2/3 of the section's length.

(4) The headline end of the first section is tied to the second section and a medium-sized buoy with a prepared line is connected. The second section is set in the same way with another two smaller floats attached.

(5) The end of the headline of the entire gillnet is now tied to another long rope three times the waterdepth as well as to a large red buoy and the boat is allowed to drift with the wind or driven slowly. Connect the end of the rope to the "eye" of the second anchor and the last flag-buoy rope to the "arms".

(6) The last step requires heavy gloves and strong arms. When the rope between the gillnets and the second anchor has been played out, the anchor is allowed to hang just over the side of the boat and the flag-buoy line is kept taut, while the outboard engine is used to straighten the entire gear as much as possible.

(7) When this is done and all the buoys form a straight line the power of the engine is reduced slightly and the anchor is allowed to sink very slowly while releasing the last rope metre by metre. The anchor has to reach the bottom while the entire gear is stretched as much as possible before the last flag-buoy is thrown overboard with the usual salute of success.

When the gear is set between the surface and 6 metres depth it has to be clearly marked with flags since it is dangerously exposed to any passing boats. These flags are preferably attached to the two large anchor buoys furthest away from the gillnets in order to minimize any tendency to affect the fish in the surface layer.

The next day, 24 hours later, the procedure is repeated in reverse. If the food habits of the fish caught is one of the major parameters of interest the gillnet should of course be examined more frequently. The gillnets are simply checked and cleaned while being hauled up into the prow in such a manner that they can be set again by backing the boat.

(1) Hauling in the long ropes against the wind requires gloves. Let the ropes fall into the bottom of the boat. The lee flag-buoy is picked up first and the attached anchor hauled onboard. From now on the ropes have to be kept in perfect order in the bottom of the boat.

(2) The first large buoy attached to the gillnet is untied and kept astern.

(3) The gillnet is hauled up into the prow by two persons, one pulling the headline and the other the sinkline. The net is laid down in perfect order in folds. Meanwhile the fish are removed and put into bags.

(4) The small floats have to be kept in the water until the section of the headline to which the float is connected is brought onboard. The knot on the float is untied and the line is checked so it will roll out another 6 metres when setting the net again. The floats are placed in order along the net in the prow with the lines loosely coiled in the sections of the gillnets where they belong.

(5) The entire gear is laid in folds in the boat, and the line of each float is released another 6 metres until the second large red buoy is reached.

(6) A rope of 6 metres is added to the buoy-line and the boat is allowed to drift backwards while the gillnets are set overboard again.

(7) Each float is thrown overboard on the same side (lee) of the boat, when the section of the headline to which the float is attached to is leaving the boat.

(8) The first large buoy is connected with a 6 metres of rope and tied to the headline end.

(9) From now on the procedure is identical to the previous description of the straightening out of the gear and the placing of the anchor on the bottom.

If everything is in order the headline of the gear will be 6 metres below the surface and the stretched gillnet will catch pelagic fish between 6 and 12 metres depth (Fig. 4).

The gear is lowered in the same way at 6 metre intervals almost all the way down to the bottom. In very deep lakes depth intervals of 12 metres may be chosen instead. This has to be decided in advance, when preparing the float and buoy lines.

VIII. APPENDIX — CHECK LIST OF EQUIPMENT

Boat:

Outboard engine
Repair kit for engine
Extra spark plug
Pressure tank
Gas tank with extra gas
Outboard oil
Oars
Oar-locks
Scoop
Funnel

Benthic gillnets:

Gillnets
Baskets (2)
Floats, 2 m (2)
        6 m (2)
       12 m (2)
       18 m (2)
       25 m (4)
       50 m (4)
Buckets
Numbered tags for
identification of the
catch in each net

Sampling:

Buckets
Plastic bags, many sizes
Measuring board
Scales (battery)
Knives
Scalpel
Tweezers
Scissors
Petri dish for otoliths
Scale envelopes
Pencils
Markers, black and red
Rubber bands
Boxes for envelopes
Gauze cloth for stomachs
Tags with numbers
String
Containers for
preservation
Formalin, 37 %
Basin
Dish brush
Paper towels

Rubber boat:

Outboard engine
Repair kit for engine
Extra spark plug
Pressure tank
Gas tank with extra gas
Outboard oil
Oars
Oar-locks
Scoop
Funnel
Aluminum floorboard
Pump
Repair kit for rubber boat
Extra valves

Pelagic gillnets:

Gillnets
Baskets (2)
Large buoys (2)
Small flag buoys (2)
Floats, prepared with
lines (1.5 mm) (5)
Anchors (2)
Ropes, 5 mm, braided
2×250 m (for anchors)
2×100 m (for flags)
2×100 m (for buoys)
Buckets

Camp:

Table with chairs
Boxes with handles for transportation
Tent and poles
Sleeping bag
Foam
Stove
Fuel
Pots
Frying pan
Plate, mug, utensils
Aluminium foil
Cooler
Buckets
Kerosene lamp with extra kerosene
Flashlight
Propane lamp with extra mantels
Backpack
Axe, hammer, saw,
pliers and nails
Tape, ruler, calculator
Paper towels
First Aid kit

Personal equipment:

Life jacket
Raingear
Rubber boots or
waders
Gloves
Sweater
Camera in water-
proof bag
First Aid kit

Instruments:

Plastic container
Shoulder bag with
testfishing form,
pencils,
knife (stainless
steel),
thermometer and
maps
Echo sounder
Plumb line
Plankton net
Bottles with buf-
fered formalin
Secchi disc
Thermistor or
water-sampler
with messenger

IX. ACKNOWLEDGMENTS

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Effects of Eutrophication on Fish Communities with Special Reference to the Baltic Sea — a Literature Review

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ABSTRACT

Discharges of nutrients to the Baltic Sea have increased considerably, from a calculated 10,000 tonnes of phosphorus and 300,000 tonnes of nitrogen annually at the end of the 19th century to around 80,000 and 1,200,000 tonnes respectively today. This has resulted in higher concentrations of phosphate and nitrate. The oxygen content has decreased in the deep waters and anoxia occurrs frequently. The biomass of benthic fauna below the halocline has decreased significantly since the 1920s, while it has increased above the halocline. It is not known to what extent this development has affected the Baltic fish communities. In analogy with fish communities in lakes and other marine areas it is, however, reasonable to assume that they have been influenced. Several authors claim that the increased fish catches in the Baltic result, at least partly, from eutrophication. Enhanced growth and changed species composition have also been reported. Data from archipelago areas indicate that the effects of eutrophication on the fish are similar to those observed in polluted lakes.

I. INTRODUCTION

The effects of eutrophication on fish have been inferred mainly from observations and experiments in lakes and ponds. This is not to say that eutrophication does not affect marine species, but rather that the effects are more difficult to study in marine environments. The water mass in lakes and ponds is, by comparison, usually more limited and hence easier to study in detail. It has also been possible to perform large scale experiments and compare numerous bodies of fresh water. In marine environments these possibilities are greatly restricted. In addition, the smaller water mass of lakes means that eutrophication proceeds much faster and is thus easier to study. In this rewiev, special reference is given to observed and suggested effects of eutrophication on fish in the Baltic Sea.

The Baltic, one of the world's largest estuaries, is surrounded by highly developed countries. It has been estimated that about 75 million people live in its drainage area. Man's activities in and around the Baltic are now influencing the sea in many ways. Annually, almost 1 million tonnes of fish are caught, which may have resulted in over-fishing of stocks (THUROW 1984). Toxic substances, such as DDT and PCB, have almost exterminated the white-tailed eagle and seals (LEPPÄKOSKI 1980). The discharge of nutrients has increased consid-erably, from a calculated 10,000 tonnes of phos-phorus and 300,000 tonnes of nitrogen annually at the end of the 19th century to around 80,000 and 1,200,000 tonnes respectively today (LARSSON et al. 1985).

This increase in the loading of nutrients is, at least partly, responsible for a considerable increase in concentrations of phosphate and nitrate in the Baltic water (e.g. NEHRING et al. 1984). The ecological consequences of these increases have been discussed in a number of articles, some of which are referred to in this paper. The most significant change probably related to this process of eutrophication is the decrease in oxygen content and the frequently occurring anoxia in the deep waters. As a result, there has been a considerable decrease in the biomass of benthic fauna below the halocline since the 1920's. During the same period, the benthic fauna above the halocline has clearly increased (CEDERWALL and ELMGREN 1980). These authors have suggested an increased pelagic pri-mary production to explain the changes. For a general discussion of eutrophication in the Baltic, see LARSSON et al. (1985).

In 1982, the National Swedish Environment Protection Board initiated a program to assess the eutrophication problems in the Swedish marine environments. The result was a number of reports, covering both hydrodynamic and biological aspects,

summarized in ROSENBERG (1984). This article is based on the report on the effects of eutrophication on Baltic fish populations. It has been my ambition to compile relevant information on the Baltic fish fauna, and to interpret these on the basis of some generally accepted ecological processes. To understand and explain which mechanisms may cause the observed changes, it is necessary to first discuss the importance of fish for ecosystem structure and nutrient recycling, as well as the general effects of eutrophication on fish.

II. THE STRUCTURING EFFECTS OF FISH PREDATION

It may seem rather far-fetched to consider the structuring effects of fish predation in a report dealing with eutrophication. This is, however, not the case, since the trophic structure of a water body can be of central importance for its production. BROOKS (1969) sums this up in the sentence "Thus, in both artificial enrichment and natural maturation there is reason to believe that a primary effect of chemical enrichment has been an alteration in the populations of planktivorous fish and that this change has in turn affected the composition of the zooplankton".

The importance of fish predation on the structure of zooplankton populations has been elucidated through comparisons of lakes and ponds with and without fish populations. Changes in the zooplankton community following the introduction of fish in previously fish-free waters have been studied, as have the differences between zooplankton communities in lakes with different fish populations. Relatively firm conclusions have been reached: fish predation can drastically change the size structure and species composition of a zooplankton population. Large species can be almost eliminated, while the proportion of small species increases. Sensitivity to predation can vary considerably between species of equal size, or within one and the same species. Pigmentation or eggs may make certain individuals more conspicuous, exposing them to heavier predation than other prey of the same size. The literature dealing with the effects of selective fish predation on the structure of zooplankton communities is extensive and

therefore the following are given as relevant examples: HRBACEK 1962, BROOKS and DODSON 1965, GALBRAITH 1967, HALL *et al.* 1970, HURLBERT *et al.* 1972, NILSSON 1972, STENSON 1972, 1976, 1978 a, b, NILSSON and PEIJLER 1973, LOSOS and HETESA 1973; ZARET and KERFOOT 1975, ANDERSSON *et al.* 1978, LANGELAND 1978, 1982, STENSON *et al.* 1978, O'BRIEN 1979, HENRIKSON *et al.* 1980 a, b, LEAH *et al.* 1980, ZARET 1980, HURLBERT and MULLA 1981. According to GRAY (1982), on the other hand, predation is of structuring importance only in small waters, and not in seas or large lakes. This is, however, contradicted by results presented by WELLS (1970), which indicate that alewife (*Alosa pseudoharengus* WILSON) predation influenced the zooplankton community in Lake Michigan.

To explain why large species of zooplankton dominate in fish-free lakes, BROOKS and DODSON (1965) suggested that larger species were able to out-compete smaller species (BROOKS 1969; HALL *et al.* 1976 and GOULDEN and HORNIG, 1980 for possible mechanisms). This theory was later questioned by DODSON himself. The alternative explanation proposed (DODSON 1974) was that invertebrate predators (*e.g.* insect larvae and carnivorous zooplankton) are also controlled by fish predation. In the absence of fish these predators can build up large populations which, in contrast to fish, prey mostly on small planktonic animals. Consequently, in lakes devoid of fish, small zooplankton become rare while larger species escape predation and can develop dense populations (DODSON 1974; DODSON *et al.* 1976, HALL *et al.* 1976, STENSON *et al.* 1978, LYNCH 1979, ERIKSSON *et al.* 1980, HENRIKSON *et al.* 1980 b). It should be stressed, however, that the general importance of fish predation compared to invertebrate predation is still debated (GLIWICZ *et al.* 1978, LANE 1979, 1981, WURTSBAUGH *et al.* 1981).

That predation and competition can be of decisive importance for the development of littoral hard bottom communities has been discussed by, among others, CONNELL (1961 a, b, 1972) and PAINE (1969). The significance of fish predation for the development of benthic communities is, however, less well understood than for pelagic systems. An important reason for this is that vegetation and/or bottom sediment make benthic

systems more complex than pelagic ones, which makes studies of species interactions more difficult.

Comparisons between fresh waters with and without fish, studies of changes caused by exclusion of fish from certain areas of lakes and investigations of effects of stocking waters with fish, all show that fish predation can have a considerable effect. Both the biomass and the production of the benthos, as well as the species composition, can be influenced (BALL and HAYNE 1952, HAYNE and BALL 1956, BERGLUND 1968, HALL *et al.* 1970, ANDERSSON *et al.* 1978, MORIN 1984). THORP and BERGEY (1981), however, argue that fish predation is not of critical importance for the benthos on shallow soft bottoms in lakes.

In marine environments, the effects of fish predation have been studied mainly through aquaria experiments, comparisons of benthic communities in different areas and through field experiments using cages to enclose or exclude predators. Some of these studies indicate that fish predation can be of great importance for the composition of benthic fauna (*e.g.* BLEGVAD 1928, VIRNSTEIN 1977, VAN DOLAH 1978, PETERSON 1979, NELSON 1979, 1981, WALLERSTEIN and BRUSCA 1982), while other studies find no such effects (BERGE and VALDERHAUG 1983, WARD and FITZGERALD 1983). ROBERTSON (1984) found that where vegetation was sparse, predation by fish structured the macrobenthos, while in densely vegetated areas it was less significant.

Attempts at controlling predation by fencing off certain areas in a water body with cages etc. can be difficult to interpret. The cage itself can influence the results. In addition, the cages often exclude only the largest predators while smaller predators (*e.g.* small fish and invertebrates) are free to enter. The cages may then act as a shelter for these small predators which therefore can increase in number and strongly influence results (VIRNSTEIN 1978, ARNTZ 1981, SCHMIDT and WARNER 1984). Another difficulty which arises in evaluating the results of cage studies is that data which show the importance of predation are often presented in the literature, whilst those which do not indicate any influence are more seldom published (PETERSON 1979). One result of both comparative studies in the field and cage experiments is, however, that those species which

react to changes in predation pressure are often those which under normal circumstances are exposed to heavy predation (BLEGVAD 1928, HAYNE and BALL 1956, VIRNSTEIN 1977, PETERSON 1979).

The significance of fish predation for the structure of pelagic and benthic communities in the Baltic is poorly known. The selective predation of planktivorous Baltic fish (SANDSTRÖM 1980, ENDERLEIN 1981, RAJASILTA and VUORINEN 1983) suggests, however, that it may be important for the structure of the zooplankton community. Indications that this may indeed be the case have been obtained by VUORINEN *et al.* (1983).

Selective predation by fish on benthic animals in the Baltic has been described by ARNTZ (1978, 1980). He found no general correlation between the density of benthos-feeding fish and the abundance of their prey. ARNTZ (1980) concluded that although the fish consume a considerable share of the benthic production in the western Baltic, the variations in benthos are mainly caused by factors other than fish predation.

In a study of particular interest from the point of view of eutrophication, L.-E. PERSSON (1981) maintained that the increase in the benthic macrofauna of the Baltic during the last fifty years had been caused by decreased fish predation. As proof of the decrease in fish predation he pointed to catch statistics and growth data for flatfish from the southern Baltic. These show that increased fishing pressure in the counties of Blekinge and Kristianstad at the beginning of the 1920's initially resulted in greatly increased catches, but that these decreased after about ten years (Fig. 1). Concurrently with these catch changes, growth of flatfish increased. This was interpreted as showing that before the increase in fishing, the area was populated with stunted fish. Heavy fishing pressure reduced these populations, resulting in decreased competition for food and increased growth rates. L.-E. PERSSON (1981) suggested that the decline in the flatfish population resulted in decreased predation on the bottom fauna, which could offer an alternative to eutrophication to explain the increase in benthos reported by CEDERWALL and ELMGREN (1980). However, according to the catch statistics available for Sweden (Sveriges officiella statistik, Jordbruk med binäringar,
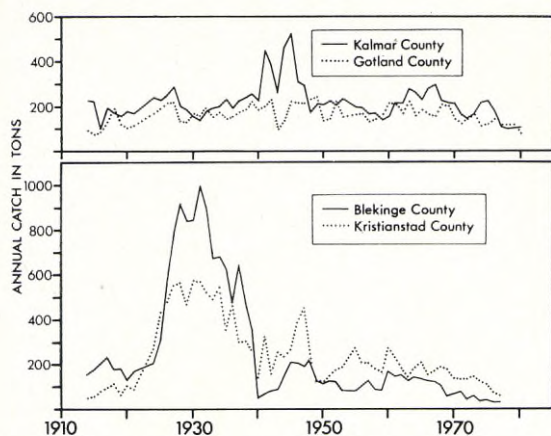
Fig. 1. Development of flatfish (plaice, flounder and dab, *Pleuronectes platessa, Platichthys flesus* and *Limanda limanda* respectively) catches in four Swedish counties.

Fiske, 1914—1963 and Fiskeristatistisk Årsbok 1964—1981) the catches of flatfish did not change in the way described by PERSSON (1981) in the area off the east coast studied by CEDERWALL and ELMGREN (1980) (the counties of Kalmar and Gotland (Fig. 1)). The differences between the catch development on the south and east coast for the period 1919—55 were also shown by SAHLIN (1959). Thus the catch data for flatfish provide no reason to dismiss CEDERWALL and ELMGREN's (1980) explanation that changes in the benthic fauna in the Baltic are caused by eutrophication.

III. THE ROLE OF FISH IN NUTRIENT CYCLING

The greatest influence of fish on nutrient cycling is probably caused by their selective predation (see above). By changing the size composition of the zooplankton community in the direction of smaller species, the speed with which nutrients are regenerated increases. This results in an increased phytoplankton production and possibly in an increased production of zooplankton. However, if fish are absent, the zooplankton is often dominated by larger species. Under such circumstances, zooplankton grazing can decrease the phytoplankton biomass significantly, reducing the primary production. This decrease in phytoplankton biomass can result in clearer water with considerably denser benthic vegetation. Fish can thus influence

the occurrence of both phytoplankton and macrophytes. The effects of fish predation can also indirectly influence both the amount of nutrients in and the pH of the water (HURLBERT *et al.* 1972, LOSOS and HETÈSA 1973, ZARET and PAINE 1973, ANDERSSON *et al.* 1978, BARTELL and KITCHELL 1978, STENSON *et al.* 1978, ERIKSSON *et al.* 1980, HENRIKSSON *et al.* 1980a, 1980b, LANGELAND and LARSSON 1980, LEAH *et al.* 1980, HURLBERT and MULLA 1981, WRIGHT and SHAPIRO 1984).

The significance of the excretion of nutrients by fish for the total nutrient regeneration in a water body has been a topic of discussion (KITCHELL *et al.* 1975, LAMARRA 1975, BERTELL and KITCHELL 1978, NAKASHIMA and LEGGETT 1980, 1982, SHAPIRO and CARLSON 1982). In general, direct nutrient regeneration by fish is considered to be less important than that of invertebrates and microorganisms.

In the Baltic proper, nitrogen is generally the limiting factor for phytoplankton production (LARSSON 1982). Assuming a C:N ratio of 4 in both fish and their prey (PARSONS *et al.* 1977) and that fish assimilate their food with 85 % efficiency (WEBB 1978), the fish in the Baltic proper annually remineralize 1 g N/m^2 (calculated from data presented by ELMGREN 1984). This remineralisation is marginal compared to the 28 g/m^2 annual nitrogen demand of the algae (primary production 165 g C/m^2yr and a C:N ratio 6, ELMGREN 1984, STICKLAND 1960). It is, in fact, considerably less than the average annual external input of nitrogen to the Baltic proper (a minimum of 4 g/m^2 according to LARSSON *et al.* 1985). These calculations, which show nutrient remineralisation by fish to be of little significance for the algal production, contradict the results obtained by LIMBURG *et al.* (1982) using an ecosystem model of a Baltic area. They found that the nutrient regeneration by fish strongly stimulated the phytoplankton production. This was probably a result of the model used, in which all trophic levels below that of fish were merged.

Considerable amounts of nutrients have, in some studies, been shown to be bound up in fish biomass. For Lake Wingra, KITCHELL *et al.* (1975) estimated that in the summer, 75 % of the pelagic P was bound in fish biomass, while the corresponding

Table 1. *Quantities of N and P incorporated in Baltic fish biomass.*

	Baltic proper	
Total fish biomass	2.3×10^6 tons wet weight	(1)
Total fish biomass	0.58×10^6 tons dry weight	(2)
Of which nitrogen	58×10^3 tons	(3)
Of which phosphorus	12×10^3 tons	(4)
mg N/m^2	270	(5)
mg N/m^3	4.5	(6)
mg P/m^2	57	(5)
mg P/m^3	0.93	(6)

	Entire Baltic	
Total fish biomass	3.5×10^6 tons wet weight	(1)
Total fish biomass	0.88×10^6 tons dry weight	(2)
Of which nitrogen	87×10^3 tons	(3)
Of which phosphorus	18×10^3 tons	(4)
mg N/m^2	233	(5)
mg N/m^3	4.2	(6)
mg P/m^2	48	(5)
mg P/m^3	0.86	(6)

(1) ELMGREN 1984
(2) 25 % of wet weight according to DURBIN *et al.* (1979)
(3) 10 % of dry weight according to DURBIN *et al.* (1979)
(4) 2 % of dry weight according to DURBIN *et al.* (1979)
(5) Area of the total Baltic $3.7 \cdot 10^5$ km², Baltic proper $2.1 \cdot 10^5$ km² (ELMGREN 1984)
(6) Volume of the total Baltic $21 \cdot 10^3$ km³, Baltic proper $13 \cdot 10^3$ km³ (KULLENBERG and JACOBSEN 1981)

proportions for zooplankton, phytoplankton and dissolved P were 18 %, 5 % and 3 % respectively. A corresponding estimate for the Baltic is hardly worthwhile since the water is stratified and nutrient content varies considerably at different depths. Furthermore, considerable volumes are often oxygen-free and therefore devoid of fish. Considering the amounts of N and P bound in fish biomass (Table 1) and assuming an annual catch of 1 million tonnes of fish, it is clear that the amount of nutrients removed from the Baltic by fisheries is small compared to the external input. For nitrogen the annual external input is 1,200,000 tonnes and the removal by fisheries is 25,000 tonnes.

In certain freshwater habitats fish migration has been shown to be a mechanism for nutrient transport. The possibility that nutrients are brought up from the bottom through the thermocline and up to the phototrophic zone by fish is discussed by SHAPIRO and CARLSON (1982). A more obvious means of nutrient transport could be spawning migrations, which can result in considerable nutrient input to the area where the fish spawn. The nutrients originate from excretion, but also from decaying sexual products and dead adult fish (DURBIN *et al.* 1979). This can increase the production in the water and it has been suggested that this type of fertilisation could be important for the survival of the young of the spawning fishes (RICHEY *et al.* 1975; LEBRASSEUR *et al.* 1979).

The most important fish migration in the Baltic, as regards nutrient transport, is probably that of herring. During most of the year a considerable proportion of the stock lives in the open Baltic (OJAVEER *et al.* 1981) and their diet includes food organisms from deep bottoms (ANEER 1980). When the fish then enter the archipelago to spawn they transport nutrients from the deep bottoms and open sea to the trophogenic layer in the coastal zone.

In the stretch of coastal zone which constitutes the primary investigation area (160 km²) of the Askö Laboratory on the west coast of the Baltic, the annual deposition of herring roe is 1000—2000 tonnes (G. ANEER, Askö Laboratory, University of Stockholm pers. comm.). Assuming a 1:1 weight ratio between roe and milt, this corresponds to about 80 and 10 tonnes of N and P respectively (if N and P are assumed to constitute 2.5 % and 0.2 % of the wet weight of roe and 2.3 % and 0.5 % of the wet weight of milt, HANSSON unpubl.). Then, if all of the nitrogen in the herring gonads was available to the phytoplankton, it would contribute to a primary production of about 3 g C/m² (for a C:N ratio of 6, STICKLAND 1960). Compared with the annual primary production in the area (165 g C/m², ELMGREN 1984) and considering that the nitrogen in the eggs and sperm is not directly available to the algae, but must first be excreted in the form of inorganic nutrients, it is clear that the spawning migration of herring is of minor significance for trophic conditions in the coastal zone.

Bioturbation by bottom feeding fish in lakes, has been suggested as an important mechanism for recycling nutrients from the sediment interstitial water to the pelagic zone (MILLER *et al.* 1961, HILSENHOFF 1965). In the Baltic, however, fish

with this feeding behavior are rare and must be considered in relation to benthic invertebrates. In Baltic soft bottoms, amphipods (*Pontoporeia* spp., in general about 2000 ind./m², ANKAR and ELMGREN 1978) often penetrate and mix the upper 6—7 cm of the sediment (HILL 1984). Thus fish bioturbation is probably negligable for the nutrient regeneration from the sediments.

IV. EFFECTS OF EUTROPHICATION ON FISH

Effects on the total amount of fish

Assuming that the availability of food is a factor which limits growth and production, eutrophication resulting in an increased production of prey can give rise to increased fish production. This has been observed in several lakes and ponds (*e.g.* SMITH and SWINGLE 1938, LARKIN and NORTHCOTE 1969, HALL *et al.* 1970, GOODYEAR *et al.* 1972, OGLESBY 1977, BIRÒ and VÖRÖS 1982). The addition of nutrients has also been used on purpose to increase the yield of fish (STOCKNER 1977, 1981, LEBRASSEUR *et al.* 1979). It can, however, be difficult to determine the long-term effects of eutrophication on the total fish catch from a water body, since some species are not fished and the effectiveness and extent of the fishing effort can change. Increases in the total catch in eutrophied lakes have been reported by *e.g.* COLBY *et al.* (1972), GRIMÅS *et al.* (1972), NÜMANN (1972), ROTH and GEIGER (1972), HARTMANN (1975, 1977a) LEACH *et al.* (1977) and SVÄRDSON and MOLIN (1981).

The effects of eutrophication on fish production in the sea have been studied to a much lesser extent than in lakes. However, a comparison between upwelling zones, coastal areas and the open sea shows a positive correlation between primary production and fish production (RYTHER 1969, CUSHING 1975, GULLAND 1976, NIXON 1982). LEE (1978) discusses the possibility that the increased catches of gadoid fish in the North Sea could be attributed to increased nutrient levels in the area, but he also gives alternative reasons such as decreased competition with pelagic species and climate changes. There is also a positive correlation between fish biomass and primary production in

different geographical areas of the Baltic (THURUW 1980, ELMGREN 1984). Eutrophication of the Baltic could thus be expected to increase the production of at least some of the fish species.

Eutrophication can influence a fish community in ways other than a change in food availability. Increased benthic vegetation can, for instance, lead to an increase in the spawning area and provide better protection for juveniles (HARTMANN and NÜMANN 1977). However, also decreased fish production can result from eutrophication. An increased sedimentation of organic material can give rise to oxygen deficiency on the bottom, thus eliminating benthic fauna important as fish prey, decreasing the fish production. In the same way, heavy blooms of planktonic algae can inhibit benthic vegetation which can in turn result in deteriorated reproduction for certain fish species.

Effects on species composition

Eutrophication often results in changes in the composition of fish communities. If the availability of food for one fish species, or group of species, improves more than for the others, this can obviously result in a relative change in the species composition, without negatively affecting the other species. Changes in freshwater fish communities resulting from eutrophication have been dealt with in many reviews (LARKIN and NORTHCOTE 1969; COLBY *et al.* 1972, HARTMANN 1977a, LEACH *et al.* 1977, WELCH 1980) and therefore no further literature review is undertaken here. A certain amount of eutrophication in an oligotrophic lake often results in increased food production and favours most fish species. Continued fertilization, however, results in deterioration for the salmonids, while percids and cyprinids benefit further. If eutrophication continues, percids begin to be negatively affected while cyprinids continue to benefit. Finally, under extreme eutrophic conditions even the cyprinids disappear. This "order" of elimination has been explained by different mechanisms. They are, however, all connected to a decreased oxygen content, resulting from the decomposition of the increased amounts of organic materials produced due to the eutrophication.

A decrease in oxygen in the bottom water may

damage reproduction in fish with benthic eggs. Especially vulnerable are species spawning on deep bottoms, where oxygen conditions are often worse than in shallow water. Species, in which the roe develops during periods when oxygen conditions in general can deteriorate, are also sensitive to eutrophication (*e.g.* autumn-spawning species with roe development during winter, BEETON 1965, LARKIN and NORTHCOTE 1969, COLBY *et al.* 1972, NÜMANN 1972, WELCH 1980). Species which spawn in relatively shallow water during the spring and summer, and species with eggs that are pelagic or attached to vegetation (so that they rise above the bottom) are less threatened by poor oxygen conditions (COLBY *et al.* 1972). Benthic vegetation is thus important for reproduction in certain species, and increased amounts of littoral macrophytes can consequently favour these fish (NÜMANN 1972). Species which spawn on shallow, clean sand and gravel bottoms can, however, sustain damage from increased vegetation (GRIMALDI and NÜMANN 1972). The decline of salmonid fish during eutrophication may therefore partly be explained by impaired reproduction. These species are mainly autumn spawners with benthic roe.

The impoverished oxygen levels which in general afflict deeper bottoms can influence the fish in ways other than through decreased reproductive success. Low oxygen levels can "force" the fish, up from deeper water, closer to the surface (HASLER 1947, TANNER 1960, LARKIN and NORTHCOTE 1969, NÜMANN 1972, HARTMANN 1977a, LEACH *et al.* 1977, FRY 1969, WELCH 1980). Low oxygen levels can also negatively influence the production of benthic invertebrates, reducing the abundance of food and thus forcing fish up to shallower bottoms (REGIER and HARTMANN 1973, HARTMANN 1977a, LEACH *et al.* 1977, HARTMANN and LÖFFLER 1978). Consequently these two mechanisms primarily afflict those species which normally live in deep water. These are primarily 'cold water species' which have a relatively low preferred temperature. Reduced oxygen concentrations thus force these species up into warmer water and expose them to a "temperature stress" (FRY 1969, WELCH 1980). An important factor in such temperature stress can be interspecific competition, of which SVÄRDSON (1976) gives some examples. The effects of changes in the abundance

of food, in combination with competition for food, in explaining changes related to eutrophication in fish communities are also stressed by HARTMANN (1979, 1982).

The "order of succession" during increasing eutrophication is well correlated to the temperatures generally preferred by the three groups of fish discussed previously. Salmonids are mainly cold water species and are the first to disappear during eutrophication, while cyprinids, which are characterized as warm water species, are most tolerant to eutrophication. Percids are intermediate, both with regard to sensitivity to eutrophication and temperature preference.

Effects on the individual fish

In fish populations influenced by eutrophication, individual fish can be affected in a number of different ways (HARTMANN and QUOSS 1983). There is no simple connection between eutrophication and growth, condition (length to weight ratio) and fat content in fish. If reproductive success decreases while the availability of food is steady or increasing, the growth, condition and fat content of the fish may improve. If reproduction remains unchanged and food availability decreases, growth and condition may, on the other hand, deteriorate. Frequently, however, species whose populations have increased as a result of eutrophication have also been observed to attain better growth, an increased fat content and a better condition. The effects of eutrophication on the growth of fish are presented in a number of articles (LARKIN and NORTHCOTE 1969, COLBY *et al.* 1972, HARTMANN 1977a, 1977b, 1978 and LEACH *et al.* 1977).

The frequency of fish diseases, including parasites and deformations, in pollution gradients are treated in reviews by amongst others SNIESZKO (1974), MÖLLER (1979, 1982), SINDERMANN (1979), SINDERMANN *et al.* (1980), and PETERS (1981). One problem which arises in the interpretation of the results is, however, that it is often not only eutrophication that has been studied, but also discharges of a very complex nature, including nutrients and metals as well as organic pollutants. Certain diseases seem to be directly correlated to discharges, while others are not, and therefore generalisations are difficult to make.

The occurrence of bacteria, including pathogens, has been reported to increase in eutrophied waters with high concentrations of organic substances (SNIESZKO 1974, LARSEN and JENSEN 1977, 1982, SPOORENDONK 1977). LARSEN and JENSEN (1982) present results which show that the occurrence of cod with 'Ulcussyndrome' was higher in areas influenced by organic pollutants. This is in accordance with the results of CHRISTENSEN (1980), which also show that the sores were often infected by *Vibrio anguillarum*. The effects of infection by this bacteria can be dramatic. EGIDIUS and ANDERSEN (1975) show heavy mortality in afflicted saith (*Pollachius virens* (L.)).

Among the more noted diseases are the tumours which can occur on pike. The connection between these and pollutants is not clear, but it appears that certain pollutants can trigger off the disease (BROWN *et al.* 1979, MULCAHY 1980). It is, however, not known whether there is any connection between eutrophication and pike tumours (MULCAHY 1980).

Increased parasitic infestion in fish has been reported in connection with eutrophication. This has been explained as a result of more abundant vegetation, which leads to denser populations of intermediate hosts (gastropods) and more substrate on which carp lice (branchiurans) can lay their eggs. If the fish populations become denser they may also become more susceptible to parasites (COLBY *et al.* 1972, NÜMANN 1972, HARTMANN 1977 a, b, LEACH *et al.* 1977).

Besides causing occasional acute oxygen depletion following the decay of organic material produced in intense algal blooms, it has been discussed whether eutrophication can cause fish mortality by stimulating phytoplankton species which produce toxic substances (CARMICHAEL 1981, PARKER 1982, MALYAREVSKAYA 1983, POTTER *et al.* 1983).

Effects observed in the Baltic

The total fish catch in the Baltic has increased ten times in the past fifty years (Fig. 2). During the last twenty years the catches have doubled. From 1980—82 the yield has been about 0.9 million tonnes, with a value of roughly 2000 million Swedish Crowns (HANNERZ 1982). Eighty to ninety per cent of the catches are made up of three species: cod, sprat and herring (*Gadus*
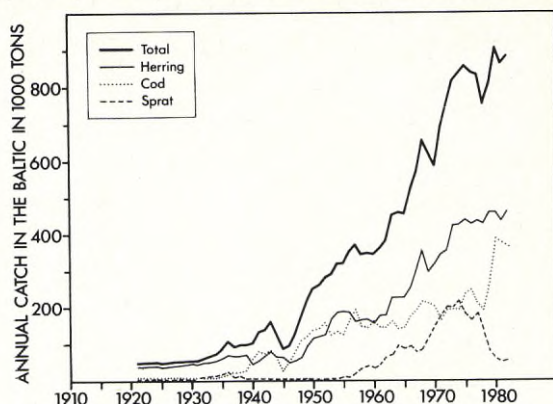

Fig. 2. Total Baltic catches according to data presented by OTTERLIND (1978, 1983 b).

morhua L., *Sprattus sprattus* (L.) and *Clupea harengus* L. respectively). These species are thought to make up 80—85 % of the Baltic fish biomass (THUROW 1980, 1984, ELMGREN 1984). The most important reason for the large increase in the catch in the Baltic is that fishing efforts have intensified and that new, more effective, gear has been introduced (CIEGLEWICZ and JENSEN 1959, OTTERLIND 1976, 1978). Whether the fish stocks and their productivity have been altered is, however, uncertain. According to THUROW (1980), the data on standing stocks prior to 1970 is poor, but drastic changes do not appear to have taken place during the 1960's. The importance of eutrophication in increasing fish production and thereby increasing the catches is, on the other hand, stressed by ZMUDZINSKI (1975, 1976, 1978), MAŃKOWSKI (1978) and NEHRING *et al.* (1984). According to OTTERLIND (1976, 1978, 1984), a positive correlation can be found between the increased nutrient levels and increased fish stocks in the Baltic. He stresses, however, that although anthropogenic factors can be of importance, nutrients released from the bottoms and transported to the surface layers during influxes to the Baltic of high salinity water from the westcoast, may also be of great significance. A positive correlation between good year classes of fish and large injections of westcoast water to the Baltic has also been stressed by RANNAK (1974). CUSHING (1982), on the other hand, considers the hydrographic changes following inflows to be more important

for the increased abundances of cod, herring and sprat than the upward transport of nutrients from the bottom water.

Eutrophication probably affects cod, herring and sprat in different ways and the species are discussed separately below. Thereafter, other eutrophication-related changes observed in coastal and archipelago regions will be dealt with.

Cod

Two main populations of cod occur in the Baltic. *Gadus morhua callarias* is found mainly in the Baltic proper and *G.m. morhua* occurs mostly in the western areas (OTTERLIND 1966, 1976, THUROW 1974, OJAVEER *et al.* 1981). Successful reproduction is limited to the deep basins with a salinity of at least 10—11 $^0/_{00}$, and is only successful if the oxygen concentrations at these deeps are above 1 mg O_2/l (OJAVEER *et al.* 1981). Low oxygen levels can also influence the adult cod, since it avoids areas with less than 1.5—2 ml O_2/l (TIEWS 1974, OTTERLIND 1976, SJÖBLOM *et al.* 1980). In coastal areas where oxygen levels have decreased due to pollution, this has resulted in considerable decreases in the abundance of cod (BERNER *et al.* 1973 a, b).

The growth of cod can vary considerably both between areas and years. This has partly been related to differences in population density, *i.e.* to intraspecific competition (DEMENTIEVA 1959, OTTERLIND 1976, BERNER and BORRMANN 1980, OJAVEER *et al.* 1981). KOSIOR (1978) presents a longtime series of growth analysis (1955—70), but no effects of eutrophication emerge. Variation in growth rates between different sampling occasions may not only be due to natural variation, but may also depend on uncertainties connected with the age determination of Baltic cod (CIEGLEWICZ and JENSEN 1959, KÄNDLER and THUROW 1959, THUROW 1974).

Catches of cod have greatly increased in the Baltic over the last forty years (Fig. 2). As mentioned earlier, the increased fishing efforts and improved gears are important reasons for this. OJAVEER *et al.* (1981) suggest that the increased yield is probably not the result of larger stocks, but that the increased fishing efforts have raised production by stimulating individual growth.

Other authors (*e.g.* KOSIOR 1974, 1978, OTTERLIND 1976, 1984, THUROW 1980, 1984) maintain that stocks have increased and thus made larger yields possible. BERNER (1979) suggests that this increase in the stocks was possible due to eutrophication. OTTERLIND (1976, 1978, 1984) also discusses the possibility that increases in the standing stocks of cod result from eutrophication. He suggests that this eutrophication can be a natural process, generated by hydrographic changes resulting in greater transport of nutrients from the deep bottoms to the phototrophic zone. OTTERLIND (1978, 1984) also points out that periodic occurrence of large stocks of cod in the Baltic is not a new phenomenon, as this probably already occurred in the 17th and 18th centuries.

Eutrophication may not necessarily be positive for the Baltic cod. An increase in primary production, with a resulting increase in oxygen consumption in the water mass and on the bottoms, could lead to oxygen depletion in deep waters. This could decrease the reproductive success of cod and decline its stocks. According to some authors, eutrophication-induced oxygen depletion has already reduced some year classes of cod (DEMENTIEVA 1972, ZMUDZINSKI 1975, 1978). The catches, however, increased significantly at the end of the 1970's and the beginning of the 80's (Fig. 2), in spite of low oxygen concentrations in the Baltic deep water. OTTERLIND (1978, 1983a, 1984) explains this paradox by suggesting that eutrophication has resulted in better feeding conditions for the juveniles, increasing their survival. In another article, OTTERLIND (1983b) discusses the effects of low oxygen concentrations in deep water in a long-term perspective, and claims that it is unlikely that oxygen shortages will be of such permanence that cod would be eliminated from the Baltic.

Herring

Baltic herring (*Clupea harengus*) has been divided into two main groups, autumn and spring spawners. These have further been classed into a number of sub-populations, some with both spawning and feeding areas in the archipelagos and others with their feeding areas in the open Baltic (OJAVEER *et al.* 1981). This division into populations, based on morphometric characters has, however, not been

verified by genetical analyses (RYMAN *et al.* 1984). ANEER (1985) suggests that the spawning time is influenced by food supply, and thus not genetically determined. He further proposes that eutrophication has improved feeding conditions for the Baltic herring explaining the decline in the proportion of autumn spawners.

In contrast to cod, herring reproduces over the entire Baltic. Spawning takes place in the littoral zone (0—20 m) and the eggs are generally attached to vegetation (*e.g.* ANEER and NELLBRING 1982). Since the roe is deposited in shallow water, herring does not normally run the same risk as cod of suffering from oxygen depletion. However, ANEER (1985) shows that low oxygen concentrations (< 1 mg O_2/l) can also develop in the algal belts. He also discusses the possibility that eutrophication may have affected the reproductive success of herring by increasing the density of the thin, filamentous algae in which such oxygen depletion most frequently occurs.

Adult herring avoid water with oxygen levels lower than 1—1.5 mg/l (OJAVEER *et al.* 1981), and locally changes in the occurrence of herring in the southern Baltic have been explained by low oxygen levels induced by pollution (BERNER *et al.* 1973 a, b). Herring have also disappeared from the most polluted areas off Helsinki (ANTTILA and MICHELSSON 1971, ANTILLA 1973, SJÖBLOM *et al.* 1979; LEHTONEN and HILDÉN 1980).

The growth of herring varies between years. It is influenced both by the abundance of food and by climate, and poor growth has been related to hard winters (RANNAK 1974, STRZYZEWSKA and POPIEL 1974). Growth rates also differ in different parts of the Baltic, being generally higher in the southern areas than in the northern areas (WEBER 1978, OJAVEER *et al.* 1981). During the last 20 years, growth rates have increased and condition (weight/length relationship) has improved in some areas (STRZYZEWSKA and POPIEL 1974, WEBER 1978; OJAVEER and RANNAK 1980; OJAVEER *et al.* 1981, FRIESS and KÄSTNER 1982, WRZESIŃSKI 1983, ANEER 1985). Considerable changes in growth of herring were, however, already observed in the 1940's (STRZYZEWSKA and POPIEL 1974, STRZYZEWSKA 1978), *i.e.* during a period when anthropogenic nutrient discharges to the Baltic were much less extensive than today. This, in combination with decreased growth rates in some parts of the Baltic (HILDÉN *et al.* 1982), makes it difficult to state the positive growth changes as results of eutrophication. An alternative explanation is that the rapid expansion in fishery (Fig. 2) has reduced herring stocks, resulting in decreased intraspecific food competition and hence better feeding conditions.

As mentioned earlier, the catches of herring in the Baltic have increased greatly since the end of the Second World War. Whether this is due only to increased fishing efforts, or whether the stocks and their productivity have increased is difficult to determine, especially since fishing is now one of the limiting factors for the herring populations (THUROW 1980, 1984). SJÖBLOM and PARMANNE (1981) present catch data from trawling in the Åland Sea and the northern Baltic proper which indicate that stocks have tripled from the 1950's to the 1970's. That herring production may have increased due to higher nutrient levels is discussed by STRZYZEWSKA and POPIEL (1974), OJAVEER and RANNAK (1980) and OTTERLIND (1976, 1978). RANNAK (1974), as already mentioned, suggests a positive correlation between year-class strength and large influxes of water with high salinity to the Baltic. According to GRASSHOFF (1975), the herring stocks were larger in the 13th and 14th centuries than they are today. GRASSHOFF (1975) further discusses the possibility of a natural eutrophication through increased nutrient flows from the bottoms to the phototrophic zone.

Sprat

According to OJAVEER *et al.* (1981), sprat (*Sprattus sprattus*), cannot be divided into such a large number of populations as herring, but a certain separation into different stocks may still occur. The species spawns during summer at salinities of at least 5 ^{0}/$_{00}$. It is probable that no spawning occurs in the Bothnian Bay but that the stocks there are recruited from the south. Generally, however, the migratory patterns of the species are poorly known, although migration is probably extensive (OTTERLIND 1978, OJAVEER *et al.* 1981).

The growth of sprat varies between different areas of the Baltic (RECHLIN 1975, OJAVEER *et al.* 1981). Growth data for Gdansk Bay are available for the period 1954—77 (GRYGIEL 1978; LIWOCK
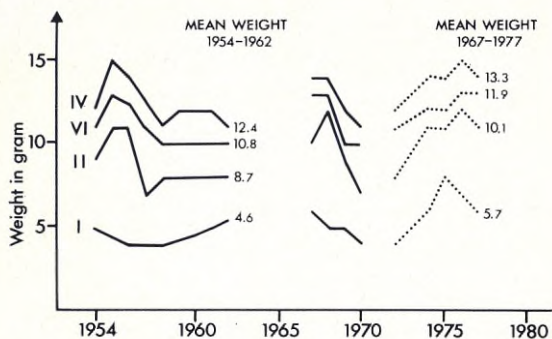
Fig. 3. Temporal changes in the mean weight of sprat at different ages (I—IV) in the Gdansk Bay. Data from LIWOCH (1978: —) and GRYGIEL (1978: . . .).

1978), and indicate higher growth rates at the end of the 1960's and 70's than during the 50's (Fig. 3). Differences between years are, however, appreciable and the changes in growth rates are small. During the same period an increase in the fat content of sprat in the Gdansk area has been observed (ELWERTOWSKI *et al.* 1974). These results can be taken as indicating that the Baltic sprat has been influenced by eutrophication, at least in the Gdansk region.

The growth of sprat has also increased along the Soviet coast (northeastern Baltic and Gulf of Finland) during the period 1961—74, while the condition of the fish has not changed significantly (VELDRE and POLIVAJKO 1975). The authors explain the increased growth as being due to stock and climate variations.

The catches of sprat increased drastically from the mid-1950's to the mid-70's. According to some authors, the increase in the size of stock during the 1960's and 70's was due to either anthropogenic or hydrographically induced eutrophication (DEMENTIEVA 1972, 1976, OTTERLIND 1976, LIWOCH 1978). Since the mid-70's, catches of sprat have decreased significantly (Fig. 2). This is probably due to a combination of overfishing (THUROW 1984) and predation from increased cod stocks which, according to ELMGREN (1984), consume at least the same quantity of sprat as human catches.

Other observations

Cod is not the only species in which reproduction can be affected by oxygen deficiencies in the deep Baltic basins. Plaice (*Pleuronectes platessa* (L.)) is probably affected even more frequently, since it requires a higher salinity for reproduction than cod (at least 12 $^o/_{oo}$, MOLANDER 1925). Poorer reproduction could explain the decreased ratio of plaice in flatfish catches in the Gdansk Bay. During the period 1954—56, plaice made up 20 $^o/_o$ of the flatfish landed in the area (MULICKI 1959), but accounted for only 5 $^o/_o$ from 1960—74 (CIEGLEWICZ 1978). For the period 1970—77 DRAGANIK and REIMANN (1979) reported only 1—5 $^o/_o$ of plaice in the flatfish catches. These three articles also show that the development was similar, though not as accentuated, in the Bornholm area.

The possible affects of eutrophication in the Baltic which have been discussed so far have all concerned fish of marine origin. Freshwater species which occur mainly in the archipelagos, may, on a local scale, be subjected to considerably more pollutants than the marine species. ANTILLA *et al.* (1975) showed changes in the fish community in the heavily polluted areas off Helsinki. The changes in the species composition corresponded well with changes observed in lakes. Trout, whitefish, burbot, ide and pike (*Salmo trutta* L., *Coregonus* spp., *Lota lota* (L.), *Leuciscus idus* (L.) and *Esox lucius* L. respectively) had become less common while roach, white bream and ruffe (*Rutilus rutilus* (L.), *Blicca bjoerkna* (L.) and *Gymnocephalus cernua* (L.)), had increased greatly in abundance. In some areas, the roach and ruffe populations were so dense that growth rates were clearly reduced. The occurrence of pike-perch and bream (*Stizostedion lucioperca* (L.) and *Abramis brama* (L.)) had on the other hand not changed to any great extent (ANTILLA and MICHELSSON 1971, ANTILLA 1973, LEHTONEN and HILDÉN 1980). In general, however, the catches of pike-perch along the Finnish coast have increased significantly since the 1950's (LIND 1977). This has been suggested to be a result of coastal eutrophication (TOIVONEN *et al.* 1982, LEHTONEN 1983, 1985). With regard to pike-perch, WINKLER and THIEME (1978) also reported greatly increased occurrence also along the East German coast during the same period, which they explained at least partly as a result of eutrophication. These authors also reported a decreased abundance of pike during the same period. According to local

fishermen, similar stock developments have been observed along the Swedish Baltic coast. In the Stockholm archipelago, pike-perch increased and pike decreased, possibly as a result of eutrophication. With improvements in sewage treatment, discharges in the area decreased and the species shift has been reversed (L. NYMAN, Institute of Freshwater Research, Drottningholm, pers. comm.). In the Himmerfjärd and Bråviken bays, south of Stockholm, the abundance of pike-perch has increased with eutrophication (HANSSON 1978, H.-G. ANDERSSON, Local Fisheries Authority, Nyköping, pers. comm.).

In the Baltic, whitefish can be divided into two different populations, coastal and river spawners. In areas where the latter group is common, changes in the whitefish abundance can result from pollution, impoundment and other human activities in their freshwater habitat. The previously described decline in whitefish catches off Helsinki has, however, been related to eutrophication. LEHTONEN (1981, 1985) presents data on Finnish whitefish catches for the period 1949—82. Apart from large between-year differences there are decreases during the last years of the period, which he considers to be an effect of eutrophication. The available Swedish statistics (Sveriges officiella statistik, Jordbruk med binäringar, Fiske 1914—1963 and Fiskeristatistisk årsbok 1964—1981) show that the trend in yields of whitefish in the Stockholm region differs from the surrounding coastal areas. In the Stockholm region, catches have decreased steadily since the mid-1950's. From the mid-1960's onwards, catches were generally lower than during the earlier part of the 20th century. In other coastal regions, catches of whitefish have either shown no tendency to decrease or else they have increased somewhat since the beginning of the century (Fig. 4). Since coastal spawners probably dominate in the Stockholm archipelago, eutrophication could be an explanation for the negative trend in yields in this area. The available statistics account, however, only for a part of the total catches. Recreational fishing is not considered, and it is possible that the shift from commercial to recreational fishing is more pronounced in the Stockholm archipelago than in other areas, and that this influences the statistics.

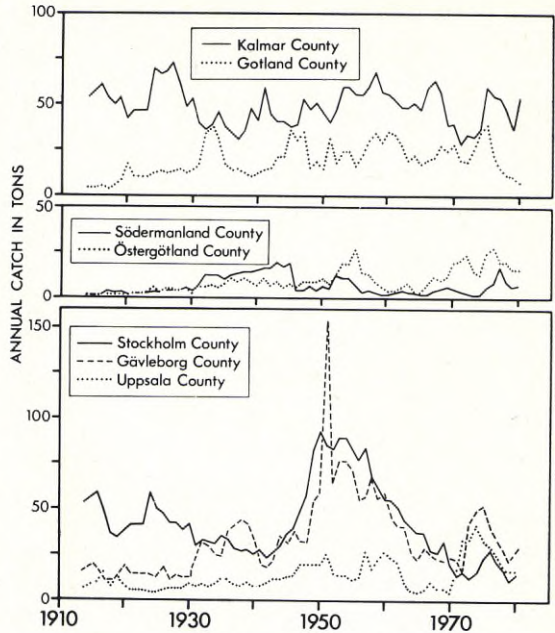To study the possible effects of eutrophication

Fig. 4. Development of Baltic whitefish (*Coregonus* spp.) catches in seven Swedish counties.

on perch in the northern Baltic proper, a comparison was made between the growth of perch in the inner, most eutrophied, part of the Himmerfjärd bay and a reference area (HANSSON and WESTIN 1985). No clear effect of eutrophication was found.

Both nutrients and organic substances are discharged from pulp and paper industries. In studies of areas close to such industries along the Swedish Gulf of Bothnia coast, fish community changes similar to those reported from the eutrophicated Helsinki area have been found. Roach and ruffe occurred in large numbers in the heavily polluted areas while the abundance of perch was considerably less than expected (HANSSON 1982, E. NEUMAN, National Swedish Environment Protection Board, pers. comm.). The discharges from this type of industries are, however, complex and factors other than eutrophication may have produced the patterns.

For several years the National Swedish Environmentment Protection Board has carried out standardized fishing programmes along the Swedish coast and has also analysed catch statistics from commercial fisheries. In general, these studies

show that cyprinids and perch have increased while fourhorn sculpin (*Myoxocephalus quadricornis* L. and sea scorpion (*M. scorpius* (L.)) have declined in abundance. These changes are thought to be due to changes in water temperature, rather than a result of eutrophication (E. Neuman, pers. comm.). Decreased catches of whitefish, perch and burbot and increased catches of pike-perch and cyprinids along the Finnish coast have, however, been proposed to at least partly result from eutrophication (HILDÉN *et al.* 1982, LEHTONEN 1985).

The occurrence of fish diseases in the southern Baltic has been reviewed by MÖLLER (1979). He found no clear correlation between pollution and the frequency of diseases. According to LASSIG and LAHDES (1980), however, fin rot is common in polluted areas along the Finnish coast. The ulcers observed on pike are one of the most widely discussed fish diseases in the Baltic. No clear connection has been found between these ulcers and pollution (LJUNGBERG and LANGE 1968, LJUNGBERG 1977, NYSTRÖM 1980 a, b, THOMPSON 1982).

In heavily polluted areas of the Baltic, muddy odour has been reported in fish (ANTTILA and MICHELSSON 1971, ANTTILA 1973, LEHTONEN and HILDÉN 1980). These have been correlated to the occurrence of the blue-green alga *Oscillatoria agadhii* (PERSSON 1981, 1982).

If eutrophication increases the frequency of heavy algal blooms, this can probably result in local fish mortality, since potentially toxic algae occur in the Baltic (*e.g.* the blue-green algae *Nodularia spumigena* and the dinoflagellate *Dinophysis acuminata*, L. EDLER, Department of Marine Botany, University of Lund, pers. comm.). In the 1920's, fish mortality was reported from the north German coast and people who had eaten fish caught in the area exhibited symptoms typical of algal-toxin poisoning (BIRGER *et al.* 1973). KALBE and TSCHEU-SCHLÜTER (1972) reported local fish mortality on the German Baltic coast caused by the chrysomonade *Prymnesium parvum*. However, despite appreciable blooms, no case of fish mortality has been reported from the Finnish coast (NIEMI 1982).

At low oxygen levels, high concentrations of NO_2^- and NH_4^+ can build up. Depending on the pH of the water, varying amounts of NH_3 can then be formed. Both NO_2^- and NH_3 are toxic to fish (EMERSON *et al.* 1975, SMITH and PIPER 1975, SMITH and RUSSO 1975, RUSSO and THURSTON 1977, THURSTON *et al.* 1978). To examine the possibility that these substances have toxic effects on fish in the Baltic, data from the eutrophied Himmerfjärd bay have been analysed (data provided by U. LARSSON, Askö Laboratory, University of Stockholm). The levels of NO_2^- and NH_3 that were found (10^{-4}—10^{-5} and 10^{-5}—10^{-6} g/l respectively) were not high enough to cause acute toxic effects, but they had occasionally magnitudes that could be expected to cause sublethal effects. It is, however, doubtful whether fish are exposed to these concentrations. They only develop where the oxygen levels are very low and hence where fish are likely to be absent.

V. EVALUATION OF DATA FROM THE BALTIC

There is a number of articles according to which the fish in the Baltic have been influenced by eutrophication. The opposite has not been claimed, but in many articles alternative factors are suggested to explain observed changes in yields and fish communities structure.

One of the reasons for the difficulties in evaluating which effects eutrophication may have had on Baltic fish is the lack of long time series on the size of the fish stocks, their age composition and individual growth rates. Available data are mainly based on the yields of the commercial fishery, and, as stated previously, these catches have increased at least partly as a result of intensified efforts and improved techniques. Different methods for quantifying fish stocks have been used by fishery research authorities around the Baltic, and the reliability of the data obtained is difficult to evaluate. BAGGE and MÜLLER (1977) compared stock estimates of cod in the Bornholm region and obtained large differences, depending on the method used. LINDQUIST (1980) also obtained considerable discrepancies between different methods when he quantified sprat. According to estimates based on quantifications of roe, the biomass of adult sprat in 1970 was 118,000 tonnes, but according to VPA (Virtual Population Ana-

lysis), their biomass was 1,116,000 tonnes, *i.e.* a difference by a factor of 10! Corresponding comparisons for some other years resulted in smaller discrepancies between the methods but the results from 1970 clearly show the difficulties involved in stock assessment.

To these difficulties in quantifying fish stocks must be added other important factors which make it difficult to evaluate the possible effects of eutrophication: 1) the dominating fish populations are influenced by the fishery 2) increased fishing can itself result in increased production, since individual growth can increase as the fish density decreases 3) fish stocks display considerable natural fluctuations 4) the three dominating Baltic fish species consist of a number of more or less independent populations and 5) the literature is probably biased, in favor of articles indicating eutrophication induced changes compared with papers showing constancy or changes which cannot be correlated to, or contradict, eutrophication.

The Baltic sprat stock provides good example of natural population fluctuations. During the period 1937—39, the abundance of sprat was very low (Liwoch 1978), while during the 1970's it was sufficiently large to yield annual catches of 100,000—200,000 tonnes (Otterlind 1983 b).

One of the most important reasons for these stock fluctuations may be changes in water temperature. Such changes have been correlated both with the annual variations in the abundance of single species (*e.g.* Sjöblom 1978, Ojaveer *et al.* 1981) and to large scale changes in species composition (Ojaveer *et al.* 1981). Even hydrographical changes such as the increased salinity of the Baltic may have contributed to changes in the fish fauna (Mankowski 1951, Cushing 1982).

The division of the species into separate populations renders analysis even more difficult since these separate groups are not absolutely bound to an area but can vary their distribution. The fishing pressure can also vary between stocks, and undergo temporal changes. This, and other factors can result in growth rate variations which differ between populations. Samples taken in different years, but in the same area may thus originate from different populations, and considerable variations in *e.g.* growth may be found.

Against this background I hesitate to positively state whether eutrophication has influenced Baltic fish communities in general. The only definite statement which I can make is that there are several signs of a large scale eutrophication of the Baltic. These are increased concentrations of nutrients, the frequent occurrence of anoxic conditions in deep water, increased benthic biomasses above the halocline and decreased biomasses below it (see references in the introduction). In analogy with lakes and other marine areas it is reasonable to assume that these changes have influenced the fish. Several authors also claim this, reporting increased fish stocks, enhanced growth, and changed species composition. It is possible, however, that some of the changes, *e.g.* in the Gdansk Bay, should be considered as local phenomena, and not as representative of the Baltic in general. Documentation of the effects of eutrophication in archipelago areas, which more or less act as direct recipients of waste discharges, is surprisingly meagre. The results from the Helsinki area are almost the only data which are available. These indicate effects similar to those observed in polluted lakes.

VI. ACKNOWLEDGMENT

VII. REFERENCES

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A Comparison of the Growth of Perch (*Perca fluviatilis* L.) in an Eutrophied Bay and a Reference Area in the Northern Baltic Proper

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ABSTRACT

Growth of perch (*Perca fluviatilis* L.) in a eutrophied bay, the Himmerfjärd, is compared with growth in a nearby reference area. The Himmerfjärd has been a recipient of nutrient discharges from a sewage treatment plant since 1974. In the reference area, growth was faster than in the eutrophied bay. No growth change, coincidental in time to the eutrophication, was detected. This suggests that the growth differences between the two areas were caused by factors other than the eutrophication.

In general, growth rates in both areas were high. The reference area had the best growth hitherto reported from the Baltic.

I. INTRODUCTION

Anthropogenic loading of nutrients to the Baltic Sea has increased from calculated 10,000 tons P and 300,000 tons N annually at the end of the 19th century, to around 80,000 and 1,200,000 tons respectively today (LARSSON *et al.* 1985). The effects of this eutrophication are not only local or limited to the coastal zone, but are also observable in the open Baltic (*e.g.* CEDERWALL and ELMGREN 1980, DYBERN and FONSELIUS 1981, NEHRING *et al.* 1984). In this paper, however, only local effects are considered.

The area studied in this article is situated in the northern Baltic proper, where the surface salinity is 6—7 $^0/_{00}$. The Himmerfjärd, in the northern part of the area (Fig. 1), has been significantly eutrophied during the last decade. A sewage treatment plant, in operation in the inner part of the bay since 1974, annually discharges 11 tons of phosphorus and 500 tons of nitrogen (U. LARSSON, Askö Laboratory, unpubl.). This has not only increased the pelagic primary production (275 gC $\cdot$ m^{-2} $\cdot$ yr^{-1} at eutrophied stations, compared to 160 gC m^{-1} $\cdot$ yr^{-1} at a reference station, LARSSON and HAGSTRÖM 1982), but via increased organic sedimentation also influenced the benthic communities. On some sublittoral bottoms the macrofauna biomass has increased, while at other localities, typically deeper ones, the macrofauna have been eliminated by oxygen deficiency. The littoral invertebrates in the eutrophied area have not been studied in detail, but available data does not indicate any clear effects (U. LARSSON, unpubl.).

In freshwater eutrophication has been shown to influence the biology of many fish species. One of the often, but not always, observed effects on perch (*Perca fluviatilis* L.) is an increased growth rate (*e.g.* HARTMANN 1975, 1978, LEACH *et al.* 1977, BREGAZZI and KENNEDY 1982). From the Baltic where perch is abundant in most archipelagoes (NEUMAN 1976), there is, however, no data on such effects. In this article, growth of perch in the eutrophied Himmerfjärd and in a reference area, not directly influenced by the discharges from the sewage plant (Fig. 1), are compared. By using back-calculation techniques on data from age readings of the opercular bone, it has also been possible to compare growth of perch in the Himmerfjärd before and after the start of the sewage plant.

II. MATERIAL AND METHODS

Perch from both areas were caught with gill nets between May 15—June 6, 1979 (*i.e.* during spawning). Using the back-calculation method described by LE CREN (1947) the total length of females at different ages was determined from measurements of the opercular bone. In order to obtain results
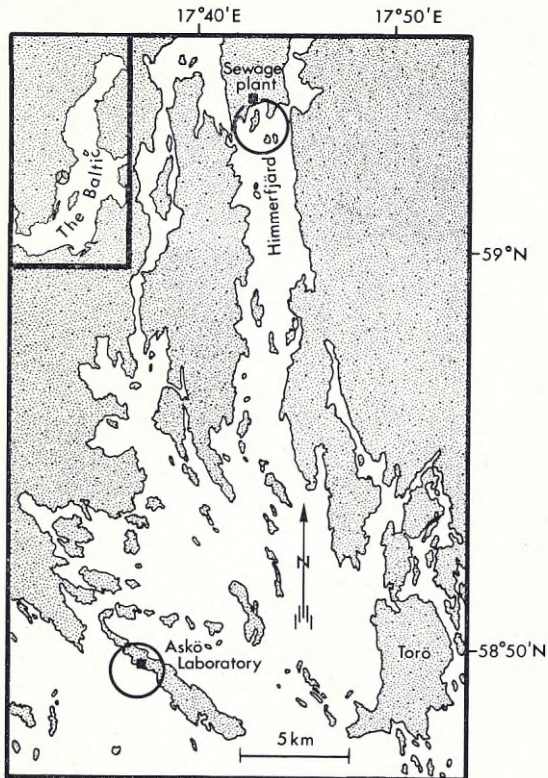
Fig. 1. The area studied, with the sampling sites encircled.

comparable to those published earlier from the Baltic (NEUMAN 1974, 1976, HANSSON 1985), the opercular bone analyses were made by the same person as in those articles, and in the back calculations for length the formula $L = 19.45 \times B^{0.861}$ was used (L=total length of fish at age a and B=opercular length in cm at age a according to the annual rings, NEUMAN 1974, 1976).

Possible differences between growth in the two areas were analysed for each age group separately, using a two-way analysis of variance (ANOVA) for unbalanced data (TEKTRONIX 1975). The variables used were the back calculated length estimates, while catch area and birth year were the dimensions considered. In this way, growth differences between year classes, and biases in the backcalculation technique, were compensated for.

To determine whether the eutrophication had influenced the growth of perch, temporal changes in age specific length in the Himmerfjärd area were analysed in the following way: for each

year class separately, the mean back-calculated length at four years of age in the reference area was subtracted from the individual length at this age for fish from the Himmerfjärd. This was done to compensate for natural interannual growth variations and backcalculation errors. The resulting differences were then correlated, using linear regression (DIXON and MASSEY 1969), to the birth year of the fish. A positive correlation would indicate that the growth rate in the Himmerfjärd had increased in parallel with the eutrophication, while a negative correlation would indicate the reverse. Length at four years of age was used in this test for different reasons. At this age the fish was about 20 cm long, and had probably passed stages when feeding on zooplankton and benthic invertebrates, and turned to a fish dominated diet. Effects of eutrophication on any of these trophic levels, which may influence the growth of perch, would thus be expected to be manifested at this age. Further, the number of observations within this age group is fairly high, increasing the reliability of the test.

III. RESULTS AND DISCUSSION

The growth rate differences between the two areas were small, but statistically significant (Table 1). In the reference area, perch grew somewhat faster than in the eutrophied Himmerfjärd. It was, however, not possible to detect any temporal trends, related to eutrophication, in the growth of perch in the Himmerfjärd ($T = -0.88$, df $= 144$, $p > 0.05$).

The growth differences between the areas cannot be explained on the basis of the data available for this study. Higher intraspecific food competition, resulting from a denser perch population in the Himmerfjärd, as indicated by the gill-net catches in the samplings for this study, is one possible explanation. Compared with other Baltic areas, growth of perch in the Himmerfjärd and the reference area is rapid. In fact, the growth in the reference area is slightly faster than reported from any of the other areas (NEUMAN 1976, HANSSON 1985).

IV. ACKNOWLEDGMENT

Table 1. Mean total length (mm) of female perch at different ages in the eutrophied area (Hfj) and in the reference area (Askö). The numbers in brackets show the number of back-calculated length data on which the age specific mean length values are based. Results of the age specific ANOVA are also shown, with 'p' representing the probability of identical mean length in the two areas.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Hfj	67 (148)	107 (148)	147 (148)	181 (147)	206 (124)	225 (98)	244 (74)	265 (48)	288 (39)	311 (32)	330 (17)	348 (7)	349 (3)	405 (1)
Askö	69 (110)	115 (110)	159 (110)	197 (109)	225 (86)	249 (75)	264 (54)	278 (30)	292 (15)	303 (10)	330 (10)	344 (5)	371 (1)	—
p	> 0.05	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.05	> 0.05	> 0.05	> 0.05	> 0.05	> 0.05	—

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Identification of Spawning Redds of Atlantic Salmon (*Salmo salar* L.) and Brown Trout (*Salmo trutta* L.) by Egg Size

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ABSTRACT

The mean diameter of eggs from spawning redds of Atlantic salmon and brown trout was obtained by recording the number of eggs covering a length of 200 mm. Eggs from 20—30 redds in three different Norwegian streams were analysed. There was a significant difference in egg size between salmon and trout, though there was some degree of overlap, especially in the River Gaula, which has a mixed population of grilse and larger salmon. For salmon, the streams having the largest spawners also had the largest egg diameters, while for trout there was not a close relationship between fish size and the mean egg diameters. Comparisons of the present results with previous data obtained by laboratory studies based on measuring each egg individually indicate that this method was sufficiently accurate to distingish between redds of salmon and trout in the field. A model analysing the interdependence of mean egg diameters from a stream and the proportions of salmon and trout is discussed.

I. INTRODUCTION

In Norwegian streams, Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) normally occur sympatrically and have similar spawning periods. Visual observation of spawning redds has been carried out for some years in Norwegian streams by using light aircraft (HEGGBERGET *et al.* 1982, 1986). By this method an assessment of the number of redds is possible, but determination of the spawning frequencies of the species is not possible. Physical caracteristics (water depth, size of the redds, size of the substratum), do not seem to be species specific in a way that make the redds distinguisable by visual observations.

Knowledge of the relative abundance of species is important for the practical management of fisheries, as in the analysis of catch regimes, and the effects of physical alterations of stream habitats and hydro-electric plants.

Although species-specific zymograms allow identification of Atlantic salmon and brown trout (MORK and HEGGBERGET 1984), the method requires advanced laboratory equipment and techniques. There is, therefore, a need for a simple field method to identify spawning redds in streams where two or more species are present.

Differences in egg size vary both between freshwater fishes (AULSTAD and GJEDREM 1973) and between marine species (BAGENAL 1971). Variation in egg size within salmonid fish species has also been described (DAHL 1918, POPE *et al.* 1961, GALL 1970).

The aim of the present study was to determine the mean size of eggs sampled from spawning redds in three different salmon and trout streams in Norway, and thereby to test a simple method for spawning-redd identification. The results of species identification based on egg size are checked with species identification based on PGI zymograms (MORK and HEGGBERGET 1984). The species composition (obtained from anglers' records) and mean egg size are compared to analyse species abundance *versus* mean egg size of the redds, within each river.

II. MATERIAL AND METHODS

Observations of spawning redds were carried out by aircraft, using the method of HEGGBERGET *et al.* 1986. Three Central and Northern Norwegian rivers, the Driva, Gaula and Alta, were investigated (Fig. 1). Eggs from 20—30 redds in each river were sampled. To reduce the effect of non-random sampling, redds sited in both shallow water (< 10 cm) and in deeper water (1 m) were analysed.
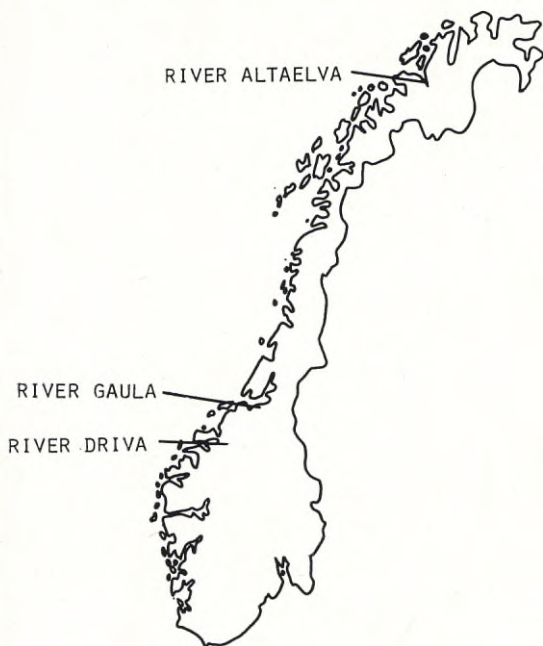
Gravel was removed from the redds and eggs

Fig. 1. Map of Norway showing the three streams studied.

were collected in a net about 1.5 m downstream from the site of excavation (BRIGGS 1953). A minimum of 30 eggs from each redd were obtained, and the mean size of eggs in the redd was estimated by determining the number of eggs covering a length of 200 mm of a ruler. Only live eggs, as determined visually, were measured. Immediately after the size determination, the egg samples from each redd were transported to hatcheries and incubated separately for further biochemical / genetic analyses (MORK and HEGGBERGET 1984).

III. RESULTS

Spawning adults of Atlantic salmon are normaly larger than those of brown trout. From this fact one would expect larger eggs in salmon than in trout (AULSTAD and GJEDREM 1973).

Diameters of eggs sampled from redds in the Gaula varied between 4.79 mm and 6.67 mm, with a mean of 5.87 mm. Corresponding measurements for the Driva were 4.76—6.06 mm, with a mean of 5.25 mm, while egg diameters from the Alta varied between 4.67 and 6.28 mm, with a mean of 5.98 mm. These mean values suggest dominance of salmon in the Alta and the Gaula, while the mean egg diameter of 5.25 mm in the Driva indicates a dominance of trout.

By using PGI zymograms, one egg of the sample from each redd was identified as either salmon or trout (MORK and HEGGBERGET 1984). When the remainder was grouped according to this species separation, the mean egg diameter of salmon was found to be significantly different from that of trout in all three streams (Table 1). The salmon eggs in the Driva had slightly smaller egg diameter than the salmon in the Alta and the Gaula. The number of salmon redds examined in the Driva was small and this difference could be due to chance alone. The fact that only two trout redds were examined in the Alta also could explain why mean egg diameter in trout for that river differs from those in the Driva and the Gaula. Comparing the trout and salmon egg measurements for all three streams, the trout had a mean egg diameter 5.14 mm and the mean egg diameter of the salmon was 6.03 mm, a difference of 0.89 mm.

Table 1. *Mean diameters of and differences (t-test) between eggs of Atlantic salmon and brown trout from the Alta, Driva and Gaula rivers. Species identification by PGI zymograms* (MORK and HEGGBERGET 1984).

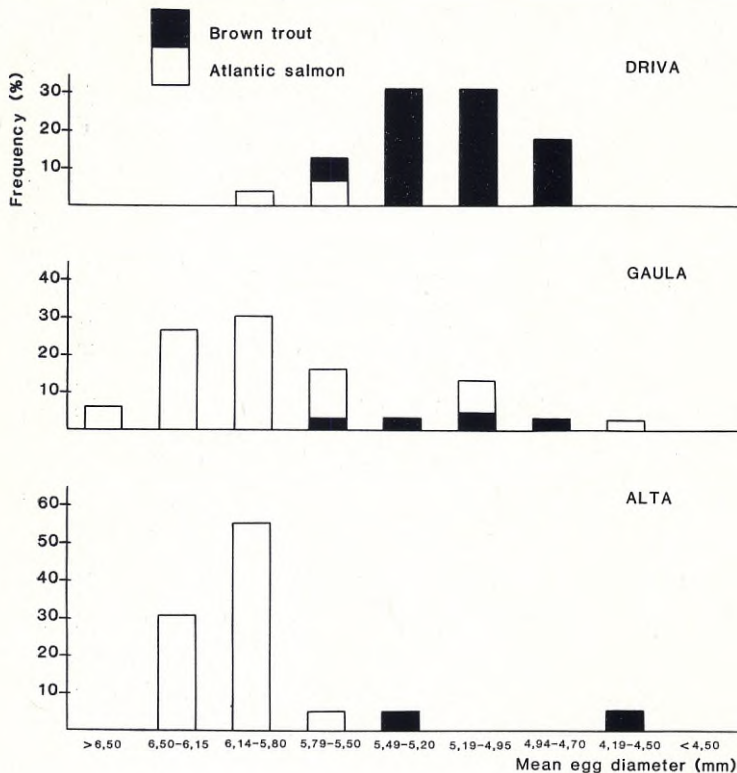|	Salmon			Trout			P
	N	x (mm)	SD	N	x (mm)	SD	
Alta	19	6.06	0.014	2	4.94	0.038	< 0.001
Driva	3	5.78	0.026	26	5.16	0.023	< 0.001
Gaula	24	6.04	0.041	7	5.18	0.023	< 0.001
All streams	46	6.03	0.032	35	5.14	0.024	< 0.001

Fig. 2. Frequencies of egg diameters in the Alta, Driva and Gaula rivers.

The mean egg diameters seem to overlap to a larger degree in the Gaula than in the other two rivers (Fig. 2). In the Alta there was no overlap, while one trout sample had an egg diameter similar to the salmon. In the Gaula, all the trout egg diameters were found to be within the range of the egg diameters of salmon, though the mean values were significantly different.

IV. DISCUSSION

The mean egg diameters varied significantly between the species, though there was some overlap, especially in the Gaula. Egg diameters from the two other streams overlapped to a lesser degree. The varying degree of overlap in egg size might be explained by the variable size of the spawners in the different streams. In the Alta, the mean size of the salmon caught in the sport fishery was 8.0 kg in 1981, while the mean size of trout was 0.5 kg in 1981 (ANON. 1981). Corresponding figures for the Gaula were 5.7 and 1.0 kg, and for the

Driva 4.8 and 2.4 kg (ANON. 1981). AULSTAD and GJEDREM (1973) observed that salmon from typical grilse rivers had the smallest egg size, showing small differences between different grilse rivers. The variation between the rivers with larger salmon was greater and some had egg diameters approximating those from the grilse rivers. In the Gaula, the salmon population is a mixture of grilse and larger salmon (GJØVIK 1981), while the Alta has a spawning population dominated by large salmon (8—10 kg). From this, one would expect a considerable overlap in egg size in the Driva, because of large trout and relatively small salmon. However, only three salmon redds were examined, the reason being that most of the presmolt Atlantic salmon in the Driva were killed in 1978 and 1979 as a result of heavy infection with the parasitic monogean *Gyrodactylus* (HEGG-BERGET and JOHNSEN 1982). The lack of overlap in egg size between salmon and trout in the Alta can be explained either by the fact that the salmon are large (8 kg) and the trout small (0.5 kg), or by the small number (2) of trout redds analysed.
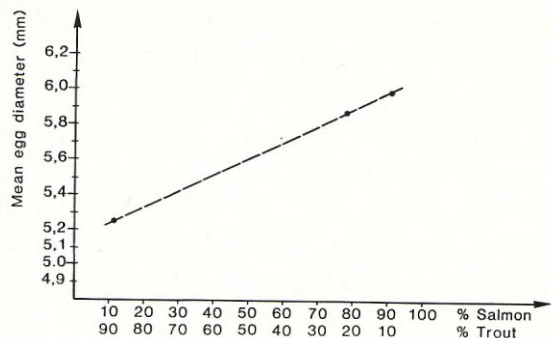
Fig. 3. Possible model of the relation between mean diameter of all eggs from each stream and the proportion of salmon to trout in the same stream. Species identification by PGI-zymograms (MORK and HEGGBERGET 1984).

There appears to be some variation in the general relationship between the recorded size of the fish in the different streams (ANON. 1981) and the mean egg size (Table 1). River Alta, with its large salmon had the largest egg diameter while River Driva had the smallest egg diameter. Concerning trout, the Alta had the smallest egg size and the smallest fish, while the trout eggs from the Driva showed an intermediate size, in spite of the significantly larger size of the spawners of trout. The Driva figures for trout are in contrast to the findings by AULSTAD and GJEDREM (1973), who reported smaller egg size from grilse than from large salmon.

The relation between egg diameters and the proportion of salmon and trout redds in the respective streams is shown graphically in Fig. 3. Based on only three streams with different proportions of salmon and trout, this model is in good accordance with the species composition shown in the anglers' records (ANON. 1982). The idea of proposing this model, is to give an example of how the data from the present study can be used to determine the species proportion of the spawning population of a stream. The model should be verified by more data on egg size from different streams to produce a regression line, before it can be used for practical fisheries management. The mean egg diameters from the three streams studied, indicate a dominance by trout in the Driva and a domi-

nance by salmon in the Alta and the Gaula (Fig. 3). Sport fishing records support this tendency: In the Driva there is a total dominance of trout due to *Gyrodactylus* infestations on salmon (HEGGBERGET and JOHNSEN 1982). In the Alta sport fishing in 1981 gave about 96 % salmon, while in the Gaula the corresponding figure was about 93 % salmon in 1981 (ANON. 1982).

Mean egg diameters for several salmonid species are given by GJEDREM and GUNNES (1978), who reported a mean of 6.2 mm for Atlantic salmon and 5.2 mm for sea trout. AULSTAD and GJEDREM (1973) reported a mean egg diameter of 5.75—5.93 mm for salmon from the Driva and 6.01 mm for salmon from the Alta. The egg size reported both by GJEDREM and GUNNES (*op.cit*) and Aulstad and Gjedrem (*op.cit*) fits well with the results of the present study. The egg size reported by Aulstad and Gjedrem (*op.cit*) was recorded by measuring each egg individually from hatchery reared fish of known strains, while the present results are based on the mean size of about 30—40 eggs from each redd. The similar results obtained by using these two different methods of measuring egg size indicate that the simple field method described in this paper is a reliable method for obtaining sufficient accuracy for egg size in the field to separate between species. The similarities between egg diameters reported by AULSTAD and GJEDREM (1973), and GJEDREM and GUNNES (1978) and the egg diameters given in this study, also indicate that a spawning redd is used either by salmon or by trout, and that there is no mixture of eggs from those species in each redd. This is also underlined by the bimodal size frequencies of the eggs from each stream analysed.

V. ACKNOWLEDGMENTS

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Validity of the Age Determination from Scales of Brown Trout (*Salmo trutta* L.)

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ABSTRACT

The present study tests the age determination from scales of brown trout of known age from 30 Norwegian mountain lakes. The scales of 2+ and 4+ trout showed mainly the true age of the fish. From age 5+ onwards, the scales commonly underestimated the fish age. This was caused by unsuccessful annulus formation and indistinct zones at the edge of the scales. A growth dependent annulus formation was documented. Specimens of age 5+ showing the true age having a length between 23—48 cm, had a minimum growth rate of 2.5 cm during the last year.

I. INTRODUCTION

Correct age determination is fundamental in fish population studies (TESCH 1971, WEATHERLY 1972), but few of the ageing methods used have been tested on wild fish of known age. Scales are most commonly used for ageing fish by counting the number of scale annuli (HILE 1970). This method assumes that the annuli are formed yearly and at the same time each year (VAN OOSTEN 1929).

However, the annulus formation may depend both on the growth rate and total age of the fish (GUNNERØD 1966). Further, JONSSON (1976) found that scales of old, sexually mature brown trout showed fewer annuli than the corresponding otoliths. This indicate that scale reading may underestimate the age of older brown trout.

The aim of the present study was to test the scale reading method on brown trout (*Salmo trutta* L.) of known age from 30 mountain lakes in Jotunheimen, Southern Norway.

II. MATERIAL AND METHODS

This investigation were carried out in lakes in Lom (Oppland County), Southern Norway (about 62°N, 9'E). The lakes are oligotrophic, subalpine and alpine situated at altitudes between 1053—1588 m, where rocks and barren ridges dominate. The lakes are usually ice free from mid-July to mid-October.

408 brown trout from 30 lakes were collected between 1971 and 1982, Table 1. The fish were sampled with series of 7 gillnets with bar mesh between 22—39 mm. The total fish length was measured to the nearest 0.5 cm. The true age of the sampled fish varied between 2—14 years. The lakes were initially barren, but were stocked with 0+ brown trout between 1961—78. Naturally reproducing stocks have not been established in any of the lakes.

Scales were removed from an area of the fish flanks between the front of the adipose and the back of the dorsal fin above the lateral line (DANNEVIG and HØST 1931, POWER 1969). From each fish, impressions of 5—6 scales containing small central plates were done on celluloid. The scales were examined and measured with use of a scale projector (100×). The least squares linear regression of fish length (y, cm) on scale radius (x, mm) were: $y = 1.58x + 71$ ($r = 0.79$). Transformation of log fish length log scale radius gave the expression $y = 1.00 + 0.80x$ ($r = 0.79$). 95 % confidence interval of the regression coefficient b were ± 0.04.

The scales from each fish were read twice. When different scales from one fish showed a varying number of annuli the largest number were used (JONSSON 1976).

III. RESULTS

The number of annuli in the scales of trout of age groups 2+ and 4+ correlated well with the true

Table 1. *Year of stocking, number of 0+ brown trout stocked and date of investigation of the experimental lakes.*

Locality	Year of stocking	Number of 0+stocked	Investigated
Glassteintjønn	1976	300	September 5, 1978
Lokkertjønn	1976	—	August 27, 1978
Mefjellstjønn	1976	—	August 27, 1978
Nedre Nufstjønn	1968	180	July 14, 1972
Sjugurdstindtjønn	1969	150	August 10, 1973
Vest Ånde	1967	60	August 8, 1971
Øvre Nufstjønn	1968	500	July 14, 1972
Øvre Høytjønn	1967	400	August 7, 1974
"	1978	312	August 9, 1982
Grunnevatn	1968	100	August 10, 1973
Ikorntjønn	1967	500	August 3, 1972
Lågtungtjønn	1967	375	August 6, 1972
Nedre Hesttjønn	1966	900	August 7, 1971
Nedre Steindalstj.	1977	100	August 11, 1982
Nedre Storgrovtj.	1977	50	August 10, 1982
Vesletjønn	1968	50	August 10, 1982
"	1977	50	August 10, 1982
Vestre Grisletj.	1967	800	August 1, 1982
Øvre Storgrovtj.	1977	50	August 10, 1982
Øvretjønn	1967	200	September 6, 1972
Øytjønn	1967	200	August 3, 1972
Nedre Uladalstj.	1969	700	August 15, 1975
Høgtungtjønn	1970	400	August 23, 1977
Vesle Lusa	1971	400	September 5, 1978
"	—	—	September 22, 1979
Merrahøtjønn	1967	1.000	August 9, 1974
Øvre Høytjønn	1969	400	August 7, 1974
"	1978	312	August 9, 1982
Leirtjønn	1967	600	August 15, 1977
Semmelholttjønn	1971	750	August 13, 1982
Aurkveé	1961	540	August 1, 1973
Bottjønn	1961	100	August 2, 1973
Nufsvatn	1961	180	July 31, 1973
Skuggevatn	1961	600	July 31, 1973
Turu	1961	200	August 2, 1973

age, and the growth rate of these specimens were high, Table 2. From age 5+ onwards, scales had often several indistinct zones at their edge (Fig. 1 a, b). The age of the oldest specimens was commonly underestimated by several years. In scales from five specimens from N. Hesttjønn the second annulus was in close proximity to the first one (Fig. 1 c), causing an underestimation of the age. Secondary annuli were detected in very few trout scales (Fig. 1 d).

Fish of age 5+ that did not form their fifth annulus, were larger at age 4 than those with a successful annulus formation (Fig. 2). The length increment from age 4 to age 5+ averaged only 2.5 cm for the former and 5.4 cm for the latter.

The length increment from age 4 to age 5 ($\Delta 5 - \Delta 4$) for specimens with true age increased with the length of the fish (Fig. 3). The minimum length in growth during this period was 2.5 and 3.5 cm for specimens with a body length between 23—37 and 38—48 cm, respectively.

The frequency of mature and immature specimens with scales showing the true age was not significantly different from that of fish with an unsuccessful annulus formation ($p > 0.05$).

IV. DISCUSSION

The experimental trout were raised to fingerlings in natural dams, subsequently most of the first

Table 2. *Mean lengths and age determination by scale reading compared to true age for different stocks of brown trout in the experimental lakes.*

Locality	Mean length (cm)	No of fish	True age	The age determined by scale reading										
				2	3	4	5	6	7	8	9	10	11	12
Glassteintjønn	23.9	34	2	33	1	—	—	—	—	—	—	—	—	—
Lokkertjønn	25.6	11	2	11	—	—	—	—	—	—	—	—	—	—
Mefjellstjønn	24.6	7	2	7	—	—	—	—	—	—	—	—	—	—
Nedre Nufstjønn	25.7	9	4	—	1	7	1	—	—	—	—	—	—	—
Sjugurdstindtj.	28.1	19	4	—	—	17	2	—	—	—	—	—	—	—
Vest Ånde	37.3	5	4	—	—	5	—	—	—	—	—	—	—	—
Øvre Nufstjønn	25.7	18	4	—	—	18	—	—	—	—	—	—	—	—
Øvre Høytjønn	23.3	6	4	—	—	6	—	—	—	—	—	—	—	—
Grunnevatn	37.4	7	5	—	—	4	3	—	—	—	—	—	—	—
Ikorntjønn	35.2	14	5	—	—	2	12	—	—	—	—	—	—	—
Lågtungtjønn	43.4	15	5	—	—	5	10	—	—	—	—	—	—	—
Nedre Hesttjønn	36.2	23	5	—	—	5	18	—	—	—	—	—	—	—
Nedre Steindalstj.	25.6	7	5	—	—	—	7	—	—	—	—	—	—	—
Nedre Storgrovtj.	26.3	8	5	—	—	—	8	—	—	—	—	—	—	—
Vesletjønn	26.3	11	5	—	—	—	11	—	—	—	—	—	—	—
Vestre Grisletj.	33.5	46	5	—	—	1	44	1	—	—	—	—	—	—
Øvre Storgrovtj.	23.7	10	5	—	—	—	10	—	—	—	—	—	—	—
Øvretjønn	32.7	16	5	—	—	9	7	—	—	—	—	—	—	—
Øytjønn	32.4	8	5	—	—	5	3	—	—	—	—	—	—	—
Nedre Uladalstj.	25.9	10	6	—	—	1	3	6	—	—	—	—	—	—
Høgtungtjønn	34.6	13	7	—	—	—	1	8	4	—	—	—	—	—
Vesle Lusa	37.4	15	7	—	—	—	4	8	3	—	—	—	—	—
Merrahøtjønn	28.2	19	7	—	—	—	8	7	4	—	—	—	—	—
Øvre Høytjønn	27.5	17	7	—	—	1	5	3	7	1	—	—	—	—
Vesle Lusa	41.3	3	8	—	—	—	—	—	2	1	—	—	—	—
Leirtjønn	42.2	22	10	—	—	—	1	—	4	12	2	3	—	—
Semmelholttjønn	36.3	12	11	—	—	—	—	—	—	1	3	7	—	—
Aurkveé	47.5	2	12	—	—	—	—	—	—	—	1	—	1	—
Bottjønn	44.5	4	12	—	—	—	—	—	—	—	1	3	—	—
Nufsvatn	43.4	7	12	—	—	—	—	—	—	5	1	1	—	—
Skuggevatn	40.7	3	12	—	—	—	—	—	—	1	—	1	—	1
Turu	43.5	2	12	—	—	—	—	—	—	—	—	1	—	1
Øvre Høytjønn	40.1	3	13	—	—	—	—	—	—	—	2	1	—	—
Vesletjønn	40.2	2	14	—	—	—	—	—	2	—	—	—	—	—

year growth rate took place prior to stocking. Naturally produced trout from a mountain lake often do not form the first scale annulus (JENSEN 1977). Thus, the scale reading of the experimental fish differs in this respect from that of self-reproducing trout stocks.

Fish of age 2+ and 4+ showed distinct zones on their scales, and annuli were mainly formed each year. Illegible zones at the edge of the scales first appeared in specimens of age 5+, and this tendency increased with age. Thus, the scale reading method is not reliable for ageing old brown trout from these high mountain lakes. However, some specimens with a good growth rate inhabiting such alpine lakes can continue to form annual zones in their scales up to an age of 17 years (HESTHAGEN 1979).

Fish between 23—27 and 38—48 cm with a successful annulus formation had a growth rate during the last year of 2.5 and 3.5 cm, respectively. For brown trout between 17—22 cm, GUNNERØD (1966) found that a yearly growth rate of 1.0—1.5 cm was sufficient to form a new annulus. Thus, it is evident that such a minimum in length increment increases with fish size. However, the age of the fish should also be considered because the time of annulus formation and seasonal growth are delayed for older trout compared to younger
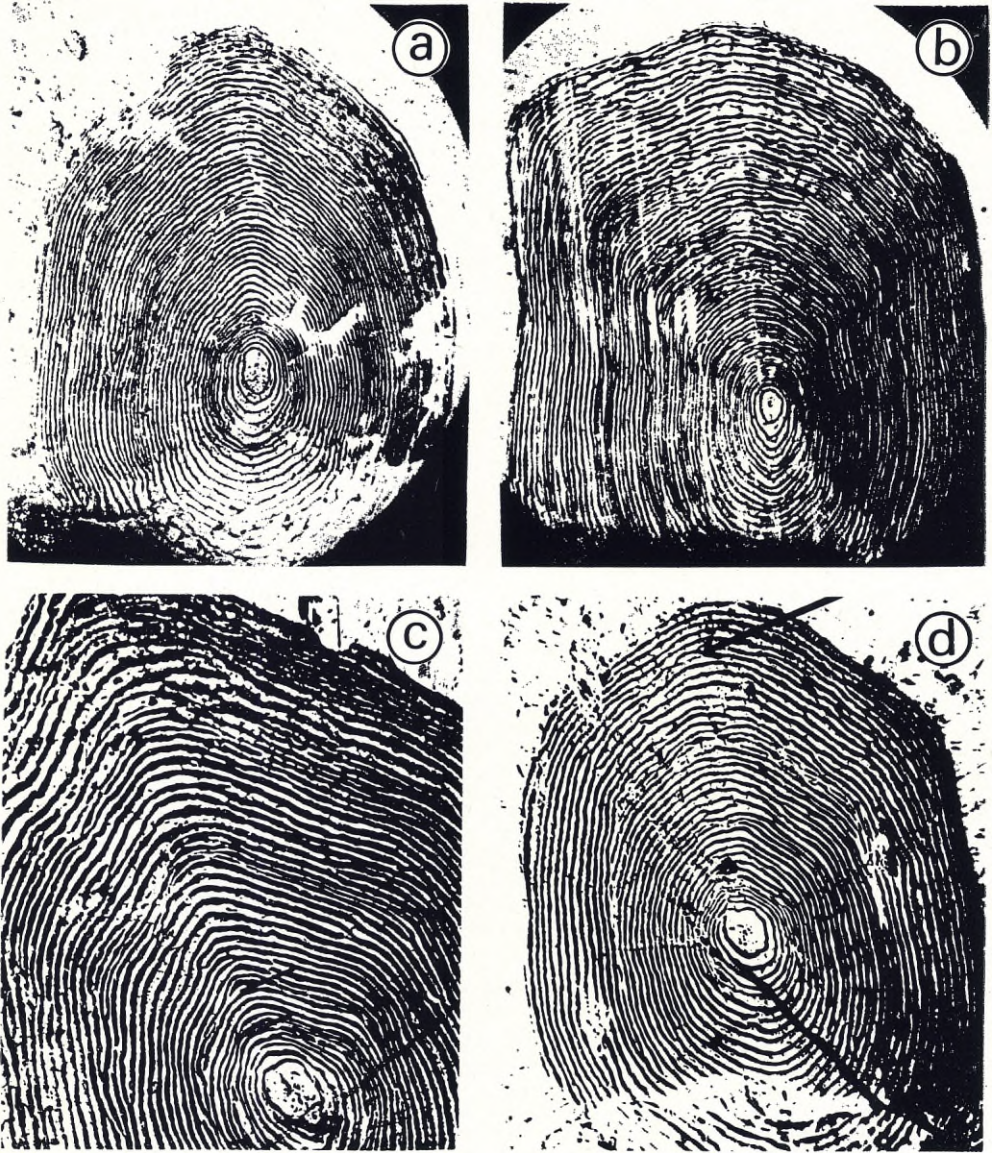
Fig. 1. Scales from brown trout from four different lakes. a) Grunnevatn: True age 5 yr. (Photo O. K. BERG). b) Leirtjønn: True age 10 yr. (Photo O. K. BERG). c) N. Hesttjønn: True age 5 yr. (Photo H. LUNDSTRØM). d) Glassteintjønn: True age 2 yr. (Photo H. LUNDSTRØM).

specimens (RUNNSTRÖM 1957, GUNNERØD 1966). The zone formation may also be different in low-land- and mountain lakes.

JONSSON (1976) found that scales from mature specimens of brown trout showed a considerably smaller number of zones than those of immature fish of the same age. However, in this study no such difference was registered. This is probably caused by a high growth rate because of low fish density and good food availabilities.

Secondary scale annuli appear to be of less importance for trout in the lakes studied. A distinct
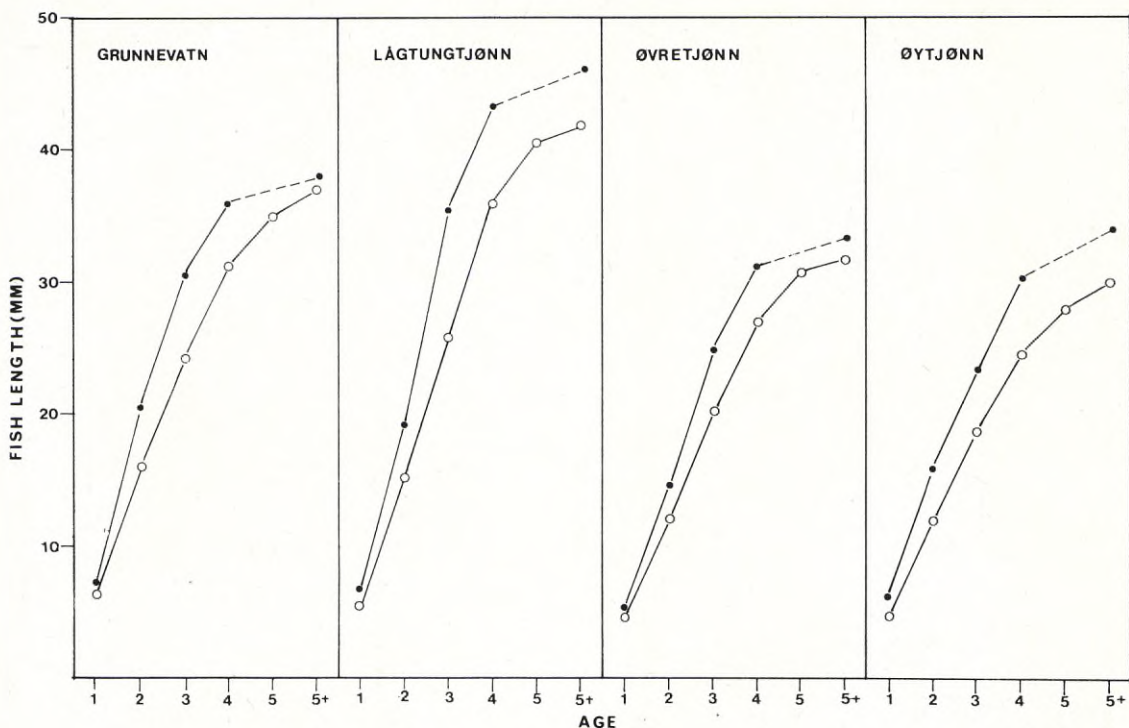
Fig. 2. Growth rate of five-year-old trout showing the true age (open marks) and that of specimens with an unsuccessful annulus formation (solid marks).
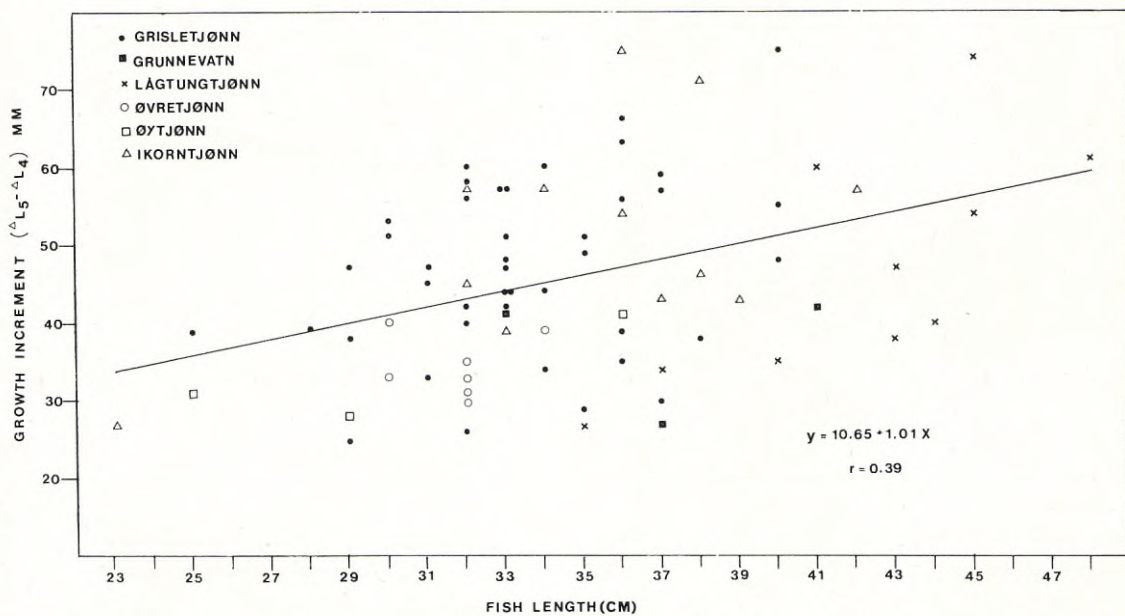
Fig. 3. Growth increment, $\Delta L_5 - \Delta L_4$, in relation to total fish length for individuals from six different populations of age 5.

growing season in such high mountain lakes is probably important in this regard. A true annulus should be fully traced around the anterior part of the scale noting distinct cutting over on each side.

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Ascent of Elvers (*Anguilla anguilla* L.) in the Stream Imsa, Norway

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ABSTRACT

Between 1975 and 1983, all elvers ascending the stream Imsa were caught. A good correlation between fresh water temperature and amount of elvers was observed.

Elver catches were best correlated to water temperature in June and July. Catches were highest during the summer, when the mean temperature in June and July was highest. Eels preferred a water temperature of 11°C or higher before migrating into the stream Imsa.

All silver eels descending the Imsa were caught before they left the stream. Average annual mortality of eels in fresh water was 14 % between 1976—79.

I. INTRODUCTION

The Imsa is situated in southwestern Norway. The water course contains 51 lakes which represent about 10 % of the total catchment area. Water quality is meso- to eutrophic (HOLMEN 1982), and the Imsa is one of the warmest streams in Norway. All ascending and descending fish are caught in fish traps. Juvenile eels migrating upstream are caught in eel ladders near the river's mouth, while downstream migrants are caught in Wolf traps (WOLF 1951) at the same location.

Eels on the northern shores of Norway, live at the limit of the species' distribution (D'ANCONA 1958 and SIVERTSEN 1962). The factors regulating recruitment of juvenile eels in this country are poorly understood. D'ANCONA (*op. cit.*) states that glass eels arrive in Denmark and Norway in May—July.

The amount of eel recruits in the Baltic is decreasing (SVÄRDSON 1976, and WICKSTRÖM 1979), and stocking of juvenile eels is common in many countries in this area (LEOPOLD 1976 and WICKSTRÖM *op. cit.*). The number of recruits required for adequate stocking is meanwhile uncertain (WICKSTRÖM *op. cit.*).

On the west coast of central Europe, supplies of glass eels have been unlimited, and TESCH (1977) claims that there is no shortage of glass eels for stocking programs. However, the recruitment of leptocephalus larvae, and the corresponding year classes of glass eels and elvers caught in the Bay of Biscay during the last 3—4 years, are small compared with previous years (TESCH *et al.* 1983).

The number of elvers in coastal and fresh waters of Norway is unknown.

This study involves the amount of elvers ascending the Imsa in the period 1975 through 1983. Water temperature is hypothesized as being the main physical factor influencing ascent of elvers into freshwater in Norway.

II. METHODS AND MATERIALS

All ascending elvers are collected in an eel ladder which is situated just below the Wolf Trap. The eel ladder was operated continuously, from the spring when the first glass eels were observed each year, until the catch was negligible. The ladder was examined at least once a week. Glass eels with an approximate length of 6.5—7.0 cm dominated catches. The other group consisted of pigmented eels with lengths 10—15 cm. One litre of glass eels contains about 2100 individuals. The total numbers of glass eels and pigmented eels were measured in ml, and they are collectively referred to as elvers.

Temperature readings were taken in the afternoon (1500—1900 Hrs), and began in August 1975.

The amount of elvers was correlated by linear correlation to the number of day-degrees. Water temperatures in May, June, July and August were used both separately and combined.

Temperatures tested were 10, 11, 12, 14, 16, and 19°C. The mean water temperature in June, July and August from 1976 through 1983 was 17.4°C. Maximum and minimum mean temperatures during these years were 19.2 and 16.4°C respectively.

Table 1. *Catch of ascending juvenile eels in the Imsa 1975—83, in. ml., and daydegrees $> 11°C$ in June and July 1976—83.*

Month/Year	1975	1976	1977	1978	1979	1980	1981	1982	1983	Total
May	3 950	—	—	—	—	—	—	—	—	3 950
June	16 500	8 150	7 675	1 450	—	4 500	—	12 750	470	51 495
July	—	13 700	5 125	2 850	330	10 110	4 390	7 300	4 070	47 875
August	—	1 300	780	1 350	840	1 950	2 880	1 700	3 120	13 920
September	—	—	—	150	—	—	100	—	—	250
Total	20 450	23 150	13 580	5 800	1 170	16 560	7 370	21 750	7 660	
Daydegrees	—	1 135	1 082	1 034	908	1 098	984	1 186	1 003	

III. RESULTS AND DISCUSSION

Strong variation in recruitment of elvers was found in the period 1975—83, Table 1, however, there was no significant decline in recruitment. The most important months for elver migration into freshwater were June, July and August (Table 1).

A positive correlation between the amount of ascending elvers and water temperature was found for the period 1976 up to and including 1983. A good correlation ($r^2=0.89$, d.f.$=6$, $p < 0.01$) between the catch of juveniles and the number of day-degrees above $11°C$ in June and July (Fig. 1, Table 1) was also discovered. Elvers apparently prefer temperatures of $11°C$ or more before ascending the Imsa, and the largest numbers were observed in years, where water temperature was $19°C$ or more in June and July ($r^2=0.94$, d.f.$=6$, $p < 0.01$).

From 1976 through 1983, water temperature in July and August was always higher than $13°C$. Therefore water temperature in June seems to be crucial for eel recruitment in the Imsa.

Juvenile eels may also enter freshwater at temperatures lower than $11°C$. TESCH (1977) quoted studies in central Europe, where water temperatures of $6—8°C$ were reported. LOWE (1951), working in the River Bann in Ireland, did not find any relationship between temperature and the start of upstream migration.

TESCH (1977) reported fluctuating annual yields of elvers in different European rivers, and the strength of a class each year often changed from river to river. TESCH (*op. cit.*) suggested that wind and surface currents in the sea should be given

more attention in order to fully understand recruitment.

Juvenile eels prefer warm water. WESTERBERG (1979) found that artificial water heating at the Barsebäck nuclear power plant on the west coast of Sweden, resulted in the congregation of as much as 10 % of the total amount of elvers destined for Kattegat and the Baltic.

The number of elvers in the Baltic area has decreased over several decades (WICKSTRÖM 1979). Many countries in the Baltic area have started stocking programs to compensate for shortages of elvers (WICKSTRÖM, *op cit.* and LEOPOLD 1976). WICKSTRÖM (*op. cit.*) recommends stocking 25—100 individual glass eels/ha/year in oligotrophic and euthrophic lakes. The Imsa is a meso- to euthrophic water-course containing 1160 ha of eel producing lakes. Necessary recruitment should be about 80,000 individuals annually. Average annual recruitment of glass eels in the period 1975—1983 was approximately 27,000 individuals, indicating that the stocking recommendation by WICKSTRÖM (*op. cit.*) is of a magnitude three times greater than that required under natural conditions in the Imsa.

The average catch of silver eels descending the Imsa was about 5000 individuals annually between 1975—1981 (HVIDSTEN 1985). Interpretation of otolith readings made age determination of eels difficult (MORIARTY and STEINMETZ 1979). HARALD-STAD (1984) used densiometry (DEELDER 1976) for age determination in the Imsa. Age was analysed in a sample of 31 silver eels collected in November, 1982. Silver eels had remained in freshwater from 3—6 years, and the mean age in the sample was 4.6 years. A total of 43,700 ml of elvers was
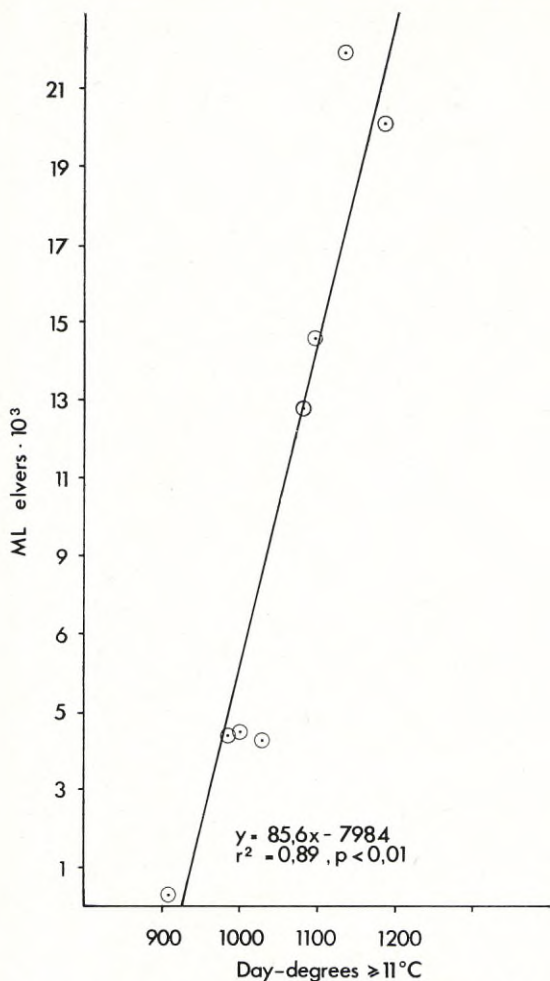
Fig. 1. Day degrees and amount of ascending elvers in June and July, 1976—83, in ml.

eels in northwestern Norway is rather low (HVIDSTEN 1982), a factor which may be partially caused by a water temperature in summer which is too low to achieve necessary recruitment.

IV. ACKNOWLEDGMENTS

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caught between 1976 and 1979. Average annual recruitment was 23,000 elvers (1976—79). In 1982, 7700 individual silver eels were caught descending the Imsa. Based upon these figures, the average annual mortality in this period was 14 %.

The mortality figures represent maximum values, as ascending elvers have always contained a minor portion of pigmented eels, and transformation of the amount of elvers in ml. to numbers of elvers leads to an overestimation of elvers.

As previously mentioned the Imsa is one of the warmest streams in Norway. The yield of silver

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Yield of Silver Eel and Factors Effecting Downstream Migration in the Stream Imsa, Norway

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ABSTRACT

All ascending and descending fish were caught in fish traps near the mouth of the stream Imsa. In the period 1975—81 the total silver eel run was caught. The average yield of silver eels was 1.9 kg/ha per year. Ten different physical factors which appear to influence the silver eel run were analysed by multiple correlation analyses. Increasing water flow was found to be the factor most important in regulating silver eel runs. The phases of the moon and atmospheric pressure were also significant factors influencing the silver eel run.

Silver eels start to descend from freshwater at a temperature of about 14°C and less.

I. INTRODUCTION

The European fresh water eel (*Anguilla anguilla* L.) is at the northern edge of its distribution in Norway (D'ANCONA 1958 and SIVERTSEN 1962). Little is known about the yield of silver eels in fresh water in Norway (JENSEN 1972, HVIDSTEN 1982). Physical parameters regulating the silver eel run have not been studied in Norwegian water-courses. The amount of ascending elvers was found to be correlated to water temperature in the Imsa. High summer water temperature occurring during June and July resulted in the greatest recruitment (HVIDSTEN 1985).

The yield of silver eels is connected with water temperature, depth of the lake, substratum and amount of food (WICKSTRÖM 1979).

JENS (1953) found that the silver eel run was correlated to synodic time in the upper River Rhine.

II. DESCRIPTION OF STUDY AREA

The Imsa is situated in southwestern Norway (Fig. 1). The 51 lakes in the water course represent about 10 %, of the catchment area. Approximately 1160 hectares of lake are eel producing. Water quality is mesotrophic—eutrophic (HOLMEN 1982). The Imsa is one of the warmest streams in Norway.

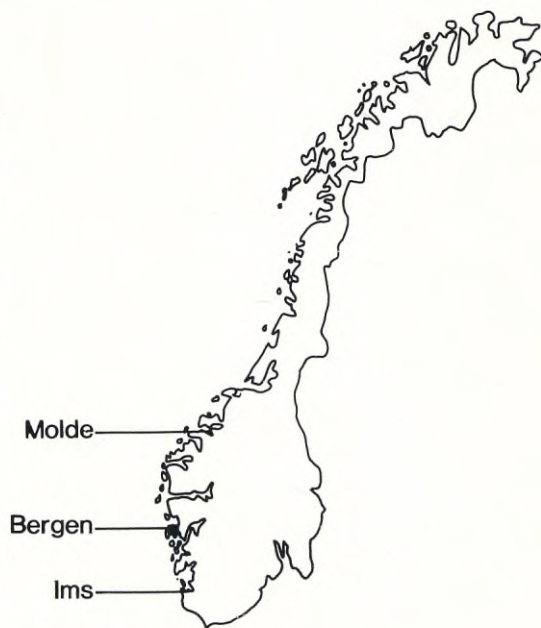In addition to eels, the fish population consists of *Salmo salar*, anadromous and stationary brown trout *S. trutta*, char *Salvelinus alpinus*, whitefish *Coregonus lavaretus* and threespined stickleback *Gasterosteus aculeatus*.

Fig. 1. Map showing Norway.

III. METHODS

All ascending and descending fish were caught in fish traps. Silver eels were caught in a Wolf-trap

(WOLF 1951) while migrating downstream. The Wolf-trap has been operated continuously since its construction in 1975.

In the period 1975 — 81 a total of 26,935 silver eels have been caught in the Wolf-trap. Additional catches, made by fishermen upstream, were included in yield estimates.

A multiple correlation analysis by the SPSS system was made (NIE *et al.* 1975) in order to study the physical parameters which were thought to influence the silver eel run.

The following parameters were analysed:

(1) Phases of the moon.

Average catch per day in synodic time as reported by JENS (1953) was used as a model for correlating the effects of moon phases and the eel run in the Imsa. JENS (*op. cit.*) found that the 22nd day in the lunar cycle was the most important day of silver eel run. In the model this day was given a score=1. All other days in the synodic period were given scores in the range 0 to 1 according to the daily catch.

(2) The average daily water flow in m³/sec.

(3) Change in water flow in m³/sec.

(4) Water temperature in °C.

(5) Positive and negative change in water temperature in °C.

(6) Rainfall measured from 07.00—19.00 hrs.

(7) Clouds were given a score 0—9.

(8) Barometric air pressure in mb. detected at 19.00 Hrs.

(9) Positive and negative change in air pressure in mb.

(10) Wind.

The effect of wind was used as a product of wind speed and direction. Wind direction was given a score +1 when the wind blew against the Imsa outlet, and score —1 with opposite wind direction.

IV. RESULTS AND DISCUSSION

The silver eel migrate downstream in the autumn. Catches in the Imsa were best in September and October in the period 1975 through 1981 (Table 1). This concurs with statements made by other authors. BOËTIUS (1967) stated that September and October are the most important times for catching silver eel in Europe.

The total average yield in the Imsa in the period 1975—81 was 1.9 kg/ha/annually. Table 1 shows the yearly catch of silver eels. Yield was unchanged during this period. Records of the yields of silver eels in freshwater are scarce in Norway. The average yield of silver eels is about 10 kg/ha/year (JENSEN 1972) in Lake Orrevatn which is located in the same area as the Imsa water-course. This lake is unique, being eutrophic, shallow and just above sea level. In some small lakes near Bergen, also situated in southwestern Norway, the silver eel yield was about 3.2 kg/ha/year (JENSEN *op. cit.*). The yields of silver eels in five different lakes situated near Molde in the Møre district (Fig. 1), were small, 0.17—1.11 kg/ha in 1980 (HVIDSTEN 1982). Peak flow hindered eel trap operation, and the results given above are minimum values. HVIDSTEN (*op. cit.*). The average weight of silver eels in the Imsa is 0.45 kg. WICK-

Table 1. *Distribution of catches of silver eels at the Wolf-trap. throughout the year.*

| Month/Year	1975	1976	1977	1978	1979	1980	1981	Total
January	—	11	25	1	1	0	0	38
February	—	1	0	0	0	1	1	3
March	—	0	10	2	0	0	0	12
April	—	1	2	0	1	1	0	5
May	0	2	16	1	2	2	0	23
June	0	0	8	3	5	2	1	19
July	0	0	27	47	8	21	72	175
August	22	12	32	230	301	73	105	775
September	2 602	55	1 971	2 371	780	548	789	9 116
October	1 508	3 006	1 955	1 509	1 083	2 182	1 168	12 411
November	932	651	1 363	258	396	229	230	4 059
December	137	85	13	5	39	49	—	328
Total	5 201	3 824	5 435	4 427	2 616	3 106	2 366	
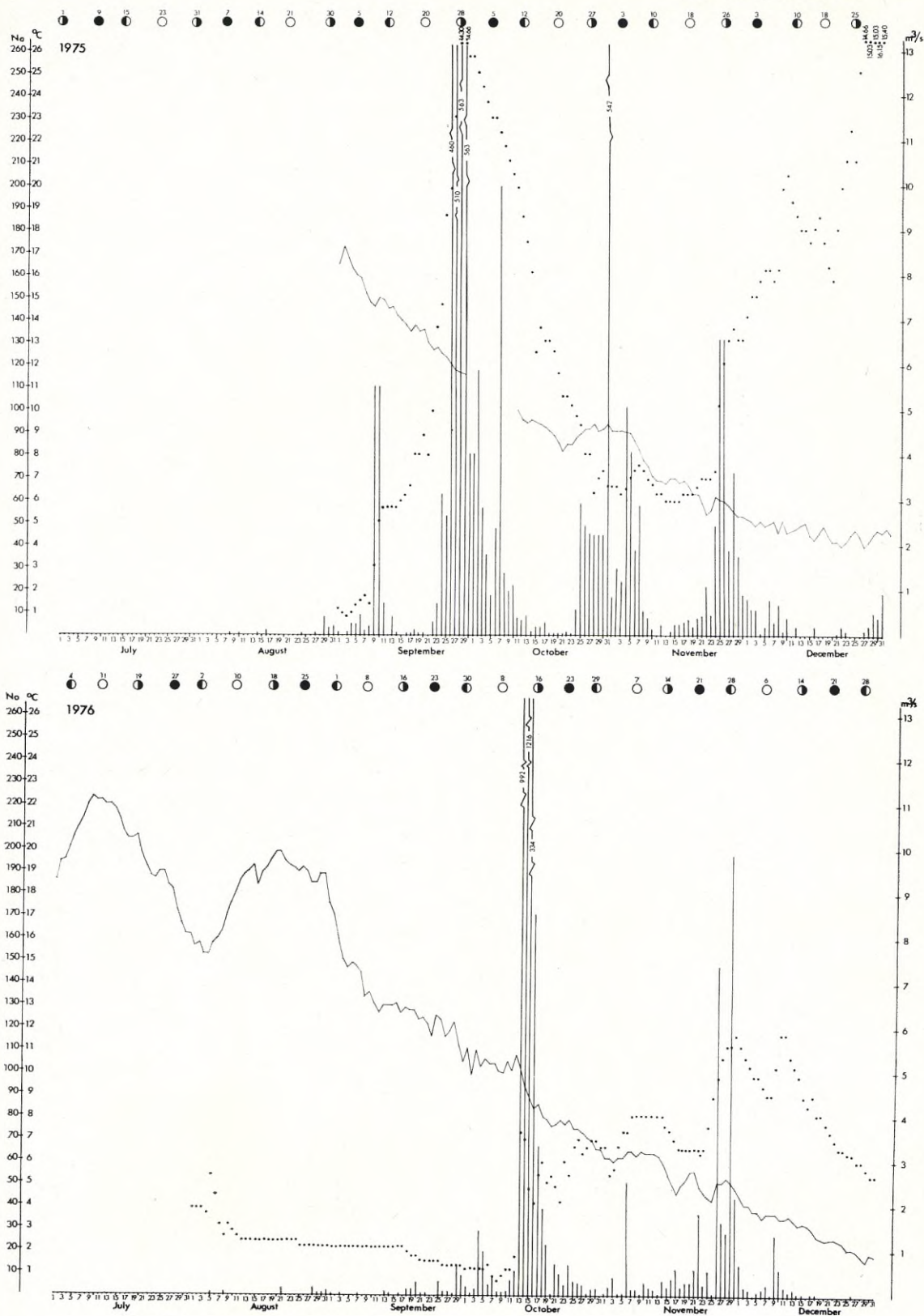
Fig. 2.
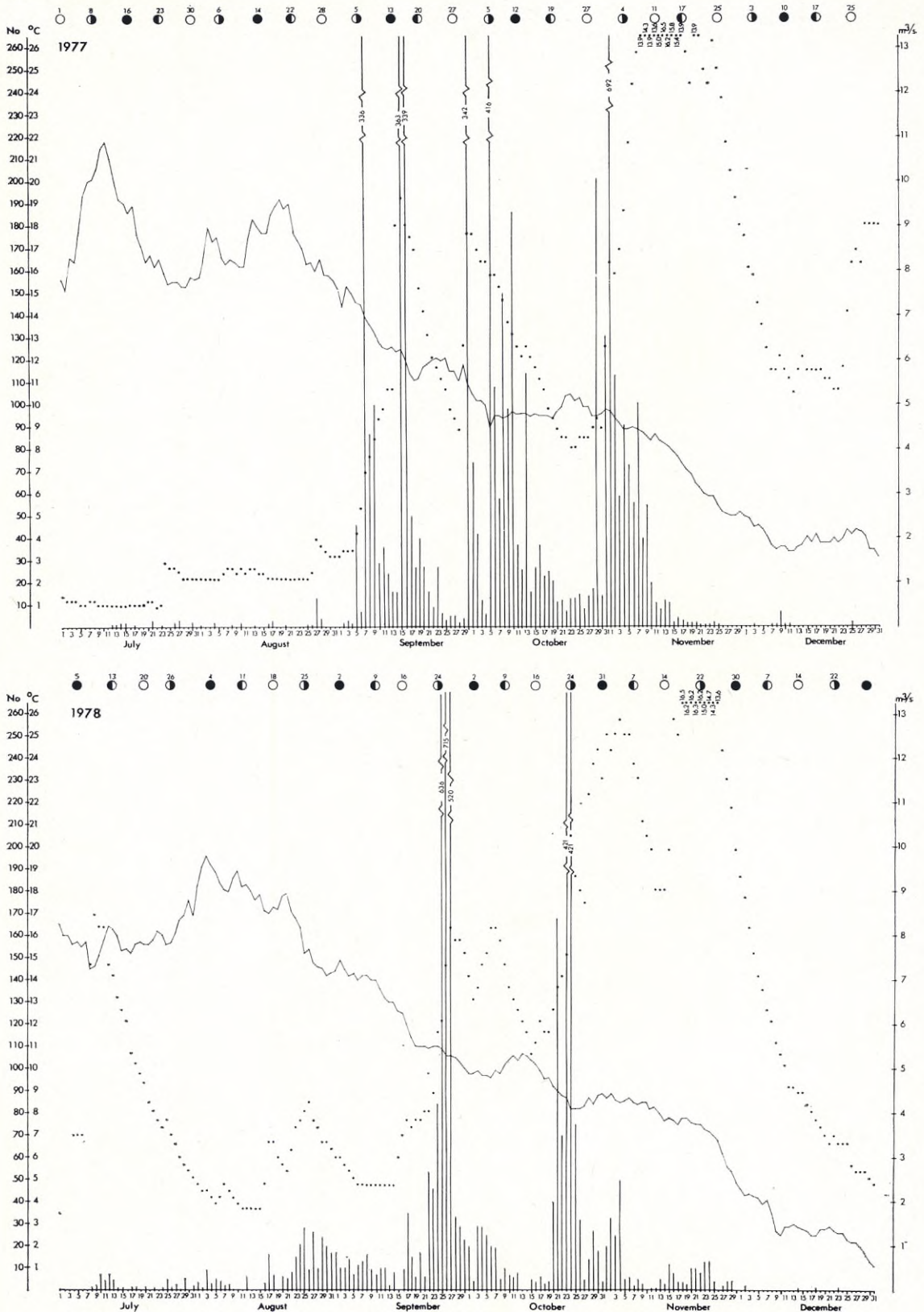
Fig. 3.
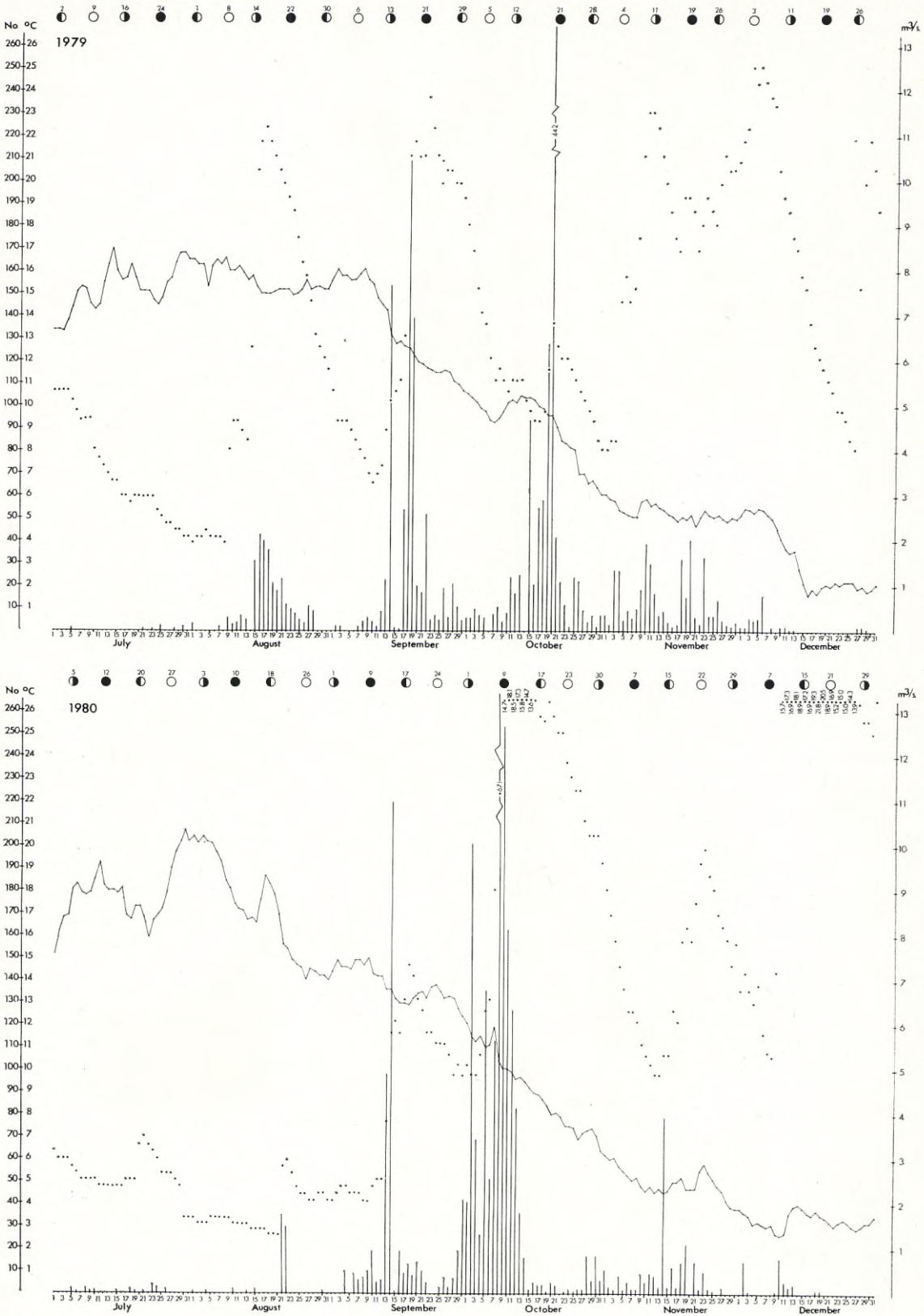
Fig. 4.
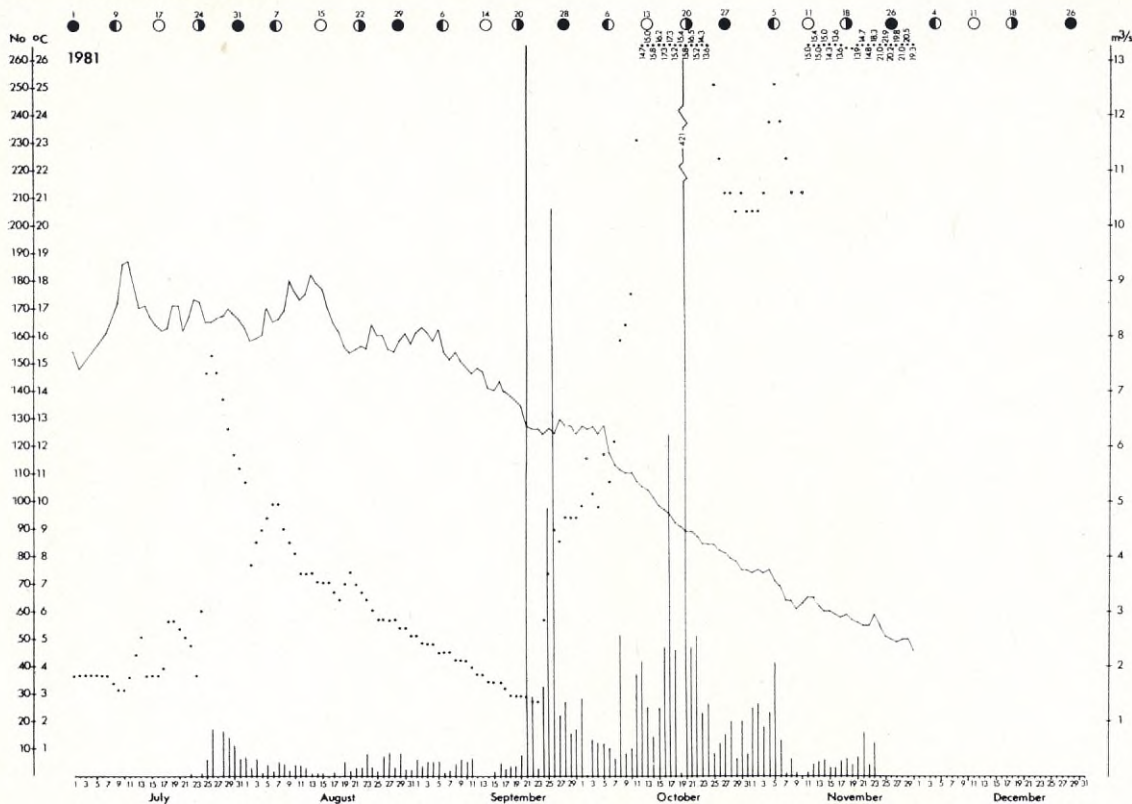
Fig. 5.

Fig. 2. The silver eel run in the Imsa autumn 1975 and 1976. The solid graph shows water temperature °C. Dotted graph shows water flow m³/s. The columns shows eel catch per day. Moon phases are also shown.

Fig. 3. The silver eel run in the Imsa autumn 1977 and 1976. The solid graph shows water temperature °C. Dotted graph shows water flow m³/s. The columns show eel catch per day. Moon phases are also shown.

Fig. 4. The silver eel run in the Imsa autumn 1979 and 1980. The solid graph shows water temperature °C. Dotted graph shows water flow m³/s. The columns show eel catch per day. Moon phases are also shown.

Fig. 5. The silver eel run in the Imsa autumn 1981. The solid graph shows water temperature °C. Dotted graph shows water flow m³/s. The columns show eel catch per day. Moon phases are also shown.

STRÖM (pers. comm.) found that 80 % of the total number were females.

JACOBSEN and JOHANSEN (1922) found a correlation between the yield of eels and water temperature in Denmark. JENSEN (1961) found a correlation between the number of eel recruits, winter and summer water temperature, and yields of yellow and silver eels in the sea. TESCH (1977) states that there is an obvious connection between the yield of eels and water temperature.

A rather low correlation was found between

the yield of silver eels in the Imsa, and the number of day-degrees from spring through the month of August. Best correlation was found when water temperature exceeded 14 and 15°C ($r=0.57$ and 0.58). The main reason for a low correlation coefficient, may be insufficient recruitment, which will prevent an optimal silver eel production (HVIDSTEN 1985).

In Figs. 2—5 the distribution of the silver eel run is shown. The parameters water flow, water temperature and moon phases are shown.

Table 2. *Water temperature* °C *and the silver eel run.*

Year	The first eel run, eels per day		The last eel run, eels per day	
	> 10	> 100	> 100	> 10
1975	14.6	14.6	6.0	4.6
1976	11.2	10.3	5.1	3.5
1977	16.0	13.9	8.9	8.1
1978	17.0	10.9	8.2	7.2
1979	15.3	13.2	9.6	5.4
1980	15.6	13.6	9.9	2.6
1981	16.5	12.7	9.5	5.9
max-min	17.0—11.2	14.6—10.3	9.9—5.1	8.1—2.6

Fig. 6. The average catch of eel per day per fishing boat in upper River Rhine, after JENS (1953).

In contrast with yellow eels, which hibernate when water temperature falls in the autumn, silver eels continue swimming when water temperature drops (WESTIN and NYMAN 1979). Table 2 shows water temperature on the day when > 10 and > 100 eels were caught in the Wolf-trap, the initial and final time in each year. Silver eels left the river over a wide range of temperature. The main silver eel run (> 100 eels) started at water temperatures from 10.3—14.6°C, and ceased at temperatures between 5.1—9.9°C. The silver eel run in the Imsa seems to start at about 14°C and less.

NYMAN (1972) stated that 14°C was a threshold temperature for yellow eel activity. When water temperature drops below 14°C yellow eels become passive.

According to Figs. 2—5 the silver eel run is influenced by periodic phases of the moon. This is evident at full moon, when the eel run is at a minimum. The interaction between the eel run and moon phases is described by JENS (1953), DEELDER (1954) and TESCH (1977).

JENS (1953) analysed the eel catch from five fishing boats (Schokker) in the upper Rhine. The distribution of these catches per day in nine years in synodic time is shown in Fig. 6. The best catch of eels was done in the moon's 3rd quarter.

Average daily catches in synodic time in the Imsa between 1975—81 are shown in Fig. 7.

Figs. 6 and 7 follow the same pattern. There are, however, differences between the results from the upper Rhine and results from the Imsa. In the Imsa, the average catch was better at the end of the moon's 4th quarter than at the beginning of
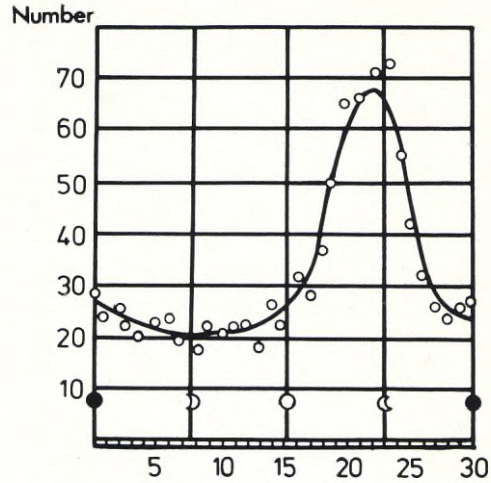
the first quarter. The results shown by JENS (1953) give the same yield in the 1st and 4th quarter.

As shown in Figs. 8 and 9, there are major differences in the time recorded for peak migrations and the moon phases in some years.

In 1979 and 1980 (Fig. 9) big catches of silver eels were recorded at the end of 4th quarter. The eel run was connected with increased water flow in both years.

In order to study the effect of possible physical parameters influencing the silver eel run, a multiple correlation analysis was made. Ten physical para-
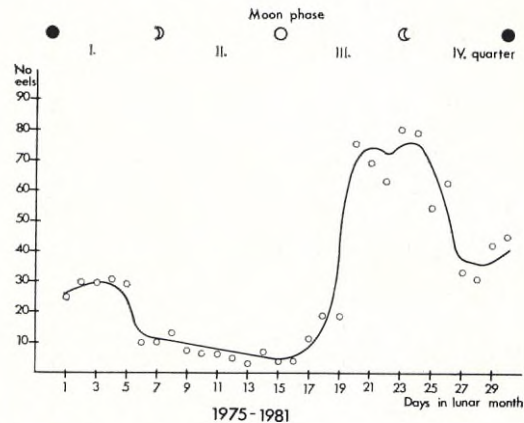

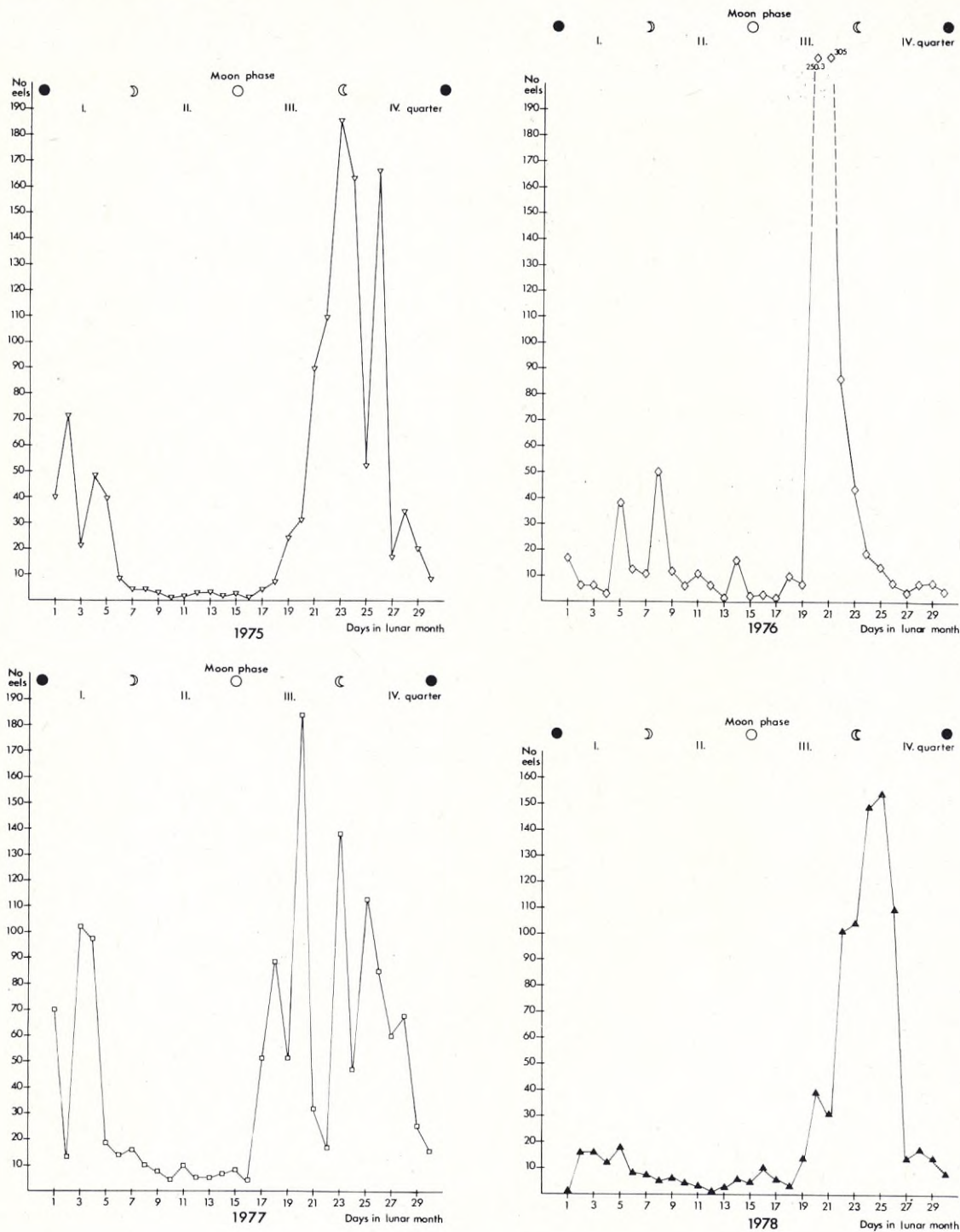Fig. 7. Average catch per day in synodic time, in the Imsa in the period 1975—81.

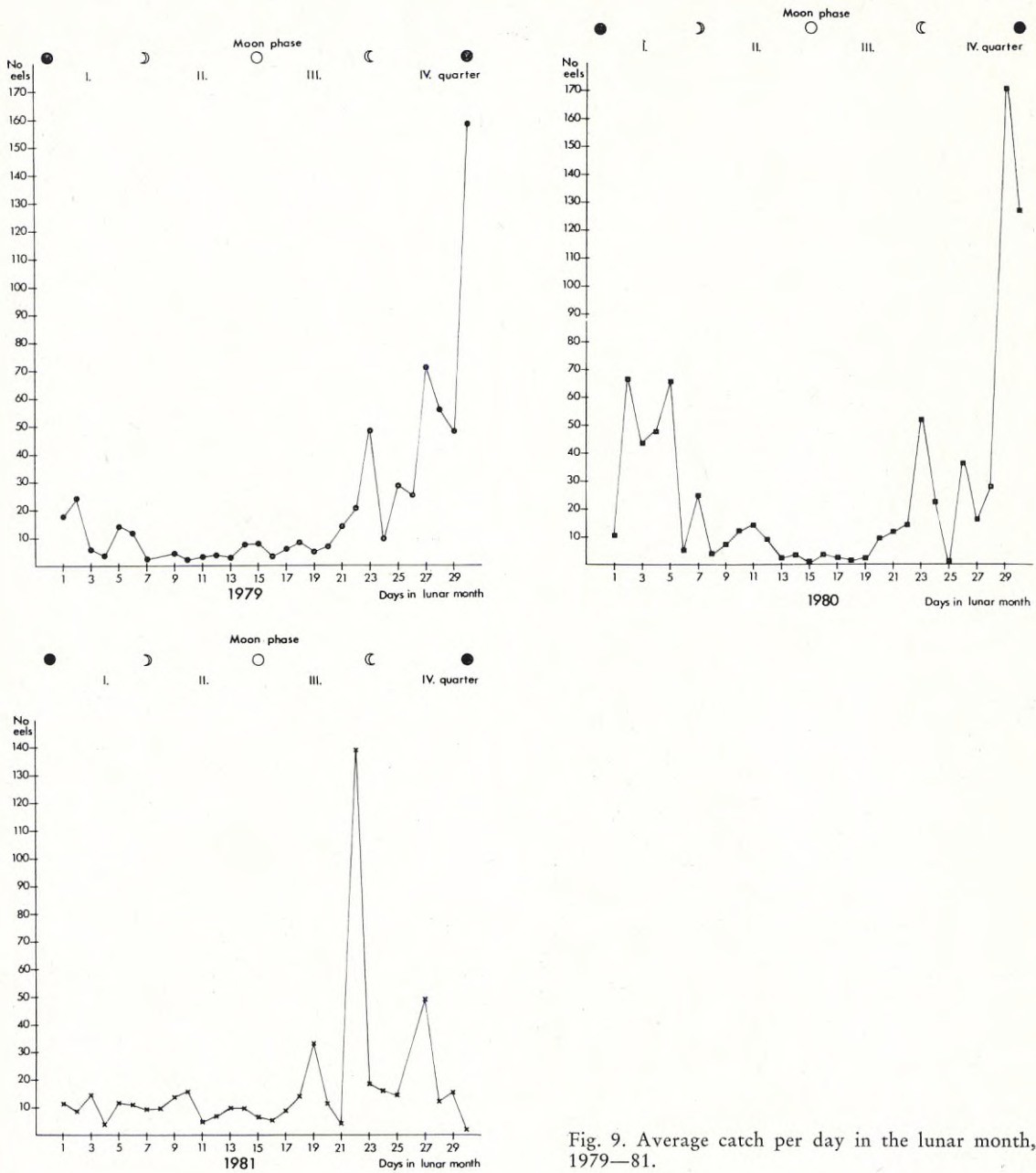Fig. 8. Average catch per day in the lunar month, 1975—78.

Fig. 9. Average catch per day in the lunar month, 1979—81.

metres were correlated to the silver eel run. In the period 1975—81 the significant physical parameters correlated with the silver eel run were ranked in order, (1) rainfall, (2) changed water flow, (3) moon phases and (4) air pressure (Table 3).

Rainfall and changes in water flow were positively correlated to the silver eel catch, while barometric air pressure showed a negative correlation.

The parameters of rainfall and increasing water flow had been expected to have the same effects on the silver eel run. The correlation between these two parameters varies because of a time-lag from commencement of rainfall until a change in

Table 3. *Multiple correlation analysis of ten different physical parameters assumed to influence the autumnal silver eel run in the Imsa.*

| Year | Score | | | | | | r^2 |
	1	2	3	4	5	6	
1975	*wat. flow p < 0.001	wat. flow p < 0.001	moon ph. p < 0.005				0.46
1976	rainfall p < 0.001	*wat. flow p < 0.001	moon ph. p < 0.001	wat. flow p < 0.025	air press. p < 0.025	wind p < 0.05	0.68
1977	rainfall p < 0.001	*wat. flow p < 0.005					0.46
1978	rainfall p < 0.01						0.09
1979	rainfall p < 0.01						0.27
1980	*wat. flow p < 0.001	air press. p < 0.001	water temp. p < 0.005				0.56
1981	moon ph. p < 0.005	air press. p < 0.005					0.31
1975—81 Total	rainfall p < 0.001	*wat. flow p < 0.001	moon ph. p < 0.01	air press. p < 0.025	;		0.18

* = change

water level was recorded. There is also a distance of 15 km between Sola, where the meterological data is recorded, and the catchment area. These factors might cause the difference in correlation between rainfall and change in water flow.

Increasing water discharge is the most important physical parameter affecting the silver eel run in the Imsa.

Connection between the rate of water flow and eel catch is well known (JENS 1953, DEELDER 1954 and SINHA and JONES 1975). JENS (*op. cit.*) correlated the eel catch to the water level in the Rhine, but increase in water flow was found to be the most significant factor in the Imsa.

In the streams Hustad, Farstad and Snipsøyrvatn in western Norway, the best catch for 1980 was made in the 2nd quarter (in August). Peak catch was connected with an increasing water flow (HVIDSTEN 1982).

In small streams in Norway, increasing water flow apparently initiates the silver eel run, despite moon phases. JENS (1953) also found that most eels are caught at high water levels, while still correlated to the moon phases. However, as shown above, in the long run there is also a significant

correlation between moon phases and the silver eel catch in the Imsa.

BOËTIUS (1967) showed that silver eels kept in aquaria in complete darkness escaped in correlation with the moon phases. The moon's 3rd quarter was the most important time for escape. BOËTIUS (*op. cit*) states that "the nocturnal, moon phase dependent, autumnal migratory activity of silver eels is independent of light, daylight as well as moonlight".

The last significant factor influencing the silver eel run in the period 1975—81 is barometric air pressure. Air pressure and rainfall are associated factors.

In some years other parameters were significant. In 1976 wind was positively correlated with the silver eel run. FROST (1950) says that when the wind blows in the direction of the outlet of Windermere, the eel catches are greatest.

V. ACKNOWLEDGMENTS

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Growth and Smolt Age of Atlantic Salmon (*Salmo salar* L.) in the Glacier River Beiarelva, Northern Norway

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ABSTRACT

The growth of the Atlantic salmon parr population in the cold, oligotrophic glacier-fed River Beiarelva in Northern Norway was studied from 1975 to 1981.

The annual growth was found to be 20.9 ± 1.4 mm, which is about the slowest growth hitherto reported for parr of Atlantic salmon. A considerable part of the yearlings still lacked scales in May.

85 descending smolts collected in May from 1977 to 1981 had a mean age of 5.4 years and an average length of 136 mm. The smolt length increased with age.

Scale analyses of 558 adult salmon caught in River Beiarelva in the period 1974 to 1980 showed a mean age at migration to sea of 4.4 years. This is obviously too low, because of problems with identifying the first winter zone in some scales, and supply of smolts from warmer tributaries.

Water temperature is supposed to be the main factor controlling growth in this river. The temperature conditions in River Beiarelva are probably close to the limit for survival of Atlantic salmon.

I. INTRODUCTION

In his paper "Age and growth of salmon and trout in Norway" DAHL (1910) showed that the age of salmon smolts at migration increased with the rise of latitude, or in other words, with the fall of water temperature. The range was from 2 to 5 winters at migration. SØMME (1941) examined scales of adult salmon taken in the River Repparfjord, one of the most northern salmon rivers in the world. He found that the smolts had migrated at surprisingly high ages, 5 winters at migration being quite common and 6 winters occurring not infrequently. He even found 7-winter-old smolts to occur. POWER (1973) investigated the growth of salmon parr in some North Norwegian rivers. He found that annual length increments averaged 30 mm, and that most salmon parr migrated to sea during their fourth or fifth summer. POWER (1969) found in the rivers of Ungava Bay, North America, high salmon smolt ages ranging from 4 to 8 years, and a mean age at migration of more than 5 years. Several workers, (EMBODY 1934, BROWN 1946, 1957, SWIFT 1961, ELLIOTT 1975 a, b) have demonstrated the effect of different temperatures on growth rates of salmonids in experimental or cultural conditions. EGGLISHAW and SHACKLEY (1977) with basis in their field observations in Shelligan burn, discuss the close relationship between the size attained by salmon and trout after one growing season, and the daydegrees above $0°C$ to this time from egg deposition.

The purpose of this investigation was to study the parr growth and the smolt age of salmon in this cold, oligotrophic glacier-fed river, with a water temperature probably close to the limit for survival of Atlantic salmon.

II. DESCRIPTION OF THE RIVER

River Beiarelva is situated in the county of Nordland, Northern Norway ($67°N$, $14,47'E$). The drainage area is about 1050 km² and the river is one of the largest salmon rivers in the county of Nordland with a total catch of salmon, anadromous brown trout (*Salmo trutta* L.) and anadromous Arctic char (*Salvelinus alpinus* (L.)) of 5—8 tons/year.

Some of the largest tributaries drain the glacier Svartisen, giving River Beiarelva a greygreen

Table 1. *Mean and range of temperatures in the River Beiarelva in July and August 1976—80. The temperature was measured at 07.30 and 17.30 each second day by the Norwegian Water Resources and Electricity Board, Hydrological Department.*

		1976	1977	1978	1979	1980
July	Min.	4.0	4.2	9.1	5.4	6.0
	Mean	6.7	6.4	11.1	8.4	9.0
	Max.	9.2	9.2	13.2	11.7	12.9
August	Min.	4.2	7.8	6.8	6.5	4.9
	Mean	7.9	9.5	9.0	9.4	9.2
	Max.	11.1	10.9	11.4	11.3	15.0

colour in summer. This makes River Beiarelva a cold river (Table 1); probably one of the coldest salmon rivers in the world.

III. MATERIALS AND METHODS

Salmon fry and parr were collected by electro-fishing in May and August each year from 1975 to 1981, and preserved in formaldehyde for laboratory study. The total length of the fish was measured by spreading the tail into a natural position.

Scale samples were taken in an area near the lateral line between the adipose and the dorsal fin (DANNEVIG and HØST 1931). Age determination was done using a binocular microscope with the scales in water. In most cases also the otoliths were analysed. About 900 salmon fry and parr were investigated.

The mean yearly growth was determined by calculating the length increment in the same year class from year to year (May to May or August to August). Most smolts leave the river as 4+, 5+ or 6+. For this reason all fish 4+ or older in August and 5+ or older in May were excluded from the growth calculations. Samples smaller than ten were omitted.

In May 1977—81 some salmon smolts were each year caught in the river. Length and age of 85 smolts have been analysed.

From 1974 to 1980 scale samples from 620 adult salmon were collected from local fishermen. In 558 the length of their river life could be determined.

IV. RESULTS

Salmon fry sampled in August were only 27—30 mm long, and in May the next year 32—40 mm (Table 2).

Table 2. *Mean length (mm) of juvenile salmon from River Beiarelva. N: number, L: mean length, CL: 95 %* confidence limit.

Age	Aug. 15, 1975 N	L	CL	Aug. 10, 1976 N	L	CL	May 3, 1977 N	L	CL	Aug. 11, 1977 N	L	CL	May 5, 1978 N	L	CL	Aug. 10, 1978 N	L	CL
0+	16	27	0.6	12	27	1.0	0	—	—	2	27	1.0	0	—	—	4	29	1.5
1+	22	49	2.7	9	46	1.7	17	32	1.0	12	44	2.5	22	33	1.3	10	55	3.0
2+	8	65	5.2	14	68	2.0	31	59	1.6	15	67	2.8	30	52	1.7	5	78	18.7
3+	7	94	6.8	6	90	5.0	17	82	2.1	6	90	2.5	45	77	1.9	8	98	8.6
4+	0	—	—	1	121	0	27	109	3.0	3	108	8.0	44	108	3.3	3	121	3.5
5+	1	127	0	0	—	—	13	130	10.2	0	—	—	23	135	5.7	0	—	—

Age	May 6, 1979 N	L	CL	Aug. 2, 1979 N	L	CL	May 8, 1980 N	L	CL	Aug. 8, 1980 N	L	CL	May 6, 1981 N	L	CL
0+	0	—	—	1	28	0	0	—	—	6	30	2.5	0	—	—
1+	26	36	1.3	7	54	7.2	30	38	1.3	34	63	2.9	38	40	1.3
2+	13	56	1.6	5	76	5.6	59	60	1.2	8	84	3.9	68	61	1.1
3+	8	71	1.3	2	102	0.7	10	77	3.0	5	109	11.5	44	80	1.6
4+	11	94	6.8	3	116	11.2	6	95	8.9	6	124	16.7	43	98	2.2
5+	11	116	5.4	1	133	0	7	114	7.4	0	—	—	29	113	4.4

Table 3. *Age and size of Atlantic salmon smolts caught in the River Beiarelva in May 1977—81.*

Age (years)	Number	Length (mm)	95 % CL
4	10	124.7	8.1
5	36	133.7	4.6
6	32	141.0	4.1
7	7	140.3	12.5
5.4	85	135.9	3.0

The yearly mean growth increment for parr was 20.9 ± 1.4 mm. The variation from year to year was rather small.

A considerable part of the yearlings caught in May still lacked scales, especially those born in 1976 and 1977 (see: Table 1 for temperature conditions). In these year classes 76 and 64 % of the yearlings lacked scales, while the corresponding data for the 1978 and 1979 year classes were 19 and 10 % respectively. Age determination by scales only will for this reason underestimate the age of a fraction of this salmon population. Further information is given by JENSEN and JOHNSEN (1982).

The age of salmon smolts caught in River Beiarelva in May varied from 4 to 7 years (Table 3). Most individuals were 5- or 6-years old. The mean smolt age of the whole material was 5.4 years, and the mean length was 135.9 mm. The smolt length increased with age.

From scale samples of 558 adult salmon the mean age at migration was 4.4 years (Table 4), while the range for seven years was 4.3—4.8 years. This is obviously too low, as some fish probably

Table 4. *Age at migration to sea of adult Atlantic salmon caught in the River Beiarelva 1974—80.*

Year	Age at migration						Mean age
	2	3	4	5	6	7	
1974	0	0	6	10	1	0	4.7
1975	0	2	14	19	3	0	4.6
1976	0	2	17	16	8	1	4.8
1977	0	3	26	39	5	3	4.7
1978	0	17	79	51	4	2	4.3
1979	0	15	79	46	6	0	4.3
1980	1	9	41	29	4	0	4.3
Total	1	48	262	210	31	6	4.4

lacked the first annulus in their scales. In addition, some smolts had apparently grown up in some warmer tributaries, with a better growth than in the main river.

V. DISCUSSION

The growth of salmon parr in River Beiarelva of 21 mm/year is about the lowest growth hitherto reported for salmon parr. POWER (1973), who investigated the growth of salmon parr in some other rivers and streams in Northern Norway, concluded that the growth was similar in all waters, with an annual increment of about 30 mm, and that most salmon migrate to sea during their fourth and fifth summers. But his raw data indicate somewhat slower growth on two localities, Rivers Storelva and Russelva, where the growth was probably not significantly higher than for the salmon parr in Beiarelva.

In the rivers of Ungava Bay in Canada POWER (1969) found annual growth rates of 30 mm. In River Leaf that supports the most northerly known population of anadromous Atlantic salmon in Canada, LEE and POWER (1976) found that the river growth averaged 40—50 mm/year. The smolts averaged 258 mm fork length and 5.3 years of age (range 4 to 7).

The very slow growth rate of salmon parr in River Beiarelva is probably mainly caused by the low water temperature. The river is to a great extent influenced by melt water from the glacier Svartisen, and is extremely cold.

ELLIOTT (1975 a, b, 1976) analysed the growth rate of brown trout fed on maximum and reduced rations at different weights and different water temperatures. This enables one to estimate the extent to which variations in growth rates of trout populations in rivers are determined by ambient temperature regimes rather than by other environmental variables or by genetic factors. ELLIOTT's growth model for trout on maximum ration has been used to the brown trout from River Beiarelva. Daily temperatures were used to calculate growth. Observed growth rates were always higher than computed maximum growth rates and indicated that food is in excess to the

brown trout in River Beiarelva. Details will be published elsewhere.

A corresponding growth model for Atlantic salmon in lacking, but the two species are very similar in methods of feeding, growth, behaviour and distribution (ALLEN 1969). The principal difference seems to be that the trout is not quite as closely related to the bottom as the salmon, lying higher in the water, consistently taking more food at the surface and feeding more on the drift and less on the bottom. Hence, we might believe that the growth rate of the Atlantic salmon too is determined mainly by the temperature regime in River Beiarelva.

At temperatures below 7°C juvenile Atlantic salmon move from riffles to pools and reduce or cease feeding (ALLEN 1940, 1941). GARDINER and GEDDES (1980) saw few young salmon when the water temperature fell below about 5°C. At water temperatures of 6 to 7°C the fish came out of hiding. Because growth of Atlantic salmon is slow at temperatures below 7°C (ALLEN 1969), SYMONS (1979) chose to define the growing season as the number of days per year in which the water temperature reaches or exceeds 7°C. He supposed that approximately 550d at or above 7°C are required to produce a 15 cm smolt. In Beiarelva the growing season according to this definition is usually 55—70 days per year, requiering 7—9 years to produce a 15 cm smolt. This is obviously too high. Hence, SYMON's definition does not fit such cold rivers as River Beiarelva.

POWER (1969), working in the most northern salmon rivers in Canada, in Ungava Bay, supposed that the limit for survival of salmon appears to be reached, at least in northern Canada, when the period with a mean temperature of 43°F (6°C) or higher falls below 100 days. Since then, LEE and POWER (1976) reported a salmon population in River Leaf, Ungava Bay, where the period with a mean temperature of above 43°F was 80 days. The corresponding period for the River Beiarelva is about 70 days. In northern Canada the Atlantic salmon may be prevented from penetrating to some areas, for example Hudson's Bay, by the distance it is necessary to travel through arctic water to reach the rivers (POWER 1969). In Norway, however, the warm Gulf Stream makes the sea water temperature high enough for Atlantic salmon to reach any river. Some of the rivers in northern Norway are extremely cold, among them Beiarelva. Hence, the limit for survival of Atlantic salmon should be sought in these rivers. The temperature conditions in Beiarelva are probably close to this limit.

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The Seasonal Growth of Brown Trout (*Salmo trutta* L.) and Arctic Char (*Salvelinus alpinus* L.) in a Man-made Reservoir, and Its Energy Basis

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ABSTRACT

The Nesjö reservoir in the central part of Norway was made by impounding 39 km² of land in 1970. In 1972 fish was netted 6 times between break-up of the ice in mid-June and the formation of ice in the beginning of November. The seasonal growth pattern was similar for brown trout and Arctic char, with exceptionally high growth rates, 1.9 % day⁻¹ for fish of initial size 20 cm or 8.7—8.9 % day⁻¹ calculated for fish of unit weight, during the first 2—3 weeks. Thereafter the growth declined. The Arctic char grew better than brown trout at temperatures below 11°C. The stomachs were fullest in mid-June, when both species ate Chironomidae larvae almost to satiation. The fullness was less, but still high, throughout the rest of the season, as the char turned more and more to crustacean plankton, and the trout to crustaceans, juveniles of burbot, and earth worms. During the whole growth season, Arctic char consumed 49 % Chironomidae, 48 % Entomostraca, and 4 % of other items. For brown trout these figures were 49, 23 and 28 %. Weighted against periodical growth, the values for trout did not change, but the production of char was based upon 38 % Chironomidae, 57 % Entomostraca and 5 % of other prey organisms. Special attention is drawn to the importance of Chironomidae as food for fish and the high production of fish in such ecosystems.

I. INTRODUCTION

The growth pattern of brown trout has been studied in ponds by SWIFT (1955, 1961) and under laboratory conditions by many fish biologists, *e.g.* WINGFIELD (1940), BROWN (1946) and ELLIOTT (1975 c). SWIFT (1964) and JOBLING (1983 b) have tested the effect of temperature on the growth rate of Arctic char.

Research on fish in the Nesjö reservoir during 1970—74 provided data for analyses of the seasonal growth and growth rates of these two species. The reservoir is located in the central parts of Norway (63°N and 12°E), just below the tree line. The reservoir was made by impounding 39 km² of land, mainly wetland, in 1970. The water level fluctuates between 706 and 729 m a.s.l. At level 722.4 m it joins the Essand reservoir of 27 km², regulated 6 m since 1950.

The situation was very favourable for seasonal growth analyses under natural conditions. The annual growth of both species was much larger than in most normal lakes at these latitudes. The growth at short intervals could therefore be measured more accurately, and the annuli of the scales

were clearly marked. Under ordinary conditions such an analysis upon Arctic char would be very difficult or impossible. Further the reservoir is unstratified, so every fish is exposed to the same temperatures. 1972 was the year sampled most frequently, and the only year when the succession of the fish populations provided enough material of both species.

II. MATERIAL AND METHODS

The fish were caught by standard series of nets of mesh sizes 19.5 to 45 mm knot to knot, effective with salmonids of length 17 to 40 cm. The brown trout population was the remainder of that of the impounded rivers. The Arctic char were mainly invaders from the Essand reservoir, after the water level passed 722.4 m on July 28, 1971. In order to exclude fish reaching the reservoir during the growth season of 1972, the fish for growth analyses were selected on the following basis. From scale readings only trout, which had stayed in the Nesjö reservoir the summer before, were considered. For each sampling, Arctic char were

chosen from the one showing the highest increase in length and downwards, until the standard deviation (s) equalled the maximum standard deviation of the samples of brown trout, defined by the equation: $s = 0.15 \, L_i$, L_i being the mean periodical length increase in cm. The fish length was measured to the fork.

For the fish length in cm (L) on scale radius in mm (R) the following linear regressions were found:

Brown trout: $L = (16.4 \pm 0.7)R + 3.7$
$(r = 0.93, \, p < 0.001)$

Arctic char: $L = (31.8 \pm 1.1)R - 1.0$
$(r = 0.90, \, p < 0.001)$

Thus the increase in fish length could be calculated proportionally from differences between annuli on the scales, which were read on impressions by a microprojector. The age of both species was from 2 to 9 years.

Linear regressions of fish weight in g (W) on length in cm (L) of fish < 30 cm caught in June 1972 gave these relations:

Brown trout: $W = 0.0130 \, L^{2.979 \pm 0.045}$
$(r = 0.99, \, p < 0.001)$

Arctic char: $W = 0.0108 \, L^{3.020 \pm 0.081}$
$(r = 0.96, \, p < 0.001)$

As regression coefficients were so close to 3, weights for the growth analyses were calculated as

$$W = KL^3 \cdot 100^{-1}$$

where K is Fulton's condition factor.

The mean specific growth rate of weight as $\%$ day^{-1} (Gw) was calculated according to

$$Gw = \frac{\ln W_2 - \ln W_1}{t} \cdot 100$$

where W_1 is the initial and W_2 the final weight in g during a growth period of t days.

From $\ln Gw = \ln a + b \ln W$

the growth rate of fish of unit weight, $Gwu = a$, was calculated. This is a convenient measure for the elimination of the size-dependent factor when comparing growth rates (JOBLING 1983 a). The exponent b has been calculated to -0.325 for both trout and char by ELLIOTT (1975 c) and JOBLING
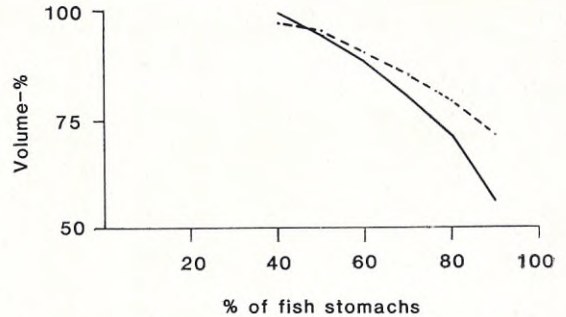

Fig. 1. The volume per cent of dominating items in different fractions of stomachs of brown trout (solid line) and Arctic char (broken line) from the Nesjö reservoir 1972.

(1983 b), a value which will be used in the following calculations.

When possible the content of at least 25 stomachs of each species were collected, but from August onwards there were fewer stomachs of brown trout available. The relative proportion of different prey organisms in the individual stomach was estimated as volume-$\%$. The fullness of the stomach of every fish caught was estimated in a 5-step scale from empty (0) to full (1). The mean volume-$\%$ (V) and mean fullness (F) were calculated for each sample.

The individual wet weights (Q) in mg of the content of 237 stomachs were found. Between QW^{-1} and the mean fullness of stomachs for each step (F), this linear relationship existed:

$$QW^{-1} = 19.0F - 0.7$$

This establishes the basis for calculating mean F. The product VF expresses the amount of each prey consumed for each sample.

These salmonids are to a high degree selective in their feeding, and this is even more the case in a reservoir, where the spectrum of prey organisms is limited (Fig. 1). Thus each individual stomach should be analysed qualitatively. The procedure followed is judged to give more correct information than methods allowing the fullest stomachs to influence to a great extent the quality of the diet, *e.g.* the often used point method of HYNES (1950).

The importance of the different species of crustacean plankton was found by pooling the content of such stomachs, counting a sub-sample

Table 1. *Increase in length (cm) of brown trout and Arctic char of different initial lengths in 1971, based on material of June 1972 from the Nesjö reservoir.*

Initial length	10—12	12—17	17—22	22—27	27—32
Brown trout	11.1±0.2	11.9±0.1	11.8±0.1	11.3±0.2	10.7±0.3
Arctic char	—	10.4±0.5	10.9±0.1	9.4±0.1	8.5±0.4

of 200, measuring the length of 30 individuals of each species, transforming their mean lengths to mean dry weight according to BOTTRELL *et al.* (1976), and multiplying these weights by the numbers counted.

Among the trout there were only two spawners. The spawning char leave the Nesjö reservoir for the spawning grounds in the Essand reservoir during August—September. This study therefore only considers immature fish. The material comprises 574 trout and 471 char, and 210 stomachs of the first and 257 of the second species.

III. RESULTS

The increase in length of both species during 1971 did not vary much for fish of initial lengths 12 to 27 cm (Table 1). The further analyses are therefore based on fish within that length interval, handled as one group.

In 1972 growth in length for both species took place from mid-June to the end of September (Fig. 2a). This was verified by control of fish caught in June and July 1973, giving the same total length increase for 1972, 9.3±0.1 cm for brown trout and 7.2±0.1 cm for Arctic char. The length increase of trout was even until mid-August, thereafter decreasing gradually. Apart from the first two and the last three weeks, the char grew less in length and very evenly throughout the entire growth season. On September 9 the mean length increase of maturing char was 4.3±0.1 cm compared to 6.0±0.1 cm for immature char. Before that date there was no difference, and afterwards the spawners left for the spawning grounds in the Essand reservoir.

The specific growth rate in weight (Gw) has been calculated for fish of initial length 20 cm, a size with increases in length close to the means of the chosen length interval (Table 1). It was

very high for both species, close to 1.9, during the first 17 days and gradually decreased thereafter throughout the growth season.

The specific growth rate is influenced by three main factors; the individual decline with increasing body size, the temperature, and the access of food. The last factor is further dependent on the biomass of the population.

In Fig. 2b the size dependent factor, set to $W^{-0.325}$ according to ELLIOTT (1975c) and JOBLING (1983b), has been eliminated by transforming growth rates to that of fish of unit weight (Gwu). For brown trout Gwu was 8.7 until mid-July. Later it fell evenly, but steeper than if controlled by temperature alone, as the optimum temperature 12.8°C (ELLIOTT 1975c) was reached in mid-
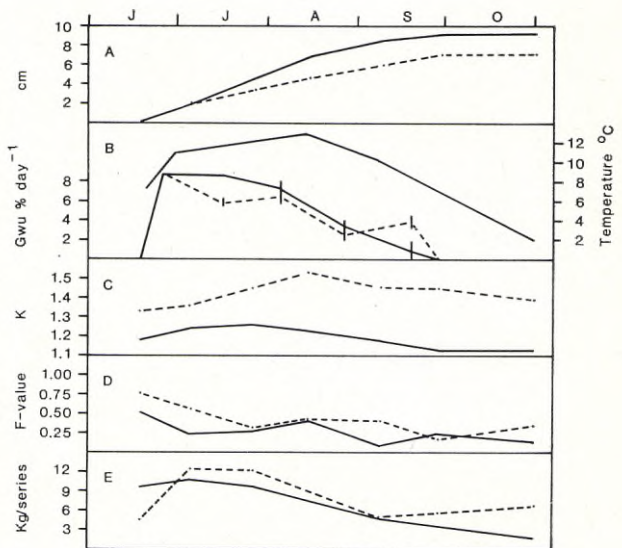

Fig. 2. Growth and factors influencing growth of brown trout (solid lines) and Arctic char (broken lines) in the Nesjö reservoir in 1972. a. Increase in length. b. Temperature and growth rates of fish of unit weight (Gwu). c. Fulton's condition factor. d. Fullness of stomachs. e. Catch per series of nets.
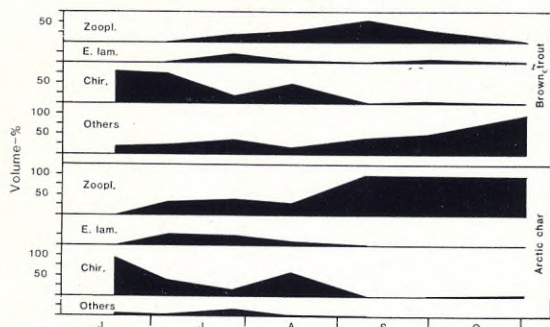
Fig. 3. Content of stomachs as volume per cent, Nesjö reservoir 1972.

August. The growth of the char varied more with time, influenced by more pronounced changes in condition (Fig. 2c). Compared to that of trout, it was higher at temperatures below and lower at temperatures above 11°C. For the entire growth season Gwu was 5.6 for trout and 5.3 for char.

The stomachs of both species were fullest in June (Fig. 2d). For Arctic char a F-value of 0.77 for a netting period of 12 hours must indicate a food consumption close to satiation. Generally there was a decline in fullness throughout the growth season, and the char had fuller stomachs than the trout.

The decline in quantities of food taken until the end of July, must partly be an effect of an increasing biomass of both species, expressed as catch per effort (Fig. 2e). This biomass increase was caused by the growth of the individual fish, and for the char population also by recruitment from the Essand reservoir. After July the biomass decreased by harvest and migration to the Essand reservoir. Taking this into consideration, the supply of prey organisms must have been better until August, as the rate of gastric evacuation declines proportionally less than the maximum food consumed in a meal, when the temperature drops from 12 to 7°C (ELLIOTT 1972, 1975a).

After the break-up of the ice the stomachs of both species were stuffed with Chironomidae larvae and later pupae (Fig. 3), as an intense emergence took place. Besides Chironomidae, the trout ate *Eurycercus lamellatus* O.F.M., *Bythotrephes longimanus* LEYDIG, a few other benthic organisms, and surface insects in July and August. In September—October the trout turned to *Daphnia galeata* SARS, and gradually more to juveniles of burbot (*Lota lota* L.) and earthworms, as the water passed the former level of flooding. The char changed from Chironomidae to Entomostraca, and ate during September—October

Table 2. *The percentages of total consumption ($\Sigma V_1 \cdot F$) and periodical consumption weighted against growth ($\Sigma V_2 \cdot Gwu$) for the growth season. V_1 is mean volume-% and F mean fullness of stomachs at dates of catch, V_2 is periodical mean volume-%, and Gwu periodical mean specific growth rate of weight according to Fig. 2b. Data from the Nesjö reservoir 1972.*

Prey	% of $\Sigma V_1 \cdot F$		% of $\Sigma V_2 \cdot Gwu$	
	Brown trout	Arctic char	Brown trout	Arctic char
Chironomidae larvae and pupae	49	48	49	39
Crustacean plankton	17	38	16	41
Eurycercus lamellatus	6	10	7	15
Other preys	28	4	28	5
Daphnia galeata	4	28	3	27
Bythotrephes longimanus	13	4	13	6
Bosmina longispina	—	5	—	7
Holopedium gibberum	—	1	—	1
Fish	4	—	2	—
Other aquatic organisms	11	4	12	4
Surface insects	8	< 1	11	< 1
Earthworms	5	< 1	3	< 1

crustacean plankton exclusively. *Bosmina longispina* LEYDIG dominated the plankton fraction in early July, *B. longimanus* made up half of the fraction in late July and August together with *D. galeata*. The latter made up 100 % of the stomach content in September—October. *Holopedium gibberum* ZADDACH was taken occasionally in very small numbers.

Of the total food consumption during the period of growth, Chironomidae made up 48, Entomostraca 48, and other items only 4 volume-% for Arctic char (Table 2). For the trout these figures were 49, 23 and 28 %, of the last fraction other aquatic organisms made 11 and surface insects 8 %. As the organic dry matter constitutes about 10 % of both Chironomidae (ELLIOTT 1972) and Entomostraca in general (BOTTRELL *et al.* 1976), the periodical consumption can be weighted against periodical growth, Gwu. This does not change the relative importance of the different prey organisms for brown trout (Table 2). The production of Arctic char was based upon the different prey organisms in the following way, Chironomidae 38, Entomostraca 57, where of *D. galeata* alone 27, and other items 5 %.

IV. DISCUSSION

The Nesjö brown trout did not grow at temperatures below 7°C, which is in accordance with field observations of EGGLISHAW (1970) and experiments of WINGFIELD (1940). In other experiments growth has occurred at temperatures as low as 3—4°C (BROWN 1946, SWIFT 1955, 1961, ELLIOTT 1975c). This is also the case in cold Norwegian lakes, *e.g.* in lakes near the Hardanger glacier, where the length increase was 3.6—4.6 cm at temperatures of 6—8°C during an ice-free season of 1.5—2 months (JENSEN 1978).

Optimal growth of brown trout has been recorded at a temperature of 12—13°C (SWIFT 1961, ELLIOTT 1975c). The very high growth rate of the Nesjö trout also indicates that the recorded temperature, 11—13°C for most of the growth season, is close to the optimum.

For brown trout fed on maximum rations in laboratory ELLIOTT (1975c) found the following dependence of Gw on individual weight (W) and temperature (T°C) for the interval 3.8—12.8°C:

$$Gw = (-1.00 + 0.29T) \, W^{-0.325}$$

This implicates a maximum Gwu of 2.7 at optimal temperature 12.8°C. The size depending relationship of ELLIOTT has been proved valid for Nesjö trout < 30 cm. A maximum Gwu of 8.7 at a mean temperature of 9.3°C, means that the temperature depending factor of ELLIOTT is much too low and that the potential growth of brown trout is higher than experienced in the Nesjö case. Neither did the Nesjö trout feed to satiation, as the mean fullness of the period was 0.38 against a maximum score of 0.77 for Arctic char.

ELLIOTT (1975a) settled the maximum dry weight of food in mg consumed by brown trout in one meal (Q) depending on temperature T°C to:

$$Q = 2.89W^{0.759} \, e^{0.133T}$$

This equation also holds for the Nesjö case as the very few fullest stomachs exceeded such values by 30 %. The Nesjö trout had therefore either to take more meals a day, for the actual interval of temperature ELLIOTT (1975b) found 1.5—1.9, and possess a higher rate of digestion, or it grows better on the same supply of energy. ELLIOTT (1975c) found his growth model valid for stream experiments as did EDWARDS *et al.* (1979) for the populations of a number of British rivers. The much better growth of the Nesjö trout must partly be a consequence of an energy-saving life in standing water. However, genetically based differences in growth characteristics and adaptions to climatic conditions are probably involved. To explain the growth and standing crop of trout in lakes near the Hardanger glacier, the author (JENSEN 1978) had to turn to the assumption that the transfer of energy through the food web is especially high in northern, alpine lakes.

SWIFT (1964) found the optimal temperature for growth of the lake Windermere S. *alpinus willughbii* between 12 and 16°C, but doubted the validity for migratory and other populations north of 64°. JOBLING (1983b) presents an optimal temperature of 14°C. The Nesjö char grew best at temperatures below 11°C, and compared to trout less at temperatures above and better at temperatures below 11°C, which here seems to be optimal. This is more in accordance with the limits of the distribution of anadromous Arctic char on the Norwegian coast

(Jensen 1981), as well as the general distribution of brown trout and Arctic char.

For Arctic char fed to satiation in experiments Jobling (1983b) established this equation:

$$Gw = (0.1643 + 0.5453T)W^{-0.325}$$

This involves a maximum Gwu of 7.5 at optimal temperature 14°C. As the Gwu of the Nesjö char was 8.9 at a mean temperature of 9.3°C, also this species possesses a potential growth higher than the established maximum one.

The fall in growth rates of both species throughout the season are steeper than can be explained by temperature and food supply alone. At the same temperature the growth rates seem to be better in spring than in autumn, which is in agreement with findings for brown trout by Wingfield (1940) and Swift (1961).

Jensen (1977) proved a positive correlation between the growth of brown trout in a Norwegian lake at altitude 1090 m and the mean June air temperature. In the Nesjö case this is obvious. An earlier break-up of the ice will not only extend the total growth season, but directly the period of high growth. A warmer midsummer would bring the temperature above the optimal one, and differences in September have small consequences.

Compared to an ordinary lake the spectrum of prey organisms for fish is very limited in a reservoir. In this case Chironomidae and three species of Entomostraca were the basis for 87 % of the production of Arctic char and 72 % of that of brown trout.

The increase in length of trout and char in a typical Norwegian lake is 5 cm a year before maturing (Dahl and Munthe-Kaas Lund 1944, Sivertsen 1952). The seasonal increase in biomass of a Nesjö fish of initial length 30 cm was twice the typical, and more for the smaller individuals. Evaluated on catch per effort the total biomass of trout and char of lengths above 20 cm was about 5 times the typical one (Jensen 1979). There were fewer smaller fish, which, according to a survival of 10 % the first and 70 % the following years, would make about 20 % of the biomass. In the Nesjö reservoir there is also a third species of fish, burbot. Altogether, the fish production of the Nesjö reservoir in 1972 was at least 10 times, and according to accepted norms, that of food orga-

nisms 100 times higher than in an ordinary Norwegian trout-char lake.

In this phase of a man-made lake, the bloom of phyto- and zooplankton is well known. Special attention is therefore drawn to the Chironomidae, the energy basis of nearly 50 % of the fish production in the Nesjö reservoir in 1972, when adult Chironomidae caught on the water surface are included. Moreover, they occurred numerously from the start of the growth season, when the salmonids seemed to have the best potential of growth. The situation is very different from reservoirs regulated only by drawing water from the natural level. In such cases there is a lack of prey organisms from the break-up of the ice and until the populations of Cladocera plankton are dense enough for predation. For the rest of the growth season predation often keeps these populations at densities too low to realize their potential production. High densities of Chironomidae larvae have been shown 30 years after impounding (Jensen 1982). The basis of their production must be the remains of the flooded vegetation, mainly peat. This situation will continue until the storage of peat is completely eroded and covered by sediments.

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Bear Island Charr

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ABSTRACT

The polar, isolated Bear Island is rich in rivers, lakes and ponds. Arctic charr is the only fish species, and the freshwater biota are of exceptionally low diversity. The charr probably immigrated in early postglacial times. Today only landlocked populations seem to exist. Anadromy is prevented by steep river outlets to the sea following land upheaval, low runoff and other factors. Most lakes had two charr morphs. As a rule fork lengths were < 20 cm for ripe small mode charr and > 30 cm for ripe large mode charr. All populations had high (0.75—1.00) EstF frequencies. Sympatric morphs had identical esterase distributions, but differed in age and growth, spawning colouration and outer morphology, gill raker and pyloric caecum counts, sex ratios and fecundity. Bear Island charr may provide good examples of incipient sympatric speciation. Three dynamic states of the double morph configuration were found. The dominating lake type is characteristically very shallow, and no crustacean plankton develops. In these lakes one charr morph was always superior in numbers. If the important prey *Lepidurus arcticus* was depleted the small morph dominated. If *L. arcticus* was abundant the large morph dominated. In Ellasjøen, the only lake with a pelagic zone and a plankton, both morphs were numerous. The crustacean plankton probably provides a suitable alternative prey for young large morph charr, thereby allowing co-dominant development of both morphs.

I. INTRODUCTION

Bear Island is a small, remote island in the Barents Sea situated at 74°30'N between Spitzbergen and mainland Norway. It has several river systems and is rich in lakes and ponds. The presence of Arctic charr was first registered by ANDERSSON (1900) and HERWIG (1900), representing Swedish and German expeditions respectively to the island in 1899. Three specimens were collected from the Lakes Ellasjøen and Laksvatn and handed over to the ichthyologist E. LÖNNBERG in Sweden. He published a detailed description of the taxon *Salmo umbla* var. *salvelino-insularis* (LÖNNBERG 1900). Today LÖNNBERG's taxonomy is antiquated, and all charr in the Barents Sea area are considered to belong to the *Salvelinus alpinus* complex (BEHNKE 1980). In spite of several scientific expeditions to Bear Island in the 20th century (SUMMERHAYES and ELTON 1923, HORN and ORVIN 1928, THOR 1930, BERTRAM 1933, BERTRAM and LACK 1933, 1938, ENGELSKJØN and SCHWEITZER 1970, FLEETWOOD et al. 1974, JACOBI and MEIJERING 1978, HUSMAN *et al.* 1979), the Arctic charr is hardly mentioned in the literature since its discovery on the island, with two exceptions. IVERSEN (1907) visited Bear Island with a fisheries vessel in 1906, and his crew caught large charr in two lakes. From a Swedish expedi-

tion in 1965 (FLEETWOOD *et al.* 1974) ARNEMO (1974) examined the stomach contents of 13 specimens from three lakes. These limited observations constituted the only published information on Bear Island charr. This was in contrast to the far more comprehensive knowledge on *S. alpinus* from mainland northern Norway (NORDENG 1961, 1971, MATHIESEN and BERG 1968, KLEMETSEN et. al. 1972, KLEMETSEN and GROTNES 1975), and the islands of Spitzbergen (DAHL 1926, GULLESTAD 1969, 1970, 1973 a, b, 1975) and Jan Mayen (SKRESLET 1973 a, b). In an attempt to remedy this the University of Tromsø Bear Island expeditions were organized in 1977 and 1978. The present contribution gives the main results of these expeditions examining the biology of Bear Island charr.

In our work on the Fennoscandian Arctic charr complex, we had adopted the Svärdson/Nyman hypothesis of allopatric development of three charr morphs in glacial refugia (SVÄRDSON 1961 a, b, NYMAN 1972) as a working hypothesis (KLEMETSEN and GROTNES 1975). It has been well documented that the Fennoscandian freshwater fauna was established by postglacial invasion (EKMAN 1922, HUITFELDT-KAAS 1918, SEGERSTRÅLE 1957). Given that the Svärdson/Nyman hypothesis is valid, we had proposed (KLEMETSEN

and GROTNES 1975) that the Est[S] charr morph of NYMAN (1972) was a pure freshwater form immigrated from the Great Siberian Ice Lake (SEGERSTRÅLE 1957) via the postglacial freshwater stages of the Baltic. Demonstration of the S-morph on Bear Island, across an extensive marine barrier, would refute the hypothesis of the Fennoscandian S-charr as a pure freshwater fish. Anadromous populations are found in the northern part of the distribution areas of the Arctic charr (JOHNSON 1980) and are common in mainland North Norway (NORDENG 1961, MATHIESEN and BERG 1968), on Spitzbergen (DAHL 1926, GULLESTAD 1973 a, b) and Novaja Zemlya (DAHL 1926). For Bear Island the record on this important point was not clear and we wanted to examine if anadromous charr were present today. By verbal communication we had indications that sympatric charr morphs might be present in some Bear Island lakes. Situations of morph sympatry are central to the charr problem and the possible existence of this phenomenon on an isolated arctic island was challenging. We decided to study the possible existence of sympatric charr morphs on Bear Island closely. Our findings are discussed in relation to the current debate on charr morph sympatry.

II. BEAR ISLAND

The discovery of Bear Island is attributed to the Dutch explorer Willem Barents in 1596 (de VEER 1609). During their short stay a polar bear was killed at sea. This incident gave name to the island (de VEER 1609, TORELL and NORDENSKIÖLD 1869, HORN and ORVIN 1928). The island's history is closely connected to the exploitation of natural resources. Coal was the most interesting mineral, and the main living resources were walrus, polar bear, polar fox, seabirds and their eggs, and marine fishes. HORN and ORVIN (1928) give an eloquent survey of the exploration of the island, also treating the sequence of scientific expeditions up to 1925 comprehensively. A survey of the island's history in relation to freshwater biological and especially Arctic charr studies is treated separately by KLEMETSEN (1985).

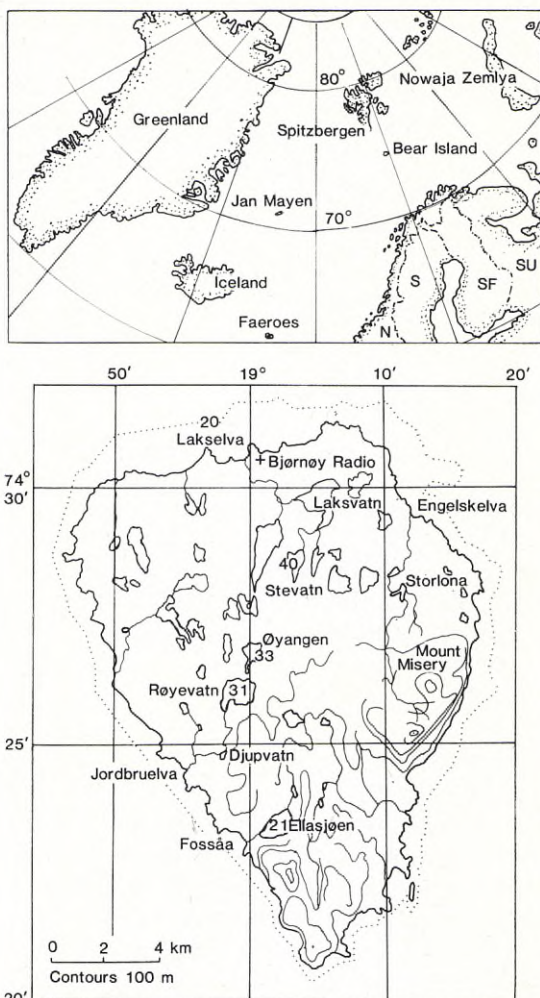Bear Island is situated at the western edge of the continental shelf between mainland Norway and

Fig. 1. Bear Island.

Spitzbergen, about 240 nautical miles north of the mainland. Of triangular shape (Fig. 1), it has an area of 178 km² and a maximum length of 20 km. The climate is relatively mild for an arctic island, with a yearly average temperature of −3.8°C. There is a midnight-sun period of 106 days. Precipitation is low (yearly normal 367 mm, Vervarslinga for Nord-Norge, *in lit.*).

Geologically Bear Island is dominated by middle Ordovician, Devonian, Culmian, Carboniferous and Triassic strata. Sandstones, limestones, conglomerates and slates dominate. A comprehensive treatment of the geology of the island is given by HORN and ORVIN (1928).

Table 1. *Temperature and pH observations with depth, Ellasjøen 1978. On all dates Secchi disc transparency was 3.5 m and the water colour greyish green.*

Depth m	Temperature °C			pH		
	July, 16	July, 27	Aug., 22	July, 16	July, 27	Aug., 22
0	5.7	6.7	7.4	7.6	7.4	7.6
1	5.7	—	7.4	—	—	—
4	5.7	6.7	7.4	7.5	7.4	7.6
8	5.7	—	7.4	7.4	—	7.6
12	5.5	6.7	7.4	7.4	7.4	7.6
16	5.2	—	7.3	—	—	—
20	5.1	6.5	7.4	7.3	7.4	7.6
24	5.1	—	7.4	7.5	—	7.6
30	—	6.2	—	7.4	7.4	7.6

The island was glaciated during the Pleistocene and the surrounding sea was certainly permanently ice-bound. Topographically the island is split into two parts, a southern mountainous area and a northern area of level plains. The highest peak of Mount Misery has an altitude of 536 m. The steep S coast constitutes perhaps the finest bird cliffs in the northern hemisphere (BERTRAM and LACK 1933). The most prominent plain of marine origin extends at 30—40 m.a.s.l. over much of the northern part. Glacial impact has left numerous shallow basins filled with water. About 740 can be counted on the Bear Island map (HOEL 1944) and their surface make up 11 % of the island's surface (HORN and ORVIN 1928). More than 600 of these lakes and ponds are found on the northern plains, rendering an impressive limnological landscape. Most water bodies are shallower than two metres. Less than 10 of the larger lakes reach depths of between 5 and 10 m (HOEL 1944), and Ellasjøen with a maximum depth of 43 m is the only deep lake on the island. The permafrost which prevails all over the island (HORN and ORVIN 1928) presumably keeps many shallow water bodies from drying up during the summer. Although ground temperatures in sediments indicate unfrozen lake and river beds, the transport of ground water is probably negligible (FLEETWOOD 1974). The ice-free period on lakes lasts from 2.5—3.5 months (BERTRAM and LACK 1933), starting in late June. Water temperatures are low. BERTRAM and LACK (1938) found typical summer temperatures in the lakes to be below 7°C and JACOBI and MEIJERING (1978) obtained a mean of 6.2°C from 35 localities in July 1975. These results agree well with our readings from

Ellasjøen 1978 (Table 1). Summer stratification did not develop because even moderate winds will turn over water masses of 5—7°C. These readings presumably reflect a typical thermal regime for Ellasjøen, and the lake is defined as subpolar (YOSHIMURA 1936) or cold monomictic, allowing for a summer circulation above the strict limit of 4°C coined by HUTCHINSON (1967). In a strict limnological sense all the other lakes are large ponds, and certainly also circulate continually through the summer.

Ellasjøen had a remarkably low transparency, its water colour was a turbid greyish green and the water was slightly alkaline (Table 1). This probably reflects a rich geology, but even more an appreciable input of bird manure. Large flocks of kittiwakes, *Rissa tridactyla*, ranging from several hundred to about two thousand birds, constantly sat on the lake bathing and preening their plumage. Their presence must imply a heavy allochthonous input to the lake which certainly contributes much to its special limnological appearance.

The typical upper littoral of Bear Island lakes is a steep, rocky margin 0.5—1 m deep. Except for occasional submerged mosses, there is no macrovegetation (ENGELSKJØN and SCHWEIZER 1970). Phytoplankton samples from Ellasjøen only comprised six species (LAGERHEIM 1900). Likewise AWERINZEW (1907) reported a low diversity of protozoans. The major invertebrate taxa of Porifera, Platyhelminthes, Annelida, Mollusca, Ephemeroptera, Plecoptera, Odonata, Culicidae, Chaoboridae, Amphipoda and Mysidacea, are totally lacking. Trichoptera, Simuliidae and Hydracarina are represented by just one species each. These are, respectively, *Apatania zonella* = *A. arctica*, *Simu-*

lium ursinum and *Sperchon lineatus* (Summer-hayes and Elton 1923, Thor 1930, Bertram and Lack 1938).

Among crustaceans the euphyllopod *Lepidurus arcticus* is a dominant species of pools, ponds and fishless lakes. In lakes with dense charr populations it is heavily cropped down. Seven species of Cladocera are recorded (Lilljeborg 1900, Summerhayes and Elton 1923, Bertram 1933, Jacobi and Meijering 1978, Husman et al. 1979). *Daphnia pulex*, *Macrothrix hirsuticornis* and *Chydorus sphaericus* occur regularly. *Daphnia longispina* is found only in Ellasjøen, and makes up an important plankton population in that lake. The locality is the northern-most known of this widespread species (Jacobi and Meijering 1978). Out of six copepods *Cyclops abyssorum* and *Megacyclops gigas* are common (Bertram and Lack 1938). Einsle (1974) concluded that earlier records of *C. strenuus* (Lilljeborg 1900, Summerhayes and Elton 1923, Bertram 1933, Bertram and Lack 1938) are misidentifications for *C. abyssorum*. Halvorsen and Gullestad (1976) agree. Bertram and Lack (1938) listed two ostracods from the island, both seemingly rare. Chironomidae is the dominant insect group, both by diversity, distribution and abundance. In all a minimum of 31 species are recorded, 21 of which are orthocladiines (Oliver 1962). During the 1977 expedition a survey of macroparasites of the Arctic charr was undertaken by Kennedy (1978). Five species were recorded from Stevatn, Øyangen and Ellasjøen. The cestode *Diphyllobothrium ditremum* dominated all the samples. Kennedy relates the low number of species primarily to the absence of suitable intermediate hosts besides copepods.

The present study added two new species to the Bear Island fauna. One imago of the dytiscid beetle *Hydroporus striola* was found in a charr stomach from Ellasjøen. This appears to be the first record of any dytiscid north of mainland Europe (J. Andersen pers. comm.). The cladoceran *Eubosmina longispina* was recorded in a few charr stomachs from Ellasjøen and Stevatn.

Our studies took place in the river systems of Lakselva, Jordbruelva, Engelskelva and Fosså (Fig. 1). Lakselva is the largest river system on the island (Hoel 1944), and also drains the two largest lakes by area, Laksvatn and Haussvatn.

Stevatn is the head lake of a tributary, situated about 7 km upstream at 40 m.a.s.l. Its area is 32 ha. Most of the lake is shallower than 3 m, and the maximum depth is 6 m (Hoel 1944). Jordbruelva drains a catchment slightly smaller than that of Lakselva towards the west. The river runs underground for several stretches (*jordbru* literally means earth-bridge) of together several hundred metres. Øyangen and Røyevatn (lit.: charr-lake) are situated close together at the upper reaches of the river (Fig. 1). Øyangen at 33 m.a.s.l. has an area of about 31 ha and Røyevatn (31 m) an area of 96 ha. These lakes are very similar, and of the typical shallow, northern plain type. Maximum depth recorded in Øyangen is 3.5 m (Fleetwood 1974). Engelskelva is the largest river system on the east coast of the plains area. The system has a few large, very shallow and turbid river pools, but no real lakes. Ellasjøen in the mountainous southern part of the island is drained by the short River Fosså. The lake is situated 0.5 km upstream at an elevation of 21 m. Its area is 73 ha, and large parts of the basin are more than 30 m deep.

III. METHODS

The 1977 expedition visited Bear Island from August 23 to September 1. In 1978 two separate expeditions were set up, the first in the period July 12—27, the second between August 18 and 27. In 1977 a base camp was established at Laksvatn and fishing was carried out in Engelskelva, Stevatn, a river pool below Haussvatn and Øyangen. A preliminary sample was taken in Ellasjøen. In 1978 the base camp was established at Ellasjøen and the main work done there. During the first period a separate party stayed for a while at Røyevatn and sampled the Jordbruelva system. In 1977 we aimed at sampling both water courses which might hold anadromous charr and water courses likely to hold resident charr only. In 1978 we concentrated our efforts on the Ellasjøen charr.

Fishing was performed with monofilament 1.5 by 25 m bottom gill nets, placed singly or in fleets from the shore and outwards and left fishing overnight. Bar mesh sizes were 16, 20, 22, 24, 26,

31 and 39 mm in 1977. In 1978, 10 and 12.5 mm nets were added to the series used in Ellasjøen, and the use of floating nets was added to the sampling procedure. These nets were 6 by 25 m and of mesh sizes 10, 16, 20, 24, 26, 31 and 39 mm and were mounted in fleets at the surface at least 200 m offshore. All fish were weighed, measured for fork length and sexed. The gonad maturity was indexed using a seven-grade scale (SØMME 1954), and the flesh colour was noted. Blood samples were taken in heparinized glass capillaries (NYMAN 1967). The samples were kept in plastic bags dug into snow before freezing aboard the expedition vessel. Otoliths, stomachs with contents, the first left gill arch and pyloric caeca were preserved in ethanol. Ripe ovaries were preserved in Gilson's fluid. Scales were taken in a few cases in order to check for possible sea-run marks.

Starch gel electrophoresis for serum esterases was performed according to NYMAN (1967). His notation of allelles is followed. Charr stomachs were opened and the degree of filling was noted using a percentage scale. After identification, all prey items were given a points number according to their relative volume. Except for stomachs collected from Ellasjøen 1978, prey items were then counted. Sub-sampling was used in some cases. Counting was not attempted with highly digested stomach contents. Finally the pooled contents of each stomach were dried for 24 hrs and weighed on a Mettler microbalance. Daily food intake was estimated using the method of BAJKOV (1935) as modified by EGGERS (1979). This gives the food intake (C) as follows:

$$C = 24 \, SR$$

where S is the mean stomach content for a 24 h period and R the gastric evacuation rate. AMUNDSEN (1984) and AMUNDSEN and KLEMETSEN (1986) have recently demonstrated that this method is usually more appropriate than ELLIOT and PERSSON's (1978) and related methods due to a general presence of large intra sample variations in stomach contents. Values for R were obtained from gastric evacuation experiments carried out by AMUNDSEN (1984) with charr from Takvatn, northern Norway. His estimates using euphausiids *Thysanoëssa* spp. as food were considered to be the best available for the present material.

The last bottom net sample from Ellasjøen in August 1978 was frozen untreated on board the expedition vessel. In the laboratory measurements were made of snout length, eye diameter (orbit length), upper jaw length, head length, pre-pelvic length, standard length and fork length. Calipers were used for the shorter measurements using the method of LOWE-MCCONNELL (1978). Age was read with the otolith immersed in glycerol on a black background. Most otoliths appeared clear and easy to read. Nevertheless, as POWER (1978) had raised doubt as to the validity of conventional otolith reading on arctic fish, a special study was undertaken with the 1978 Ellasjøen material (KRISTOFFERSEN 1982). On a selected sample conventional reading was compared to reading after burning and breaking the otoliths, using Power's technique slightly modified. Discrepancies between the two reading techniques were found in less than half of the cases. About 90 % of the readings were within 2 years of each other. Mature fish below 25 cm showed significantly higher readings with the burn-break technique. The differences were far less than those reported by POWER (1978) for other arctic fresh-water fish, and we concluded that the use of the more laborious burn-break technique was not justified for the present purpose.

IV. RESULTS

Distribution and density

Arctic charr was caught in all sampled river systems except Engelskelva. Nets were placed in two pools; one along the middle reaches and one very large pool at the upper reaches (Storlona), without result. Pool depths generally appeared to be less than 1 metre, and *Lepidurus arcticus* was abundant. This system probably harbours no charr. In the Lakselva river system both Laksvatn and Haussvatn have long been fished by the radio station staff (S. JENSEN pers. comm.), and we caught charr in Stevatn and a river pool below the entrance of the Hausselva tributary (Fig. 1). This system therefore holds charr all along its course. The same is the case with the Jordbruelva river system. In addition to samples from Øyangen and Røyevatn, one specimen was caught in Djupvatn and a small sample was taken in a pool close to

Table 2. *Net selection expressed by modal cm length class* (m), *range* (r) *and number of fish* (n). *Ellasjøen, August 1978.*

		Bar mesh size mm								
		10	12	16	20	22	24	26	31	39
Bottom nets	m	9	12	15	18	22	24	26	34	36
	r	8—22	9—35	13—25	15—46	13—39	15—40	16—39	13—45	17—52
	n	47	168	112	148	58	28	24	15	18
Floating nets	m	(35)	—	18	22	—	—	28	33	34
	r	—	—	14—26	17—47	—	—	22—38	16—38	30—42
	n	1	—	22	137	—	—	84	20	39

the river mouth. In the Fossåa river system Ellasjøen holds the only charr population. In addition to these localities, Arctic charr is present in other shallow lakes on the north plain, such as Lomvatnet, Vomma and Krokvatnet. ARNEMO (1974) examined specimens from Daudmannsvatnet. The north plain lakes Stevatn, Øyangen, Røyevatn and Djupvatn had small charr stocks. Catches were always ≤ 1.0 charr net^{-1} night^{-1}. Ellasjøen contrasted sharply to this with bottom net catches of 5—20 charr per net-night.

Population structures

The net selection statistics showed a smooth increment of the modal sizes and ranges with mesh size (Table 2). We therefore accept the mesh size ranges as giving a representative picture of the population structures. A conspicuous bimodal length distribution was established for the 1977 Ellasjøen sample (Fig. 2). Median lengths of the two groups were 16 and 38 cm. Only one fish fell between 19 and 29 cm. A similar bimodal grouping appeared for Stevatn, although large mode fish were few. The combined Øyangen samples showed a similar size range, but large sized fishes dominated. The few charr from Røyevatn hints of a population structure similar to that of Øyangen. In Djupvatn one specimen 30 cm in length was caught. The bottom net catches in Ellasjøen 1978 showed a bimodal distribution similar to that of 1977, but with a lower length class of 8 cm caused by the addition of smaller mesh sizes (Fig. 3). The catch of pelagic fish filled the gap obtained with the littoral material. The bimodality reappeared when ripe fish were plotted separately (Fig. 4). Two size modes emerged, one in the 8—21 cm range and the other above 29 cm.

The age and growth characteristics of the 1977 material displayed some striking intra sample and inter sample variations (Fig. 5). Small mode charr from Ellasjøen and Stevatn were very similar.
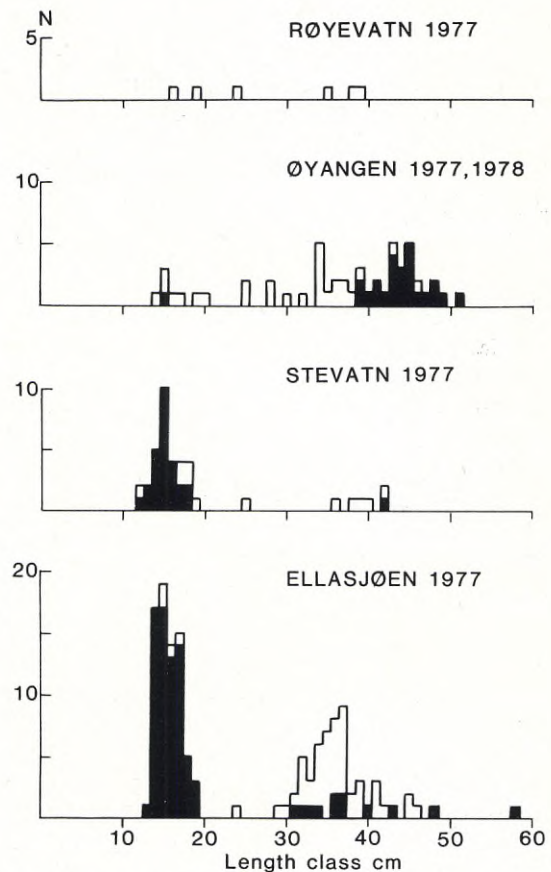
Fig. 2. Length frequency distributions of Arctic charr samples from Bear Island. Black bars indicate sexually ripe fish.
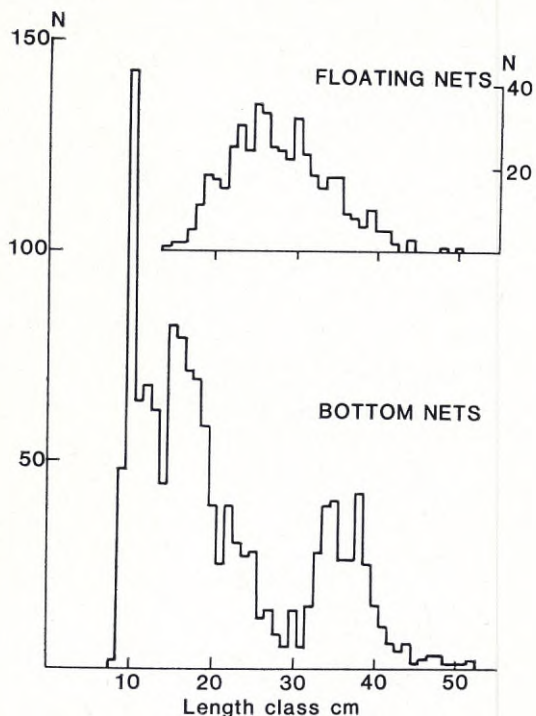
Fig. 3. Length frequency distributions of Arctic charr samples caught with bottom nets and floating nets, Ellasjøen 1978.
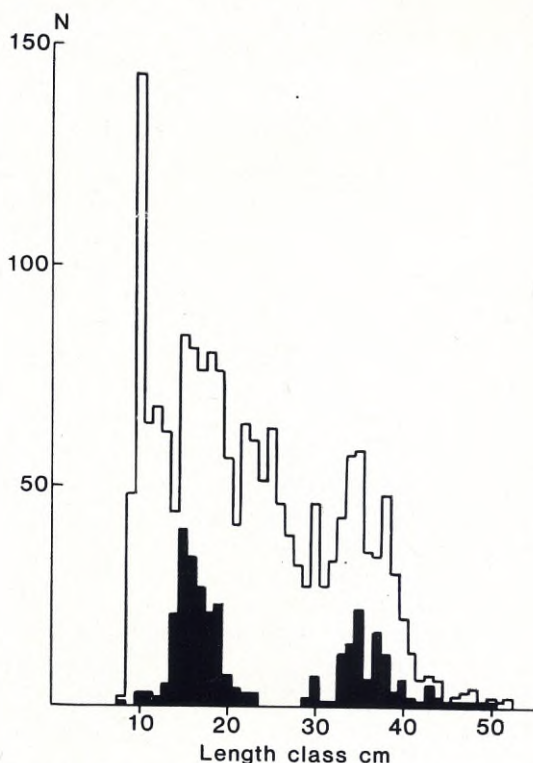

Fig. 4. Length frequency distribution of the total sample, Ellasjøen 1978. Black bars indicate sexually ripe fish.

Their age range was 6—14 and 6—16 years, both samples had a modal age of 8 years and both displayed a pronounced growth stagnation in the 15—20 cm size range. The presence of one ripe fish below 20 cm in Øyangen may indicate the presence of a small charr mode also in this population. Large mode charr from Ellasjøen were 12—23 years old with a modal age of 16 years. Even allowing for a slight underestimation of the age of small mode charr (KRISTOFFERSEN 1982), large mode charr were clearly older than the small mode charr. The ages of the few large charr from Stevatn corresponded well to large mode charr from Ellasjøen, but the growth was somewhat better at Stevatn. The Ellasjøen large charr showed no clear indication of growth stagnation with age, and many were not ripe. The large Øyangen charr differed markedly. Age readings did not exceed 10 years and their growth was much more rapid. Nearly all fish above 40 cm were ripe, and the

sample indicates a growth stagnation in the 40—50 cm range.

The extended sampling procedure in Ellasjøen 1978 complemented the picture of the population structure, essentially with the much stronger representation of 20—30 cm fish and the addition of the yearclasses 3+, 4+ and 5+ (Fig. 6). Bimodality is evident from age 8 upwards, and the very different growth characteristics of the two size modes are apparent. The maximum age was extended to 25 years.

We found no indications of anadromous life cycles among Bear Island charr. A substantial proportion of the material was taken in the latter part of August when the sea-run charr was likely to have returned to freshwater. Only two specimens caught in Lakselva had the silvery appearance resembling sea-run fish. Both were 27 cm long, immature males and 8 years old. Even allowing for a high smolt age, their growth was too
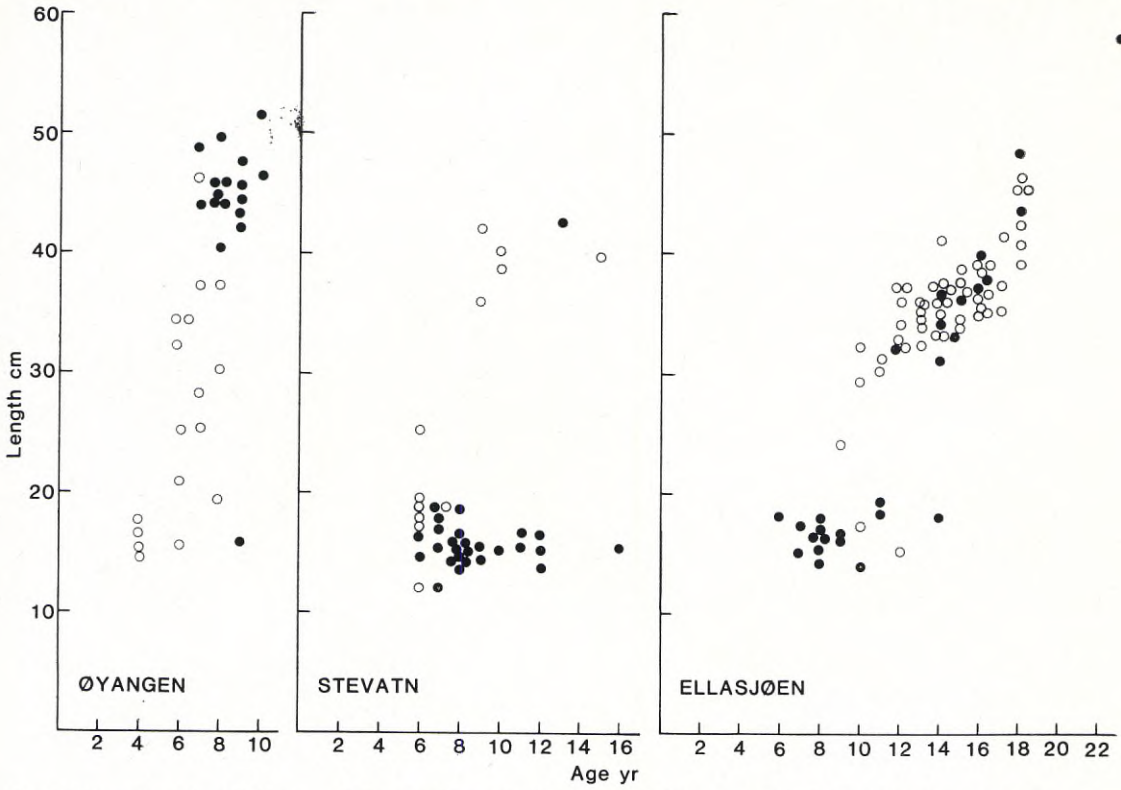
Fig. 5. Length and otolith age of Arctic charr from Bear Island 1977. Small-mode charr from Ellasjøen were subsampled, the other samples represent total catches. Black dots indicate sexually ripe fish.
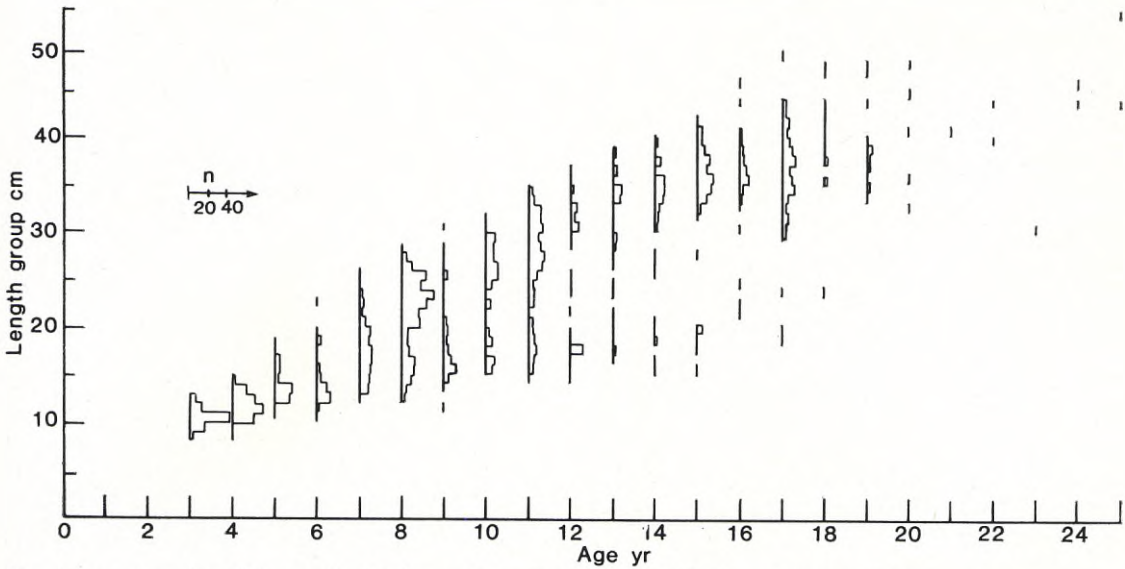

Fig. 6. Length and otolith age distributions of Arctic charr from Ellasjøen 1978 (n=1312).

Table 3. *Blood serum esterase electrophoresis of Arctic charr from Bear Island. No tested sample deviated significantly from expectation under Hardy-Weinberg equilibrium (χ^2, .05).*

Sample	Observed phenotypes			Frequency of allele F	χ^2 deviation
	F/F	F/S	S/S		
Stevatn 1977	20	17	1	.75	1.41
Jordbruelva 1978	8	6	0	.79	1.06
Øyangen 1978	18	0	0	1.00	0
Røyevatn 1978	4	2	0	—	—
Ellasjøen 1978	1408	5	0	1.00	$< \cdot 01$

slow for sea-run fish. Their scales showed no change in growth rate corresponding to a feeding period at sea. The riverine charr from Jordbruelva were small, sexually mature and obviously not sea-run fish.

Serum esterases and morphology

Blood serum Est^F frequencies of all Bear Island charr samples were ≥ 0.75 (Table 3). All tested samples agreed well to expected Hardy-Weinberg equilibria. The small sample from Røyevatn was not tested but did not deviate from the general pattern. Neither did large-mode fish from Stevatn (4 F/F, 3 F/S). Of the five heterozygotes from Ellasjøen, one was a ripe small-mode fish, one was a ripe large-mode fish and three belonged to the unripe large-mode group. These results give no indication of more than one panmictic population in any of the studied localities. The results also refute the presence of S-charr on Bear Island.

Pyloric caecum and gillraker counts (Fig. 7) were significantly different between small-mode

Fig. 8. Position of pelvic fins of Bear Island Arctic charr expressed as prepelvic length fractions of fork lengths, Ellasjøen 1978. Black dots indicate sexually ripe fish.

and large-mode Ellasjøen charr (t, .05). Inclusion of small charr from Stevatn and large charr from Øyangen gave consistently significant differences for both characters between small-mode and large-mode samples, while within mode tests showed no differences. These results indicate a size mode dependency of pyloric caecum and gill raker numbers among Bear Island charr. The characters are, however, not diagnostic due to overlapping. In spite of a tendency for larger charr to have the pelvic fins forward of half the fork length (Fig. 8) and small-mode charr to have them behind, range overlap also precludes the use of this character diagnostically as did SEPPOVAARA (1969). The same applies to relative head length (Fig. 9) which was significantly larger in ripe small mode charr (t, .05) as compared to fish > 21 cm. The actual difference was small and range overlap extensive. Relative eye diameter fell very clearly with fish

Fig. 7. Mean numbers of gill rakers and pyloric caeca of Bear Island Arctic charr samples. Standard deviations are indicated. S: Stevatn, E: Ellasjøen, Ø: Øyangen, s.m.: small-mode charr ≥ 15 cm, l.m.: large mode charr. Sample sizes for gill raker and pyloric caecum counts were, respectively, 24, 27 (S, s.m.), 64, 63 (E, s.m.), 74, 79 (E, l.m.) and 26, 26 (Ø, l.m.).
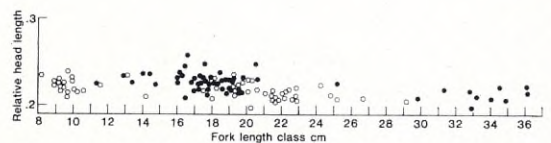

Fig. 9. Head length of Bear Island Arctic charr expressed as fractions of fork lengths, Ellasjøen 1978. Black dots indicate sexually ripe fish.
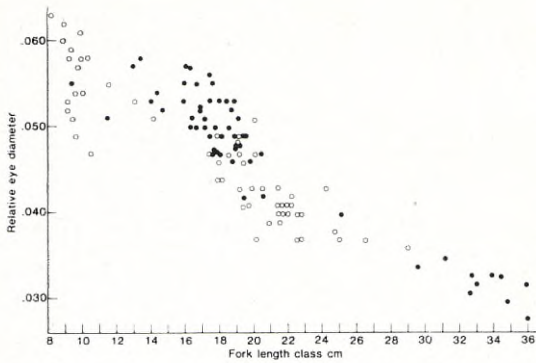
Fig. 10. Eye diameter (orbit length) of Bear Island charr expressed as fractions of body lengths, Ellasjøen 1978. Black dots indicate sexually ripe fish.

Table 5. *Sex ratios of Arctic charr from Bear Island. Italics indicate significant deviations from 50/50 expectations (χ^2, .05).*

Charr sample	♀♀	♂♂	♀♂ ratio %	p
Stevatn Aug. 1977				
Unripe, small mode	15	8	65/35	.86
Øyangen 1977, 1978				
Ripe, large mode	*18*	*8*	*69/31*	.95
Ellasjøen Aug. 1977				
Ripe, small mode	*9*	*61*	*13/87*	1.00
Unripe, large mode	*20*	*39*	*34/66*	.99
Ripe, large mode	6	7	46/54	.23
Ellasjøen July 1978				
Ripe, small mode	*23*	*11*	*68/32*	.96
Ellasjøen Aug. 1978				
Parr	31	29	52/48	.20
Unripe, small mode	86	102	46/54	.76
Ripe, small mode	*80*	*132*	*38/62*	1.00
Unripe, large mode	133	151	47/53	.72
Ripe, large mode	*27*	*10*	*73/17*	.99

size (Fig. 10), with a doubling from the smallest to the largest eyes. This presumably reflects restricted growth of orbits as rigid parts of the skull from early life. Size dependency is, however, not the only explanation because testing showed that ripe 17—21 cm fish had significantly larger eyes than unripe fish of the same lengths (t, .05; see also Fig. 10). The clear tendency for a shift from a short to a long snout with increasing fish size and the similar tendency of a short jaw in small fish and a long jaw in large fish (Table 4) are obviously directly dependent on the relative eye diameter. None of these morphometric traits are diagnostic for separating large and small-mode Bear Island charr. Relative eye size and its two dependent characters are, however, useful additional tools in the field because small mode ripe charr showed a tendency towards larger eyes irrespective of body size.

Sex ratio and fecundity

The samples from Stevatn, Øyangen and Ellasjøen in August 1978 displayed a sex ratio shift from 50/50 among young parr via a male dominance among the small ripe fish to a female dominance among the large mode spawners (Table 5). The July 1978 Ellasjøen sample of ripe, small mode fish contradicts this. In this sampling period small, ripe fish (≥ stage III) were notably rare, indicating that gonad growth had just started. We suggest that the female dominance in this sample was simply caused by females starting their gonad growth earlier than males. The results for large

Table 4. *Comparison of eye diameter and snout length, and of upper jaw length in relation to eye position for Arctic charr groups, Ellasjøen August 1978. Significant deviations from a 50/50 expectation (χ^2, .05) are indicated by italics.*

Charr group	Eye diameter		Upper jaw	
	< snout	> snout	under eye	behind eye
parr, < 11 cm	*1*	*15*	*16*	*0*
ripe, 17—21 cm	16	13	22	7
unripe, 17—21 cm	*18*	*1*	7	12
all, > 21 cm	*31*	*0*	*2*	*29*

Table 6. *Absolute and relative (eggs kg⁻¹ fish weight) fecundity of large mode and small mode Arctic charr, Ellasjøen 1978.*

	Absolute fecundity			
	Range	Mean	St.dev.	N
Small mode charr	45—120	76.3	23.6	16
Large mode charr	700—1450	1117.3	244.6	18

	Relative fecundity			
	Range	Mean	St.dev.	N
Small mode charr	835—1852	1422.8	291.1	16
Large mode charr	1485—3092	2019.0	651.3	18

Table 7. *Check list of prey found in stomach contents of Arctic charr, Bear Island 1977—78.*

Prey identified	Locality				
	Stevatn	Røyevatn	Øyangen	Jordbruelva	Ellasjøen
CRUSTACEA					
Euphyllopoda					
Lepidurus arcticus	×	×	×	×	×
Cladocera					
Daphnia longispina	—	—	—	—	×
Eubosmina longispina	×	—	—	—	×
Chydorus sphaericus	—	—	—	×	—
Copepoda					
Cyclops abyssorum	—	—	×	—	×
Megacyclops gigas	×	—	—	—	×
Indet.	—	—	—	×	—
Ostracoda					
Indet.	×	—	—	×	×
INSECTA					
Collembola					
Indet.		—		—	—
Coleoptera: Dytiscidae					
Hydroporus striola	—	—	—	—	×
Coleoptera: Staphylinidae					
Indet.	—	—	—	—	
Trichoptera					
Apatania zonella	×	×	×	×	×
Diptera: Chironomidae					
Heterotrissocladius subpilosus	—	—	—	—	×
Orthocladius consobrinus	—	—	—	—	×
Micropsectra sp.	—	—	×	—	×
Diamesa sp.	—	—	—	—	×
Procladius sp.	×	×	×	—	—
Psectrocladius barbimanus	×	×	×	—	—
Stictochironomus rosenschoeldi	×	—	×	—	×
Indet.	—	—	—	×	—
Diptera: Simuliidae					
Simulium ursinum	—	—	—	×	—
Diptera: Cyclorrhapha					
Indet.	×	—	—	×	—
ACARINA					
Hydracarina					
Sperchon lineatus	×	—	—	×	×
PISCES					
Salvelinus alpinus	×	—	×	—	×
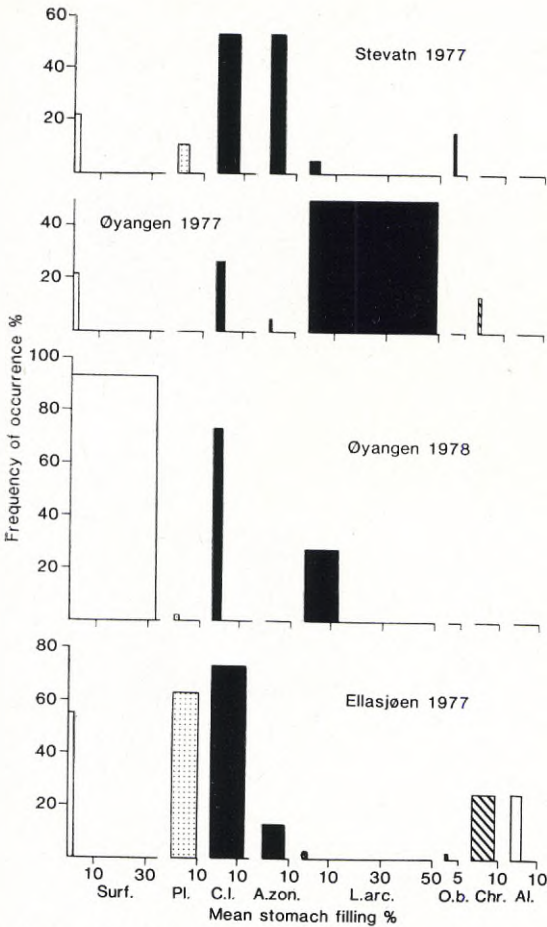
Fig. 11. Stomach contents of Arctic charr from Bear Island August 1977 and 1978. Frequencies of occurrence and mean stomach fillings are combined for each food category. Surf.: surface food, predominantly hatching chironomids; Pl.: crustacean plankton; C.l.: chironomid larvae; A.zon.: larvae of *Apatania zonella* (Trichoptera); L.arc.: *Lepidurus arcticus* (Euphyllopoda); O.b.: other benthos; Chr.: arctic charr; Al.: allochthonous material. Stevatn 1977, small mode charr (n=31); Øyangen 1977, large mode charr (n=33); Øyangen 1978, large mode charr (n=15); Ellasjøen 1977, large mode charr (n=73).

mode fish from Ellasjøen 1977 is also somewhat conflicting. We feel, however, that confidence should rest with the far more comprehensive material from August 1978.

With the great difference in size between the two modes of ripe fish, a large difference with no overlap in egg counts of the type observed in Ellasjøen (Table 6) was to be expected. The material also supports the conclusion that large-mode fish had a significantly higher relative fecundity (t, .05). The mean difference amounted to about 600 eggs pr. kg fish weight.

Food and feeding

The prey list of Bear Island charr comprised only 22 taxa (Table 7). This reflects the low diversity of the island's fresh water fauna. A few species of phyllopods, copepods, trichopterans and chironomids were the main elements of the diet. Terrestrial surface food items were exceptional. Ellasjøen charr had the highest number of prey items in their stomachs, and certain species were only found in that lake.

The quantitative analysis of stomach contents also showed greatest variety for Ellasjøen charr. Plankton, charr and allochthonous items were significant only from this lake (Fig. 11). The plankton food comprised four crustaceans, with *Daphnia longispina* in strong dominance (Table 8). Allochthonous food consisted of gulls' feathers, crab legs and non-charr fish bones. The marine food elements must have come from gull's gulpings, most probably from Glaucous Gull *Larus hyperboreus*. The same phenomenon was noted by SKRESLET (1973a) on Jan Mayen. Besides plankton chironomid larvae was the most important food item of the Ellasjøen 1977 large-mode charr sample. Small-mode charr were not quantitatively

Table 8. *Numbers of zooplankton prey in charr stomachs. Ellasjøen August 1977, large mode Arctic charr.*

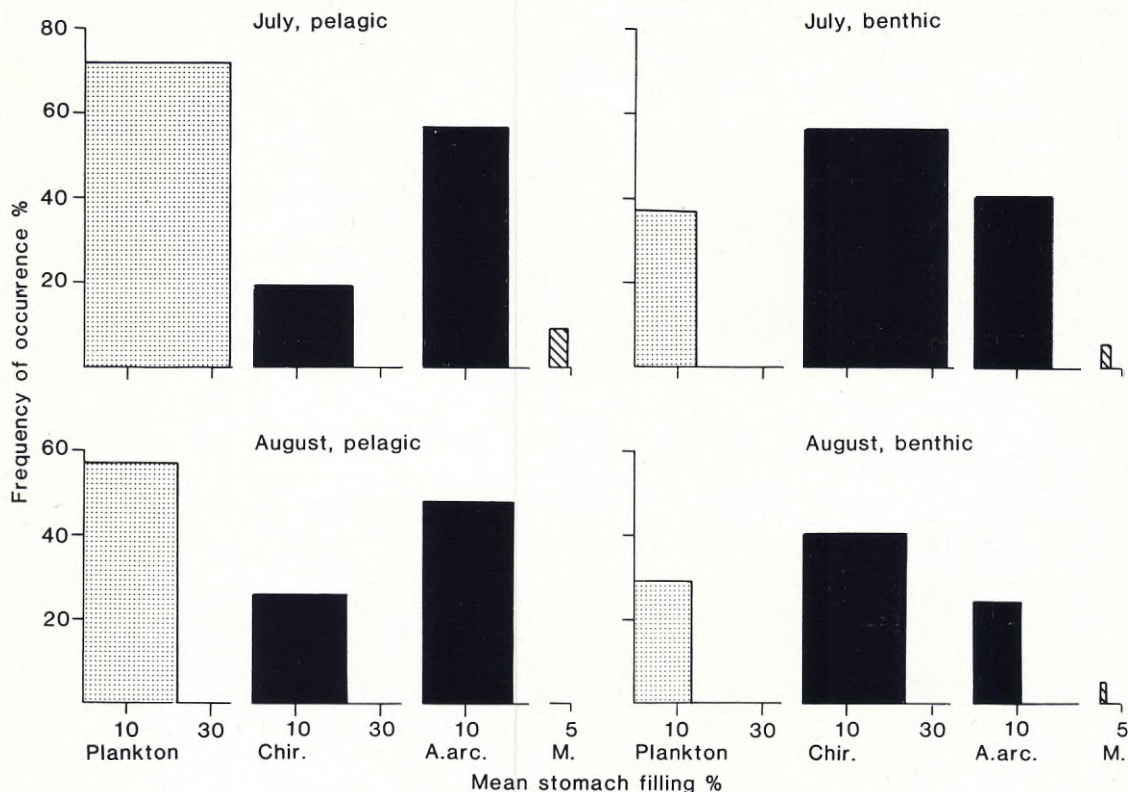| Prey	Range of prey numbers	Median prey number	Number of stomachs
Daphnia longispina	1—3240	465	37
Eubosmina longispina	1	—	1
Cyclops abyssorum	1—15	8	14
Megacyclops gigas	1—35	5	23

Fig. 12. Stomach contents of Arctic charr from parallel floating net and bottom net catches, Ellasjøen July and August 1978. Frequencies of occurrence and mean stomach fillings are combined for each food category. Chir.: chironomids, mainly larvae; A.zon.: larvae of *Apatania zonella* (Trichoptera), M.: miscellaneous. Sample sizes were 38 (July, pelagic), 95 (July, benthic), 44 (Aug., pelagic) and 103 (Aug., benthic).

analysed because most stomachs were empty, presumably because their spawning had started (ultimo August 1977). The few food remnants found indicated a prey picture similar to that of the large-mode charr.

The stomach contents of pelagic and benthic charr from two sampling periods in Ellasjøen 1978 showed a striking similarity (Fig. 12). Plankton (*D. longispina*) chironomids and caddis larvae were co-dominant. This is again similar to the result from the previous year (Fig. 12). The general conclusion that Ellasjøen charr of all sizes and both modes, depend on *Daphnia longispina*, Chironomidae and *Apatania zonella* for their chief food seems therefore to be substantiated. Although plankton was more important to the pelagic fish (Fig. 12), the co-dominance of both benthos and plankton prey implies that the Ellasjøen large-mode charr exhibits frequent habitat shifts be-

tween the littoral and the pelagial. Small mode charr were not often caught in the floating nets. Their capture of *D. longispina* therefore probably takes place close to the littoral zone.

The stomach contents from the north plain lakes were completely dominated by benthic prey (Fig. 11). Surface food consisted of little more than hatching chironomids and caddis flies. Plankton had little or no importance, and cannibalism was exceptional. The small-mode charr from Stevatn had taken mostly chironomid and *A. zonella* larvae. Six large-mode Stevatn charr stomachs were not treated quantitatively, but their contents were very similar, with the exception of charr remains in one stomach. The large charr of Øyangen had different stomach contents in 1977 and 1978. In the first year *Lepidurus arcticus* dominated, in 1978 chironomid pupae dominated. Presumably the hatching of one chironomid species

Table 9. *Numbers of Lepidurus articus, and larvae of Apatania zonella and Chironomidae in Arctic charr stomachs, Bear Island 1977 and 1978. r: range of prey numbers, m: median prey number, n: number of stomachs.*

Prey	Stevatn 1977 small mode charr			Øyangen 1977, 1978 large mode charr			Ellasjøen 1977 large mode charr		
	r	m	n	r	m	n	r	m	n
Lepidurus arcticus	10	—	1	2—1010	200	16	4	—	1
Apatania zonella	1— 4	2	8	1— 3	2	3	1— 360	12	11
Heterotrissocladius subpilosus							1—2080	6	47
Orthocladius consobrinus							7	—	1
Micropsectra sp.				2		1	1	—	1
Diamesa sp.							1	—	1
Procladius sp.	2— 27	5	6	1— 9	3	12			
Psectrocladius barbimanus	1— 3	2	6	1	—	1			
Stictochironomus rosenschoeldi	1— 2	2	6	1— 27	3	14	3	—	1
Chironomidae pupae	1—440	35	4	1—3412	51	17	1— 380	6	24

coincided with sampling time that year. The moving, unsheltered chironomid pupae are probably very attractive prey especially when concentrated at the surface for the actual hatching process. *L. arcticus* biomass is much more stable than that of hatching chironomids, and is probably reverted to in other periods. The six large-mode charr from Røyevatn 1978 showed the same general picture; dominance of benthic prey species, notably *L. arcticus*, and no cannibalism or plankton food. The two fish from Lakselva 1977 were both packed entirely with *L. arcticus*, and six small charr from Jordbruelva 1978 had chironomid pupae as the dominant food.

In Ellasjøen *Heterotrissocladius subpilosus* made up nearly all the chironomid larvae in the stomach contents (Table 9), while *Procladius* sp. and *Stichtochironomus rosenschoeldi* appeared to be the most preferred in the shallow lakes. *L. arcticus* and *A. zonella* were found in all samples. High numbers of the first occurred in Øyangen and of the latter in Ellasjøen charr stomachs. Both *L. arcticus*, *H. subpilosus* larvae and chironomid pupae were counted by the thousands in several stomachs. Even higher numbers than those shown in Table 6 were found among the few large charr from Stevatn. For *S. rosenschoeldi* the maximum count was 5520 larvae. Another charr had taken 7618 chironomid pupae. These high prey numbers probably reflect both a heavy predation activity and a slow rate of digestion at the low temperatures that prevailed in Bear Island lakes.
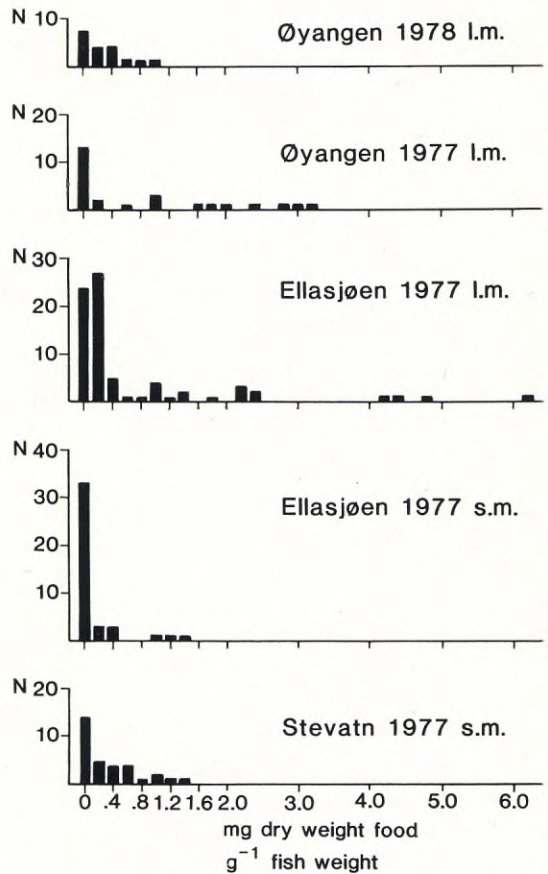
Fig. 13. Stomach contents weight distributions of Bear Island Arctic charr samples given as frequencies of empty stomachs and 0.2 mg classes of dry weight food g⁻¹ fish wet weight.

Table 10. *Daily food consumption rates of Bear Island Arctic charr 1977, 1978, given as mg dry weight of food g^{-1} fish wet weight.*

Charr sample	Consumption rate	95 % conf. limits	N
Stevatn Aug. 1977 small mode	.52	.16—1.43	32
Ellasjøen Aug. 1977 small mode	.18	−.14— .84	42
Ellasjøen Aug. 1977 large mode	.80	−.11—2.45	75
Øyangen Aug. 1977 large mode	1.08	.32—3.34	26
Øyangen July 1978 large mode	.34	.15— .98	18

Stomach content weight distributions were skewed to the right for all samples (Fig. 13). The strongest skew was found for large-mode charr from Ellasjøen and Øyangen 1977. The fishes with the high relative food contents had taken large amounts of *L. arcticus* (Øyangen, see also Fig. 11 and Table 9), or had recently eaten small charr (Ellasjøen, see also Fig. 11). The chironomid pupae-dominated 1978 stomachs from Øyangen (Fig. 11, Table 9) had low relative biomasses (Fig. 13). These findings indicate a relation between stomach content weight distributions and prey size. The presence of large prey (fish) gave a strong skew to the right while dominance of small prey (pupal chironomids) rendered a weak skew and low stomach content weights. Intermediate prey (*L. arcticus*) gave intermediate skew. The Ellasjøen sample of small mode charr had probably especially low stomach contents because most fish were spawners. The sample from Stevatn was caught 10 days earlier, before the onset of spawning. This sample is taken to represent a more typical picture of Bear Island small-mode charr feeding. Skew to the right was again present, but far less pronounced than with large-mode charr from Ellasjøen and Øyangen 1977.

Even ruling out the Ellasjøen small mode spawners, the estimated rates of daily food intake were low, *i.e.* < 1.0 mg g^{-1} (Table 10). The food-restricted, stunted charr studied by AMUNDSEN (1984) had intake rates in the 1.5—2.5 mg g^{-1} range, *i.e.* above the present results. Only his late autumn rates were below 1 mg. In spite of large confidence limits, which seems to be a much igno-

red but general phenomenon in fish feeding (AMUNDSEN and KLEMETSEN 1986), these results indicate low food intake rates among Bear Island charr of both size modes.

V. DISCUSSION

The Arctic charr was apparently well established in Bear Island river systems by its discovery in 1899 (ANDERSSON 1900, HERWIG 1900). There is nothing in the 19th century Bear Island literature to indicate introduction by man (KLEMETSEN 1985). Before that time artificial propagation of salmonids was unknown, and transport over large distances unlikely. The island was glaciated during the Weichselian (HORN and ORVIN 1928) and the surrounding sea either glacierfilled or frozen (BOULTON 1979). The existence of habitable conditions for Arctic charr is therefore not feasible. We conclude that the Arctic charr invaded Bear Island in postglacial times in the manner discussed by HUITFELDT—KAAS (1918) for mainland Norway, without human intervention. The relative ocean level was higher (HORN and ORVIN 1928) and the steep brink probably not shaped in early postglacial times. Access for straying anadromous charr and the maintenance of anadromy was probably easy. Once established, the populations presumably developed co-existent resident life cycles like those of most other sea-run Arctic charr systems (JOHNSON 1980).

Our results deny present-day anadromy among Bear Island charr, despite the presence of large

charr in all the sampled lakes. In 1978, Ellasjøen was studied extensively both in July, when any anadromous charr should have been at sea, and in August when they should have returned to freshwater (GULLESTAD 1973 a, b). No change in the population structure caused by ascending sea-run fish was detected in August, and no specimen with a sea-charr dress was caught. The slow growth rate of 2 cm or less per year (Fig. 5 and 6) also precludes marine residence for this population. Large-mode Stevatn charr had also grown slowly compared to the observations of GULLESTAD (1973 a, b) of 5—7.5 cm year^{-1} for Spitzbergen anadromous charr. The charr from Øyangen had a growth rate of 5—6 cm year^{-1} (Fig. 5) which could have been attained at sea. On the other hand, no other observations from Øyangen or other parts of the Jordbruelva system gave reason to believe that anadromous life cycles existed. The good growth probably resulted from good feeding conditions in the lakes themselves, especially through sustained production of the *Lepidurus arcticus* populations. These matters are discussed more closely in the following.

There are no biological reasons for the disappearance of anadromy. Bear Island is situated in the middle of the highly productive Barents Sea, and anadromy is found both to the north and to the south (DAHL 1926, GULLESTAD 1973 a, b, NORDENG 1961). We believe that combined hydrological and erosional factors are involved. In postglacial times the north plains area was raised above the ocean, and wave and pack-ice erosion on the soft rocks started shaping the steep brink so characteristic of Bear Island. This process is still going on. Precipitation is low and catchments are small. Consequently, river run-off is also small after the spring discharge. Fluvial erosions are often too weak to cut a deep profile through the brink. Most river outlets to the sea are therefore too steep and high to allow fish ascent. This is the case with Fosså, Jordbruelva and Engelskelva. Lakselva is an exception. Its valley is wide and flat and the slope itself is no hindrance for upstream migration, except perhaps for a small waterfall below Haussvatn. Nevertheless, we obtained no indication that sea-run charr existed, neither through our own studies nor through interviews of the neighbouring radio station staff. Because it is wide and

flat and consists of loose deposits, the estuary is constantly reshaped by spring flood and marine erosion. Deep channels do not develop and the river is very shallow. During low runoff the water may simply disappear into the gravel. These physical conditions probably obstruct sustained anadromy in the Lakselva river system. In effect, Bear Island Arctic charr populations are landlocked in the sense discussed by NILSEN and KLEMETSEN (1984) and NORDENG and SKURDAL (1985). Descent is possible but ascent is physically prevented.

Since all samples had high frequencies of the Est^F allele, no S-charr seem to have immigrated to Bear Island. The result supports the proposition that Fennoscandian S-charr populations may be descendants of freshwater immigrants from the east (KLEMETSEN and GROTNES 1975, 1980, KLEMETSEN 1984). This seems to be contradicted by HAMMAR (1982) who claims to have found S-charr on Spitzbergen. The claim is probably based on the collection of three resident fishes homozygous for the S-allele on Nordaustlandet 1980 (HAMMAR 1984). This case does not necessarily refute the hypothesis. The homozygoty suggests that fixation of the S-allele through a founder effect may have taken place, for instance, via piscivorous birds. The presence of a relatively high (0.67) Est^S frequency population on Spitzbergen (HAMMAR 1982) makes this plausible. Nevertheless, HAMMAR's report from Nordaustlandet challenge the hypothesis, and more extensive studies of Svalbard charr populations may eventually lead to its contradiction (HAMMAR 1985). In a comprehensive analysis of serum esterases in Icelandic charr GYDEMO (1984) found one clear-cut case of S-charr; the anadromous population of the River Hvita, W. Iceland. This undoubtedly demonstrates that sea-run S-charr exist. The case is, however, of doubtful relevance for Fennoscandia because of Iceland's geographic position. Immigration from the nearctic side seems as likely, especially for the West coast of Iceland. Our hypothesis does not deny anadromous S-charr for other regions, it seeks to explain the Fennoscandian situation by suggesting a freshwater immigrant.

As discussed by KLEMETSEN (1984) and NILSEN and KLEMETSEN (1984) the presence of high frequency Est^F populations on Bear Island fits into a

geographic situation in North-Norway with F-charr populations having a northernly-easternly distribution. NYMAN *et al.* (1981) and HAMMAR (1984) found that the Swedish F-charr distribution was alpine and northern. This preference for cold environments may have been selected for in the Siberian coast refugium suggested by KLEMETSEN (1984). If the Laptev Sea region was habitable for Arctic charr the climate undoubtedly was high arctic, *i.e.* an environment exposing strong selection pressure towards cold adaptation, and for a long time. Pre-adaptation to short summers and low temperatures and a NE immigration route may explain present-day distribution of Fennoscandian F-charr populations.

The establishment of Bear Island charr by invasion of high Est^F frequency ancestors seems to be substantiated. The apparent fixation (Øyangen, Table 3) or near fixation (Ellasjøen) of the F-allele may later have been aquired by a founder effect or by genetic drift. The presence of a very low number of heterozygotes in Ellasjøen (Table 3) possibly provides an example of a genetic drift process close to termination in homozygosity. Genetic drift resulting in homozygosity for serum esterase alleles has earlier been discussed by CHILD (1977) for Welsh charr populations.

The two-morph situation in Bear Island lakes is clearly different from the many Swedish cases (NYMAN 1972, HENRICSON and NYMAN 1976, NYMAN *et al.* 1981, HAMMAR 1984) and the cases from the Skjomen mountains, N. Norway (KLEMETSEN and GROTNES 1975, 1980, KLEMETSEN 1984) with respect to serum esterase frequencies. In Skjomen the sympatric morphs could be referred to segregated Hardy-Weinberg equilibria with markedly different serum esterase frequencies; they were separate populations living together in the same lakes. Life histories and ecology were different. On Bear Island, esterase analysis failed to separate the morphs into discrete biological units. On the contrary, the analysis seemed to put them together in the same gene pool. This biological situation resembles the Salangen charr system (NORDENG 1961, 1983) with its two resident morphs in addition to anadromous charr. The three morphs have identical esterase frequencies (H. NORDENG *in lit.*, KLEMETSEN 1984) and NORDENG (1983) concludes that they belong to the

same population. The situation is also similar to the system of two resident charr morphs in Vangsvatnet, W. Norway. (JONSSON and HINDAR 1982, HINDAR and JONSSON 1982). Again the serum esterase frequencies were identical (K. HINDAR pers. comm.) and HINDAR and JONSSON (1982) concluded that the morphs belonged to one population.

Mature Bear Island charr morphs were readily sorted in the field because of their non-overlapping size ranges (Fig. 2, 4). Spawning colours were different with bright yellow to carmosine belly colours in large-mode charr and bronze-greyish, drab belly colours in small-mode charr. Small mode charr often had parr-marks on the flanks. Additional clues were relative eye-size and related morphometric traits (Fig. 10, Table 4). Whether the large eyes of the small morph are phenotypically linked to sexual maturation or if the character is hereditary is an open question. Eye size, snout length and jaw length are, however, characters used frequently in fish taxonomy, and should therefore not be ruled out as being genetically influenced in Arctic charr. FROST (1965) discussed gillraker number differences of the same magnitude as in the present material for autumn and spring breeding Windermere charr, and suggested that the differences were influenced by the environment. Also gillraker numbers have been found to depend on body size (VLADYKOV 1954, RESHETNIKOV 1961, NILSSON and FILIPSSON 1971, HINDAR and JONSSON 1982), at least up to a certain size. The same has been discussed for pyloric caeca (RESHETNIKOV 1961, ANDERSSON *et al.* 1971). On the other hand both characters are used taxomically in Arctic charr (McPHAIL 1961, SAVVAITOVA 1966, BEHNKE 1972, 1980, 1984), and SVÄRDSON (1952, 1979) has shown that *Coregonus* gillraker numbers are genetically determined. Because CHILD (1980, 1984) reported that the Windermere autumn and spring breeders belonged to different gene pools by using serum esterases, the question of a hereditary basis for the differences in gillraker numbers among Windermere charr must be reconsidered. We conclude that the small, but significant differences in gillraker and polyric caecum numbers demonstrated for the Ellasjøen charr morphs may have a genetic basis. Relative fecundity is a quality which varies much among charr populations (JOHNSON 1980), and its geneti-

cal basis is neither much studied nor understood. Fecundity is, nevertheless, central to life history strategies, and may therefore be supposed to be under considerable selection pressure. Again the difference found between Ellasjøen charr morphs (Table 9) may indicate a hereditary segregation.

The qualities discussed above, the discrete size modes of spawning fish, the corresponding age patterns, the sex ratio differences and the ecological differences together make up a sum which cannot be put aside as purely phenotypical. The question of a genetic basis cannot be ignored, and the presence of sympatric selection processes is suggested. This possibility has been discussed earlier for Arctic charr, notably by SAVVAITOVA (1980 a, b, 1985) and BALON (1980, 1984, 1985), but also by SKRESLET (1973 b), CHILD (1980) and others. KLEMETSEN (1984) proposed that the arctic charr complex is a result of both allopatric speciation processes and postglacial segregation processes in sympatry. The Bear Island charr may provide good examples of sympatric speciation at work.

In Ellasjøen charr of both morphs were numerous and each made up a large part of the population (Figs. 2, 3, 4, 6). In Øyangen and Stevatn one size mode dominated, the other was present but insignificant. Interestingly the dominant morph was opposite in the two lakes, large-mode charr dominated in Øyangen and small-mode charr in Stevatn (Figs. 2, 5). In the following these three manifestations of the two-morph configuration are discussed in relation to lake morphology and prey availability.

Stevatn and Øyangen are morphologically similar and represent the dominant Bear Island lake type, the shallow north plains lake. Apart from cannibalism, the charr of these lakes must rely on benthos as the only source of food. In terms of relatively important prey, this involve very few species: *Lepidurus arcticus*, *Apatania zonella*, *Heterotrissocladius subpilosus*, *Procladius* sp., *Stichtochironomus rosenschoeldi* and perhaps one or two other chironomids (Table 9). The notostracan *L. arcticus* clearly gave the highest stomach content weights and food intake rates (Fig. 13, Table 10). SØMME (1934) found this prey to be very much preferred by salmonids. In alpine and arctic conditions it probably constitutes a very important link in salmonid — and

especially in charr production (P. HAGALA pers. comm., AASS 1969, BORGSTRØM 1970). Its high value is probably through a combination of relatively large size and possibly high energy content, conspicuousness, availability and easiness in capture, although these matters have not been studied in an optimal foraging context. It is, however, easily cropped down if predation pressure gets too high. There may be a close link between a sustained density of *L. arcticus* and the charr morph configuration at Bear Island, exemplified by Stevatn and Øyangen. Small-mode charr stomachs from Stevatn were dominated by chironomids and caddis larvae (Fig. 11, Table 7). *L. arcticus* was rare, and obviously cropped down in this lake. Stomach content weights and consumption rates were low with this food, indicating that the immature insects constitute a poor food, leading to stunted growth and consequently a population dominated by small-mode charr. The few large-mode charr had eaten the same aquatic insects, but also small charr. Their better growth may therefore depend on cannibalism. This situation resembles very closely the alpine Lake Finsevatn, S. Norway (KLEMETSEN and ØSTBYE 1967) and Nordlaguna, Jan Mayen (SKRESLET 1973 a). Both lakes have numerous, small charr with a few large cannibals on top. The river pools of Jordbruelva were similar to Stevatn with stunted charr, decimated *L. arcticus*, and aquatic insects as the prevailing food. Large cannibals were, however, missing, due obviously to restricted space and small prey fish populations. Engelskelva represents another extreme, with no fish and dense *L. arcticus* populations.

In Øyangen a high sustained yield of *L. arcticus* is probably the main reason for the rapid growth of the charr. Plentiful food at the critical size may prevent growth stagnation and sexual maturation, and the majority of the charr grow to large sizes. Cannibalism is probably also important to uphold this dynamic state, although this was not documented by the present material. The intake of chironomid pupae, probably at a time of concentrated hatching, gave low food consumption rates also in this population (Table 10).

These two configurations may illustrate Balon's hypothesis of altrical—precocial dynamic states of charr life histories (BALON 1984, 1985), with

Stevatn representing a state of dominance by altricial dwarfs and Øyangen a state of dominance by large, precocial fish. BALON's hypothesis involves an element of stability for the precocial dynamic state. The present results points to *L. arcticus* as a probable stabilizing element, in combination with cannibalism. If *L. arcticus* becomes grazed down, unstable conditions prevail and altricial dwarfs take over.

Morphologically Ellasjøen is fundamentally different from the north plain lakes. All three limnetic zones are developed, and the pelagial holds a plankton community dominated by *Daphnia longispina* and *Cyclops abyssorum*. This adds a dimension to the environment and may explain why both charr modes are numerous. As in Stevatn *L. arcticus* is grazed down by littoral charr, and immature insects are the dominating prey (Fig. 11, Table 7). At the critical point, however, the pelagial space and its plankton production is available for continued growth through a habitat shift. This is a common situation found among charr, both with a single population (*e.g.* HINDAR and JONSSON 1982, RUBACH 1985) and with two genetically separate morphs, where one morph exhibits the habitat and food shift and grows to large sizes (*e.g.* KLEMETSEN *et al.* 1972, KLEMETSEN and GROTNES 1975, 1980, NYMAN *et al.* 1981, HAMMAR 1984). The numerous two-mode cases from the Canadian Arctic (JOHNSON 1983) also fit into this picture. Many of Johnson's cases imply anadromous charr, which perform the habitat shift by descending to the sea to prey on marine food animals. In principle this is not different from a space shift into a limnetic pelagial (KLEMETSEN and GROTNES 1980). The important point is the added dimension of another space and a food source outside the lake littoral zone. The extremely low diversity of prey communities in Bear Island lakes combined with the two clearcut morphological lake types provide good illustrations for the life history models of Arctic charr under current debate.

VI. ACKNOWLEDGMENTS

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Consequences of the Rotenone Treatment of a Subarctic Swedish Lake on the Fish and Zooplankton Communities

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ABSTRACT

The practice of diverting water from one water system to another for hydroelectric purposes has had an increasing influence in Scandinavia during the last few decades. This paper deals with the problem of undesireable fish species invading water systems with valuable fish species.

To avoid such a disaster occurring due to the diversion of water from Lake Särvsjön to Lake Grundsjön in northern Sweden, it was decided that Lake Särvsjön should be reclaimed by rotenone treatment. This was carried out in August 1974.

It appeared that the fish community of Lake Särvsjön consisted mainly of dwarfed whitefish (*Coregonus* sp.), perch (*Perca fluviatilis*) and pike (*Esox lucius*), whereas the community of Lake Grundsjön consisted mainly of Arctic charr (*Salvelinus* sp.), brown trout (*Salmo trutta*) and some burbot (*Lota lota*). Through catch-recapture experiments the population of mature whitefish was estimated to be about 1,000,000.

The invertebrate plankton community changed strikingly after the treatment. The smaller species increased in size, and the larger species, which had not been observed in the lake before, became the most abundant. This superabundance of nourishment resulted in fast growth and good condition in the introduced fish species (Arctic charr and brown trout).

I. INTRODUCTION

The practice of diverting water from one water system to another has appeared to be an economically profitable method for providing hydroelectric power in Scandinavia. Recently, discussions on whether the diversion of water from water systems with different fish communities can be carried out without serious damage to the fish populations in the receiving lake, have been urgent. One case will be discussed here. It concerns the diversion of water from Lake Övre Särvsjön (surface area 8 km², altitude 650 m asl) in the River Särvån water system to Lake Övre Grundsjön (surface area 6.5 km², altitude ca 640 m asl) in the River Mittån water system. This construction was completed in the autumn of 1965. Of extraordinary interest in this context was the fact that the two water systems contained quite different fish communities. The River Särvån system contained three species of whitefish (SVÄRDSON 1979): *Coregonus fera maxilaris* "storsik" (a large whitefish with sparse gillrakers), *C. wartmanni*, an introgressed "blåsik" or blue whitefish and *C. nilssoni* "planktonsik" (a southern densely-rakered whitefish). The growth rate of the "planktonsik"

was extremely low, the fish becoming mature at a mean weight of 0.038 kg. The first two species were large, bottom-dwelling, benthos-feeders, and the "planktonsik" was a typical, very abundant plankton-feeder which was the numerically dominant species in the lake. Moreover, the system contained a very sparse population of small brown trout (*Salmo trutta* L.), a few grayling (*Thymallus thymallus* L.) pike (*Esox lucius* L.), an abundant population of perch (*Perca fluviatilis* L.), burbot (*Lota lota* (L.)) and a few roach (*Leuciscus rutilus* L.). The River Mittån system, on the other hand, contained only three species of fish: brown trout (*Salmo trutta* L.), Arctic charr (*Salvelinus alpinus* complex) and perch (*Perca fluviatilis* L.). To obtain permission to divert water from the River Särvån system to the River Mittån system, the hydroelectric power company (Bergvik & Ala AB) was obliged to eliminate the fish population of Lake Övre Särvsjön by rotenone treatment. This was done to avoid serious damage to the River Mittån system due to the invasion of "planktonsik" and pike, both known to eradicate charr populations and disturb fish communities in other ways.

The project was initiated by the Regional Director of Fisheries. A detailed description of the

background and the manoeuvres done, was published earlier in Swedish (GUSTAFSON *et al.* 1981). (See map Fig. 1.)

II. MATERIAL AND METHODS

The mapping of the lake and its tributaries revealed that the water volume of Övre Särvsjön amounted to about 50 million m³, which meant that about 25,000 l of rotenone would be necessary for an effective treatment. The tributaries would need about 400 l.

In addition to routine test fishing, an analysis of the zooplankton communities of the two river systems was carried out, Lakes Övre Särvsjön and Nedre Särvsjön in the River Särvsjön system and Lakes Övre Grundsjön, Nedre Grundsjön and Messlingen in the River Mittån system were investigated. (Table 1 and Fig. 1).

The table supports the idea formulated by NILSSON and PEJLER (1973) and NILSSON (1978) that lakes containing typical plankton-feeders such as 'planktonsik' (in this case, Lake Övre Särvsjön and Nedre Särvsjön) are characterized by zooplankters of smaller size, such as *Daphnia cristata* and *Ceriodaphnia* spp), while lakes containing larger fish species such as brown trout and charr (Lakes Övre Grundsjön, Nedre Grundsjön and Messlingen) are populated by larger zooplankters such as *Daphnia galeata*, *Acanthodiaptomus denticornis* and *Heterocope saliens*.

To obtain an approximate measure of the 'planktonsik' population, *sensu* SVÄRDSON (1979), 1000 specimens were marked (fin-clipped) during
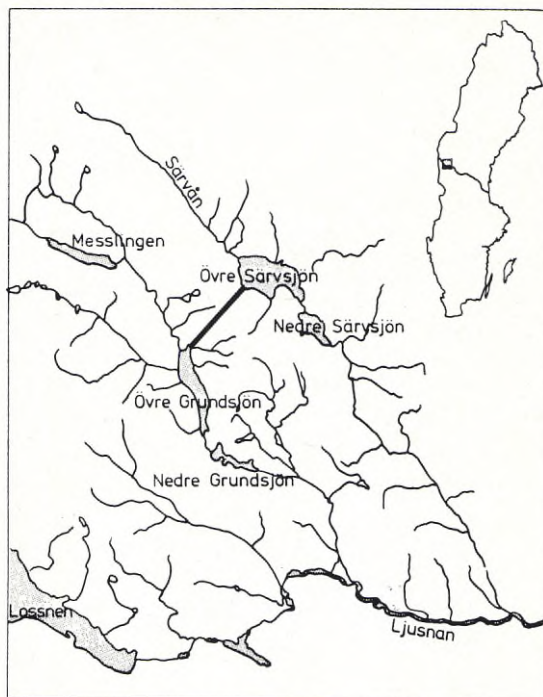
Fig. 1. The water systems of the Rivers Särvån and Mittån, and the position of the tunnel between Lake Övre Särvsjön and Lake Övre Grundsjön.

the period of August 12—20, 1974. The fish were caught with floated nets, and, judging from their condition at recapture, their survival was good, albeit we have no exact data at all as concerns the possible mortality immediately after the marking.

As mentioned above, 25,000 l of rotenone were

Table 1. *Crustacean plankton in the lakes of the River Mittån and River Särvsjön systems.*

Crustacean plankton species	River Särvsjön system		River Mittån system		
	Övre Särv-sjön	Nedre Särv-sjön	Övre Grund-sjön	Nedre Grund-sjön	Mess-lingen
Bosmina coregoni	×	×	×	×	×
Daphnia galeata	—	—	×	×	×
Daphnia cristata	×	×	—	—	—
Ceriodaphnia sp.	—	×	—	—	—
Holopedium gibberum	—	—	×	—	×
Eudiaptomus laticeps	—	×	×	—	×
Acanthodiaptomus denticornis	—	—	×	—	—
Cyclops sp.	×	×	×	—	×
Cyclops scutifer	—	×	—	—	—
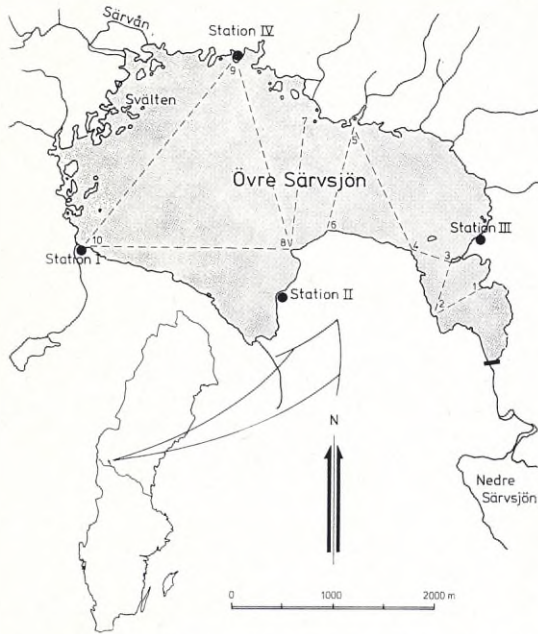
Fig. 2. The sampling stations in Lake Övre Särvsjön 1974. Broken lines indicate the tracks of the diving team.

spread in about 50 million l of water, which gives a concentration of about 0.5 l rotenone per million l water in the lake itself. The fluid was spread by 10 aggregates driven by Homolite pumps, through 20 m long perforated plastic tubes which could be prolonged to 40 m. In this way 270 l of rotenone per minute could be added to the lake.

To gain as much information as possible, four sampling stations were placed at strategically important parts of the lake (Fig. 2). A team of divers also collected fish that sank to the bottom within sampling areas 10 m in diameter.

The rotenone treatment lasted from August 26—28, 1974 and about 30 persons were engaged in the sampling of dead fish. Six members of the staff of the Institute of Freshwater Research, Drottningholm measured, weighed and identified the catch. Fin-clipped whitefish were carefully noted, and samples were collected for later age determination.

III. RESULTS

One of the prime interests of the biologists involved was to obtain information on the composition of the fish community in a "typical" whitefish-lake. Such lakes are frequent in the northern Swedish highlands and also in the vast arboreal areas of northern and central Sweden. The theories about size selective predation also could be tested in this experiment.

Table 2 shows the result of the sampling. In spite of the very intense sampling activity, the figures represent only a small fraction of the real fish population.

Fig. 3 gives the relative contribution (numbers, biomass) of major species in the fish community of Lake Övre Särvsjön in its original condition (the figures are based on the samples of dead fish collected after the rotenone treatment). The planktivorous whitefish was extraordinarily dominant in the context of SVÄRDSON's "dominance-subordinance theory" (1976). The catch of 25,000 whitefish included 28 of the 1000 marked whitefish ("planktonsik"), which means that there were probably about 1 million mature 'planktonsik' in the lake before the treatment. Second in importance numerically were the small perch (mean weight

Table 2. *Lake Övre Särvsjön. The catch resulting from the rotenone treatment in August 26—28, 1974.*

Species	Number	Weight, kg	Mean weight
Planktivorous whitefish	25,071	975.1	0.038
Large whitefish (two species)	52	78.0	1.5
Large perch	101	59.3	0.587
Small perch	5,516	227.6	0.041
Pike	116	443.2	3.820
Burbot	85	115.4	1.358
Roach	4	0.4	0.1
Brown trout	3	0.3	0.1
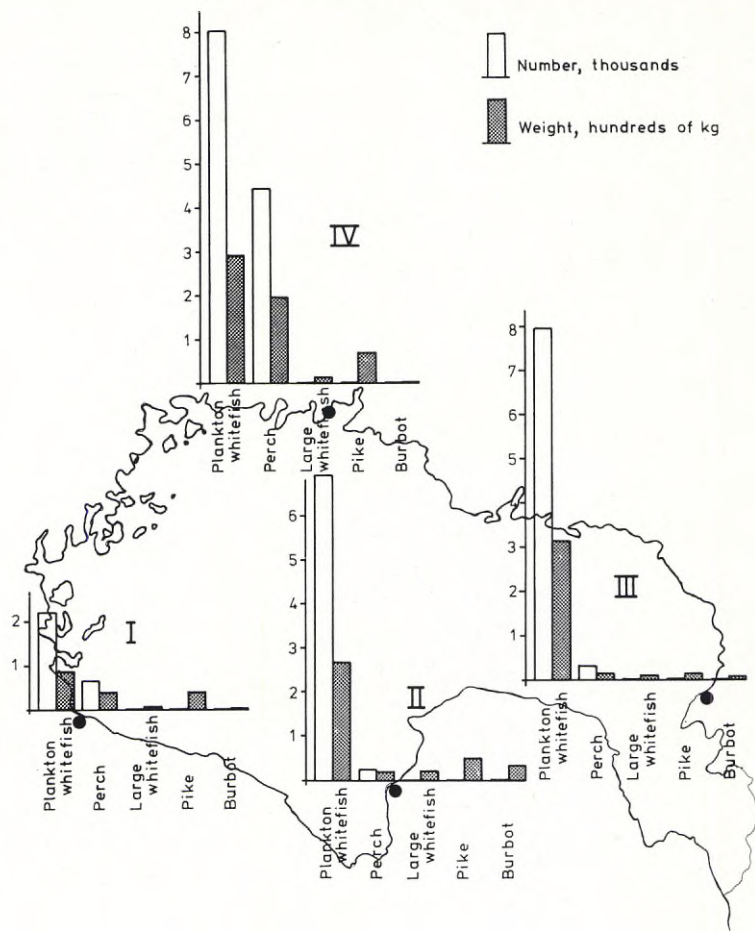
Fig. 3. The amount of fish sampled at stations I—IV.

0.041 kg) amounting to about 2,000 specimens at station IV. This biotope consisted of shallow, former marsh areas submerged by the damming of the lake. The remaining species; large benthic whitefish, grayling, brown trout, large pike and burbot on the whole constituted a relatively small fraction of the standing crop.

On the whole the rotenone treatment was successful, although some of the fish species reappeared in the lake later on. The most important of these was the burbot, which probably migrated down from high mountain lakes (the Sameh people are known to have introduced burbot into high mountain lakes to secure their need for vitamin B₉). Some grayling and brown trout were also found. These species had probably also migrated down from lakes at higher altitudes.

IV. THE REACTION OF THE ZOOPLANKTON COMMUNITY

The sampling was carried out for three years before the rotenone treatment and continued ten years afterwards. To obtain mature specimens, the net hauls were taken in August every year at fixed stations and without changing the procedure.

A drastic change in body size occurred after rotenone treatment within the zooplankton community (Fig. 4). All of the orginal species (*Daphnia cristata*, *Bosmina longirostris* and *Cyclops* sp.) tended to increase in length after the treatment. *Daphnia cristata* increased in mean length from about 0.8 mm in 1974 to about 1.5 mm in 1977. After that it disappeared completely. *Bosmina longirostris* increased from 0.4 mm to about 0.8 mm
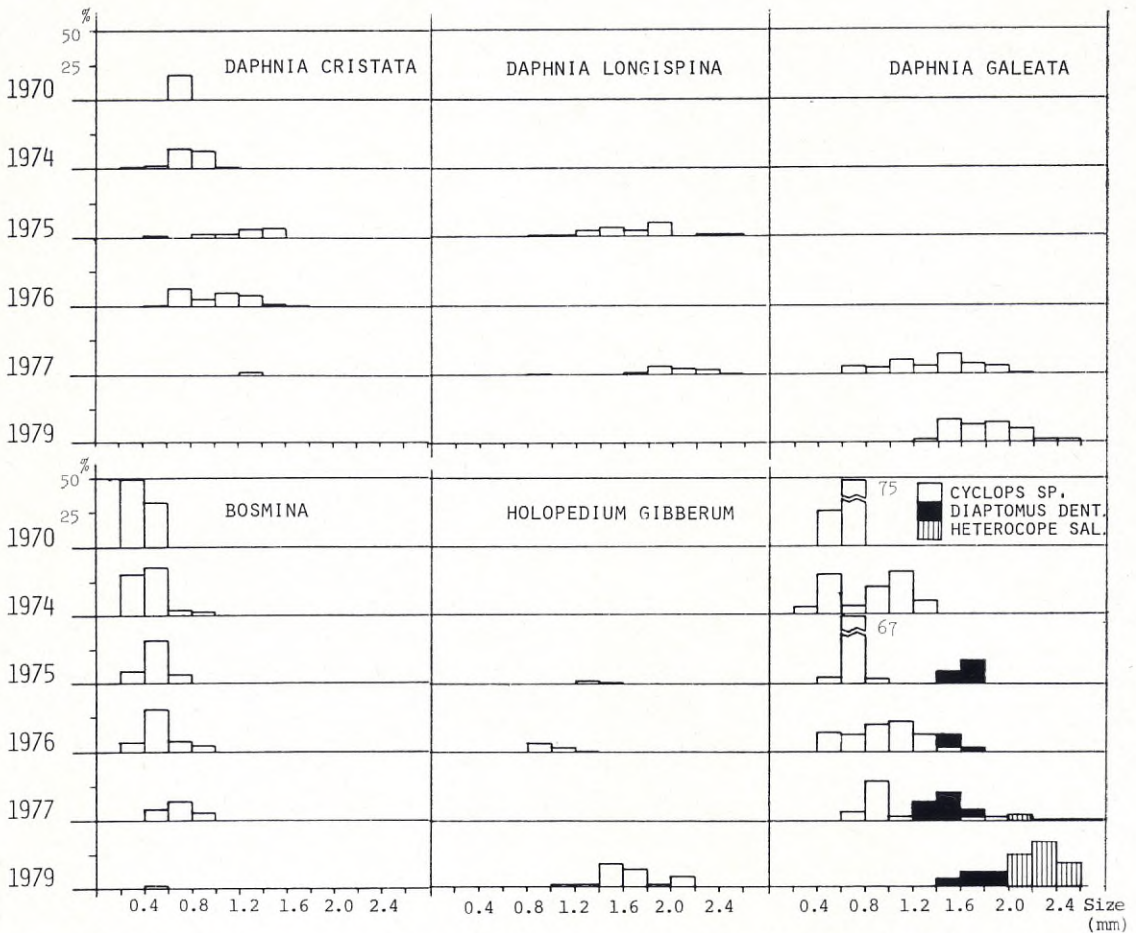
Fig. 4. The change in the structure of the zooplankton community in Lake Övre Särvsjön after rotenone treatment. Species composition and size of the zooplankters.

and had almost disappeared by 1979. *Cyclops* sp. was on the whole the most abundant zooplankter before the treatment. After the treatment its size increased sligthly from about 0.7 to 1.0 mm. In 1979 it disappeared from the samples.

After the disappearence of *Daphnia cristata* it was replaced by the large *Daphnia longispina* (*sensu* PEJLER 1973). It first appeared as early as 1975, when it had a mean size of about 1.6 mm, but it disappeared in 1977, when it had a mean size of about 2.0 mm. It was thereafter succeeded by the extraordinarily large *Daphnia galeata* (cf. NILSSON and PEJLER 1973), which reached a mean size of about 1.6 mm (maximum size 2.4 mm) in 1979. At the same time, *Bosmina* almost disappeared. *Holopedium gibberum* appeared for the

first time in 1975, and there attained a mean size of about 1.6 mm.

Changes in body size of copepods were even more drastic. After completely dominating the crustacean zooplankton community, *Cyclops* (mostly *C. scutifer*) increased in size and suddenly disappeared after the rotenone treatment. Then, in 1975, the large and colourful diaptomid species *Acanthodiaptomus denticornis* appeared in the lake. This species is known to be very rare in lakes containing fish (NILSSON and PEJLER 1973). According to plankton specialists, however, it interacts with other large copepods such as *Heterocope saliens*, which first appeared in the lake in 1977. *Heterocope saliens* dominated the crustacean zooplankton fauna (with *Holopedium gibberum*)

in 1979, although large *Acanthodiaptomus denti-cornis* were still present. *Heterocope saliens*, which is large and brightly coloured red and green, reached approximately the same size as *Daphnia longispina*. It is easy to imagine the former species being very vulnerable to predation by plank-tivorous fish.

V. DISCUSSION

The rotenone reclamation of a lake as large as Lake Övre Särvsjön was at that time probably one of the most comprehensive such projects ever carried out in Europe. Of extraordinary interest was the record of the fish community in a rather typical Fennoscandian 'whitefish-lake', situated in the subarctic region of the Swedish highlands.

The dominance of the small planktivorous whitefish was even more pronounced than expec-ted, as was the relative scarcity of large predators. The results of the sampling indeed provide strong support for SVÄRDSON's "dominance-subordinance" principle (1976). This principle postulates that the standing crops of fish in lakes are hierarchical in nature, which means that the reduction or elimina-tion of the dominant species tends to lead to drastic changes in the lower ranked species. On the whole, pelagic fish species are dominant over littoral species.

The eradication of planktivorous whitefish and small perch (Fig. 3) was *per se* a reversed illustra-tion of what happens to invertebrate communities when new species of fish are introduced into rela-tively stable fish communities (cf. STENSON 1972). Much writing has been produced on selective predation since the work by IZAAK WALTON (1653), HRBÁCEK *et al.* (1961) and BROOKS and DODSON (1965). NILSSON (1978) tried to sum up the evi-dence for size selective predation as an important factor in competition and interactive segregation in fish, and many North American and European scientists are now devoted to far-reaching research in this context (*e.g.* STENSON 1972, ANDERSSON 1979, WERNER *et al.* 1977, TONN *et al.* 1983).

What strikes the researcher in this case, apart from the extraordinary dominance of small plank-tivorous whitefish, is the rapid change which occurred in the zooplankton community after the treatment.

The adult size of most zooplankton species increased and a pronounced succession of new dominant species occurred. The change took place during a relatively short period (ca 5 years). Some of the species had never been observed in the lake before but became abundant after a few years. This very rapid invasion of new species is at pre-sent difficult to explain. One probable theory is that they have always occurred in the lake as rare species and have only accidentally been caught by plankton nets or foraging fish, rather like 'rare birds', hiding in inaccessible habitats, but suddenly becoming common due to environmental changes. Little is also known about the speed at which eggs, ephippia etc. can be spread from one distant place to another.

On the whole, the composition of the zoo-plankton community in Lake Övre Särvsjön be-came more and more similar to that characteri-zing the brown trout — Arctic charr lakes typical for the River Mittån system.

VI. MANAGEMENT AND COMPLICATIONS

In 1975 and 1976, Arctic charr and brown trout were introduced into Lake Övre Särvsjön in the following numbers:

Brown trout	23,000 newly hatched fry	1975
,,　　　,,	12,360 1-year old fry	1976
,,　　　,,	5,000 2-year old fry	1975
Arctic charr	11,400 1-year old fry	1976

Moreover, as mentioned earlier, some fish spe-cies may have re-entered the lake from upstream refugia. Of greatest interest is the appearance of the burbot (*Lota lota* (L.)), which now occurs in abundance. In addition, the opossum shrimp, (*Mysis relicta* L.) seems to have invaded the lake through occasional "backstreams" through the tunnel between Lake Övre Särvsjön and Lake Övre Grundsjön, where it was earlier introduced. The recapture and growth rates of the introduced or re-invading fish were, as expected, excellent. For instance, 50 brown trout caught in June 1976 averaged 22.5 cm in length, with a mean weight of about 89 g. Brown trout caught in November 1977 had a mean length of about 30 cm and a mean weight of 250 g. The charr had also grown

Table 3. Dominant food organisms of brown trout and Arctic charr in September 1979. Percentage of mean volume.

Food organisms	Brown trout						Arctic charr		
	< 150 mm	151—200 mm	201—300 mm	301—400 mm	> 400 mm	Average	301—400 mm	> 400 mm	Average
Burbot	8	—	67	45	22	38	—	—	—
Bythotrephes longimanus	—	—	—	1	—	1	—	30	10
Daphnia longispina	—	—	—	5	—	1	1	10	—
Daphnia galeata	—	—	—	2	—	3	8	57	25
Eurycercus	33	—	—	—	—	4	—	3	1
Mysis relicta	—	—	—	<1	—	<1	—	—	—
Chironomid larvae	—	—	—	23	1	13	<1	—	<1
Trichoptera larvae	3	—	3	<1	—	3	1	—	1
Water bugs (Dytiscidae etc.)	14	—	2	—	<1	—	—	—	—
Corixa	—	—	—	—	<1	<1	1	—	1
Chironomidae, imago	24	—	29	20	72	34	90	—	60
Terr.insects	—	—	1	3	4	4	4	—	2
No. of samples	3	—	3	15	7	28	4	—	4

well. The 33 charr caught in November 1977 averaged 31 cm in size and weighed about 252 g.

The food of the introduced fish

Table 3 indicates the exploition by fish of the changed prey fauna in the reclaimed lake.

The table shows that the brown trout primarily made use of the abundant burbot, in addition to chironomids and Trichoptera. The table does not indicate that gill-breathing invertebrates were damaged by the treatment. Apparently recolonization by many rotenone-affected invertebrates occurs very rapidly. This does not necessarily include sensitive organisms such as gill-breathing molluscs and *Gammarus lacustris*. The Arctic charr primarily consumed the abundant crustacean zooplankton, as well as terrestrial insects (*e.g.* Diptera, Hymenoptera and even spiders) trapped on the water surface. A superabundance of food should have provided the main basis for the good growth of the introduced charr.

Unfortunately, severe acidification during the last few years seems to have influenced the lake in an almost catastrophic way. No complete summary of the effects of this is yet available but is being assembled by the Institute of Freshwater Research.

VII. ACKNOWLEDGMENTS

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The Niche Concept and the Introduction of Exotics

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ABSTRACT

The niche concept has caused some confusion and semantic discussion ever since it was first introduced by, for instance, GAUSE (1934) and ELTON (1946). ELTON's simple definition still stands well as a working paradigm: "The status of an organism in its community".

As it became clear that the seemingly stiff quotation that "two or more species cannot live in the same niche" was not true, many students of the coexistence of species objected, mainly because of the obvious fact that niches very often overlap, or even temporarily seem identical. HUTCHINSON's (1967) definitions of 'fundamental' versus 'realized' niches, as well as his definition of "the N-dimensional hypervolume" as a handy instrument to study niches mathematically, has given rise to an ever-growing literature on 'niche overlap', 'niche breadth', etc. Hand in hand with these discussions the concepts of "interactive segregation" and "species dominance" has shown some importance; many parallels between insects (BRIAN 1956), birds (SVÄRDSON 1949) and fish (NILSSON 1978, SVÄRDSON 1976). As regard fish, the recent finding that exploitative competition by selective feeding force species to segregate into their 'realized niches' (literature compiled by NILSSON 1978) has given us a clue to monitoring introductions of 'exotic species', including subspecies, 'stocks' etc.

It is suggested that the introduction of 'exotics' leads to any of the following results. The introduced stock:

(1) is rejected, because there is no 'vacant niche' or predators graze down the population at early stages,
(2) hybridizes with very closely related stocks, formerly adapted to the ecosystem,
(3) eradicates a stock that is either an 'ecological homologue' or a very available prey,
(4) finds a 'vacant niche' within the community, which means that it adapts to resources that are not fully exploited by other species, and finally makes it able to survive as a member of the community.

The four alternatives suggested are demonstrated in the paper by European and North American experiences.

I. INTRODUCTION

In 1982 EIFAC held its XII Session in Budapest, Hungary. The main object of discussion was the value of introductions of fish — conspecific or 'exotic'. This paper is an abstract of a lecture held at the Symposium which was published as an EIFAC Technical Paper 42/Suppl/2.

II. THE NICHE CONCEPT

The niche concept has (as had once the concept of competition) caused some confusion and semantic discussion ever since GRINNEL's (1904), LOTKA's (1932), GAUSE's (1934), ELTON's (1946), HUTCHINSONS's (1957) and many other trials to define the concept. ELTON (1946) termed the phenomenon "the status of an organism in its community",

which still stands as a simple as well as a good definition.

To fisheries biologists, forced as they are to use theory as a 'superstructure' to practical action called 'fishery management' (cf. KERR's and WERNER's (1980) enlightening discussion about 'academic' and 'fisheries' approaches to niche analysis), it was quite consistent that they objected to the seemingly stiff imperative that "two or more species cannot exist in the same niche", as they frequently observed that fish for instance very often consume similar food or share other essential resources (e.g. FORBES 1914, HARTLEY 1948, STARRETT 1950, NILSSON 1955, LARKIN 1956). In that context phenomena called 'niche overlap', niche breadth", etc. were stressed by many scientists, interested in species interaction (cf. e.g. HURLBERT 1971). The Swedish zoologist LÖNN-

BERG (1929) perhaps was the first one to formulate this by pointing out what he in Swedish named "det dukade bordets princip", by JOHNSON (1980) translated to the "principle of the smorgasbord" that is "in Nature — miscellaneous animals make use of one kind of food that is available in plenty, also such animals, the 'natural' or common food it does not seem to be" (LÖNNBERG, *op. cit.* quoted by NILSSON 1960).

HUTCHINSON (1957, 1967) defined the term niche as an "N-dimensional hypervolume" designating "the requirements of an organism abstracted from the specially extended habitat. The habitat of two species may overlap completely; it is empirically probable that at equilibrium, their niches never do". Thus he distinguished between 'the fundamental niche', which means the virtue of a species to make use of available resources through its physiological capabilities, and the 'realized niche', which is that portion of the hyperspace that is actually occupied, the difference being due to exclusion from certain parts of the niche by other species in the community.

This philosophy is in good agreement with the theories of "interactive segregation" and "dominance-subordinance". This firstmentioned theory (NILSSON 1978) means in a simplified way that interaction between species or subpopulations of species is a fundamental variable creating 'realized niches' *sensu* HUTCHINSON. In even more simplified terms: cohabiting species are forced by interaction to refine their virtues, when resources are at a minimum. Many biologists have spent much painstaking thinking on this problem. For example, entomologists like BRIAN (1956), PARK (1954), ROSS (1957), ornithologists like SVÄRDSON (1949), CODY (1968), MCARTHUR (1958), fish ecologists such as SVÄRDSON (1976), NILSSON (1967, 1978) and WERNER (1977), have arrived at very similar conclusions which probably could be of help in judging whether or not 'exotics' should be introduced in a stabilized ecosystem. SVÄRDSON's (1976) theory of 'dominance-subordinance' points to the fact that the standing crops of fish in lakes are hierachical in nature, which means that the reduction or elimination of the dominant species tends to lead to drastic changes in the lower ranked species. On the whole species with pelagic capabilities generally are dominant over littoral species

(SVÄRDSON 1976, SKUD 1982, RYDER and KERR 1982).

The study of competition is, of course, closely related to the abovementioned problems. PARK (1954), BRIAN (1956) and others distinguished between two components in interspecific competition: interference and exploitation. Interference means a direct harm to one or both species, for instance by aggressive behaviour such as fighting for territories etc. Exploitation, on the other hand, means an interaction that develops whenever one species is more efficient to use available resources more easily and quickly than their competitors.

To turn from theory to practice, it seems that when introducing a new species (population, subspecies etc.) into a new community, it may face any of the following fates:

An exotic species:

(1) gets rejected, because there is no 'vacant niche', or predators graze down the population at early stages, or gets harmfully infected by native diseases, or abiotic factors like temperature, pH, etc. do not fulfil the needs of the species at crucial circumstances,

(2) hybridizes with very closely related stocks, formerly adapted to the ecosystem,

(3) eliminates (completely or partly) a species that is either an 'ecological homologue' or a very available prey, or is sensitive to foreign diseases and parasites, carried by the exotic species,

(4) or finds a 'vacant niche' ('potential niche', WELLCOME pers. comm. 1982) in the community, which means that it adapts to food, space, spawning sites, etc. that are not fully exploited by other species or stocks. It means also, however, that because of competition, niche overlap, etc., the species within the community have more or less to purify their specific virtues, *i.e.* to restrict themselves to their 'realized niches', through interactive segregation.

Fig. 1 is an attempt at modelling a Scandinavian example as regards the 'fundamental' and 'realized' niches of three salmonine species. The hypervolumes of the niches are in the graph hypotheti-

POLYARTEMIA FORCIPATA
HETEROCOPE SALIENS
DAPHNIA LONGISPINA

HETEROCOPE SALIENS
DAPHNIA LONGISPINA

HETEROCOPE SALIENS
DAPHNIA GALEATA

HETEROCOPE APPENDICULATA
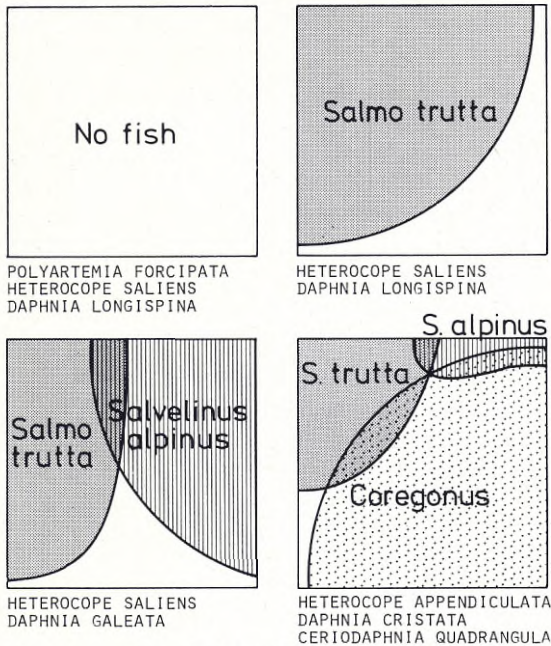DAPHNIA CRISTATA
CERIODAPHNIA QUADRANGULA

Fig. 1. Model of the "dimensions" of the niches of brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus* sp.) in allopatry and sympatry, and the dominant species of zooplankton. (After NILSSON and PEJLER 1973.)

cal, the indications of the zooplankton communities based on quantitative information (NILSSON and PEJLER 1973).

III. SOME PALEARCTIC EXAMPLES

European and American immigrants have enthusiastically tried to introduce species from one continent to another for a very long time, in attempts to 'improve' the native fauna. European starling, house sparrow, European carp and brown trout are wellknown American exemples. Many of these attempts, however, have failed or become disastrous. Our North American colleagues have reviewed this story in some detail (COURTENAY and TAYLOR 1984, RYDER and KERR 1984), it will in this paper mainly be commented on some European experiences, using the introductory scheme (1—4) above.

Rejection

This should by theory be the most likely outcome, as the indigenous fauna should *a priori* be best

adapted to the ecosystem in question, and thereby should not accept an 'intruder'. However, several experiences such as the overwhelming Australian ones, as well as the worldwide plant introductions have provided terrifying lessons (cf. HARLAN 1981). Freshwater fish species on the whole, however, are less disastrous as they mainly are introduced into more closed systems as compared to terrestrial organisms.

Rainbow trout (*Salmo gairdneri*) a western North-American salmonid, originally native to lakes and streams from Alaska to Mexico, with many migratory and resident stocks and subspecies, has been spread all over North America and later to most continents: New Zealand, Australia, Tasmania, South America, Africa, Japan, southern Asia, Hawaii and many parts of Europe (MAC-CRIMMON 1971).

In Europe it has, on the whole, been used as a "put and take" species, or a species cultured for direct consumption. However, as far as natural reproduction is concerned it has on the whole not been suited to European habitats. For instance, WHEELER and MAITLAND (1973) stated that in the British Isles "in spite of such widespread introductions the species appears to have appeared in relatively few places", and WORTHINGTON (1941) listed only about 14 waters in the south of England and one in Ireland. The same is true as regards Scandinavia, where many thousands of introductions have been made since the turn of the century. In spite of thousands of lakes being stocked with rainbow trout ever since the 1880's, just two or possibly three reproducing stocks have been recorded. There has been much speculation on why these introductions have failed. Just to mention a few possible reasons why, the presence of strong competitors or predators may be mentioned. Also the genetics of the species must be taken into account, evolved as it has at the American west coast, rich in lime as a buffering substance, and with very few competing or predatory species present (cf. NILSSON and NORTHCOTE 1981). In Scandinavia the very disastrous acidification problem, should imply a severe threat to the species.

Another apparently non-successful exotic species is the kokanee (*Oncorhyncus nerka*) native to the American west-coast as a landlocked variety. It

was introduced in Sweden in 1960 and onwards into some ten lakes and also in the Baltic.

The result was, on the whole, discourageing although the stocking of kokanee fry in some lakes reclaimed with rotenone proved to be successful. For instance, in one case, one third of the introduced fish were recaptured in a very esteemed shape. This experience has led to the idea that kokanee might be a possibility for fish farming. Some evidence for natural reproduction have appeared, but has hitherto had very little significance. Of course, the increasing acidification problem in Scandinavia leads us to be less interested in trying to introduce species from less acid environments, for instance the American west coast, to our extremely acid-stressed environment.

Another example is the brook trout (*Salvelinus fontinalis*) which was introduced into Scandinavia at about the same time as the rainbow trout. Although it appeared to be more successful than rainbow trout in establishing breeding populations it is now confined to cold headwaters of small streams where apparently it could compete with the native brown trout. This is consistent with the introductions of brown trout at the American east coast, where, on the contrary, the introduced exotic forced the brook trout to inhabit head water refugia of small streams (cf. *e.g.* BRYNILDSON et al. 1964).

The Danube salmon (*Hucho hucho*) can in this context be treated very briefly. It was imported in 1963 to Sweden from Yugoslavia, and the general idea was that — in addition to being an exellent game-fish — it could possibly use habitats apart from its "ecological homologue", the Northern pike, or even compete with it. The introductions, however, completely failed. No Danube salmon has hitherto for certainty been recaptured in Sweden, although the places of release were chosen very carefully.

As to a more comprehensive review of the introductions of this species, I refer to Dr. HOLČÍKS (1984) paper in the FAO symposium in Budapest 1982, and I certainly appreciate his statement that the failures of introduction mostly "are due to the ignorance of the ecology of this species", which is now threatened with extinction.

Similar results have characterized many other introductions of 'game fish' in Europe — mainly centrarchids such as rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*) — and above all largemouth bass (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*). As to the two last mentioned species, WHEELER and MAITLAND (1973) have stated that no population has been established in the British Isles. The same is true for Scandinavia (SVÄRDSON, pers. comm.), in spite of early attempts of introductions. Long winters and too cool summers for spawning have been put forward as a main factor in context with these failures of acclimatization (SVÄRDSON pers. comm.).

This last theory of 'rejection' is also to be considered in the case of introductions of grass carps (mainly *Ctenopharyngodon idella*) into temperate European areas where water temperature and other factors like water flow at crucial stages are unsatisfactory.

The introductions of 'exotics' should apparently not be done without careful consideration, where scientists have a very important responsibility.

Hybridization

Mayr (1963) very early stressed the significance of hybridization between closely related species or subspecies, often leading to a 'subspeciation in regress' (SVÄRDSON 1970). Sibling species hybridize, like coregonids and *Salvelinus* (SVÄRDSON 1970, NYMAN et al. 1981). Rainbow and cutthroat trout, cyprinids and many other taxa also hybridize, as well as 'stocks' introduced to improve fishery. Hybridization (cross breeding) can be devided into two categories: intraspecific crosses between strains 'stocks', 'races' etc. or interspecific crosses between species. Hybridization can achieve either of two favourable outcomes: *viz.* (1) heterosis or hybrid vigour, (2) non-heterotic effects, "the performance of the progeny as the result of simple combination of parental genotypes" (FAO 1981).

Apparently the effects of hybridization can be favourable or disastrous, which all prompts for careful decision. New 'sibling species' should not be stocked without the serious consultation of genetical expertise.
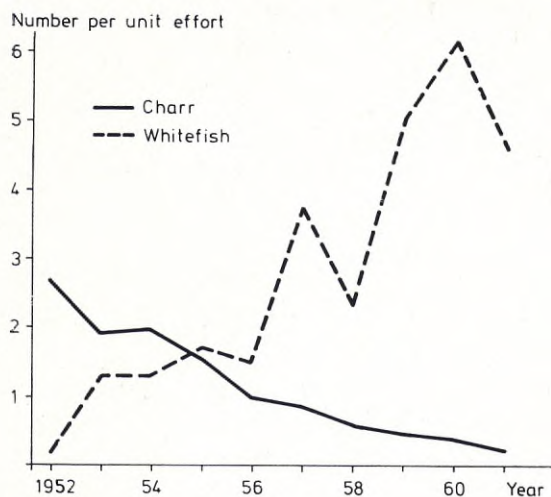
Fig. 2. Decrease in the gillnet catch of charr (*Salvelinus alpinus*) as the catch of the introduced whitefish (*Coregonus* sp.) increased, Lake Västansjö, north Sweden. From NILSSON (1967).

Elimination

The elimination of organisms by introducing exotics has for many decades been one of the most delicate discussion subjects, ever since the naive attempts of the pioneers to improve the natural resources.

Experiences from the introductions of terrestrial animals or plants have taught us that the outcome can — from an anthropocentric view — be manifold, simply speaking either:

(1) an 'exotic' eliminating a less esteemed species, or

(2) an 'exotic' eliminating a more esteemed species.

The agents provided by the introduced 'exotic' can be *e.g.* competition, predation, introduction of diseases, parasites etc.

There are few evidences of really favourable introductions caused by exotics eliminating native species, apart from successful introductions of carp, grass carp or brown trout in areas where these species are looked upon as more favourable than native species. For instance, brown trout or rainbow trout have been looked upon as good alternatives to native species. Brown trout, however, has been shown to interact with brook trout

where it has been introduced — especially at the American east coast.

More severe have been deliberate or accidental introductions of species harmful to the native fish community, profoundly considered by our North American colleagues (COURTENAY and TAYLOR 1982, RYDER and KERR 1982).

I have chosen two cases of disastrous introductions of exotics into European water, one by predation the other by classical Darwinian competition.

Every fisherman knows that the Northern pike (*Esox lucius*) most often has made impossible the coexistence of many species sensitive to predation. For instance TONER (1959) estimated that 2594 pike in two lakes consumed approximately 112.5 tons of brown trout in one year, and WENT (1957) gave strong evidence that pike was not native to Ireland but has eliminated the salmonids in some very important salmonid waters because of introduction. In Scandinavia the presence of pike has made the introduction of, above all, salmonids impossible. Strong evidence has been offered by the many experiments of reclaiming 'coarse fish waters' by rotenone.

The introduction of pike into salmonid waters, thus, is a good example of unfortunate predation on esteemed species.

The elimination of 'ecological homologues', however, seems to imply a still more important problem. This means a competition that is not only a matter of interactive segregation but a real elimination of a species that is unable to defend the niche it was once adapted to.

In this paper no world-wide review of this problem has been possible but one example has been selected because it has since long been very carefully studied. My example is the introduction of whitefish (*Coregonus* spp.) into brown trout-Arctic charr lakes in the north of Sweden. This is a very complicated story, which has been elucidated through SVÄRDSON's (1985, 1979) important studies of the ecology of Arctic charr-whitefish interactions. Already EKMAN (1910) observed that introductions of coregonids tended to eliminate charr populations. SVÄRDSON's (1979) studies have shown that notably one species of whitefish, the 'älvsik' (*Coregonus lavaretus*) has been especially adverse to charr populations. Fig. 2 shows the
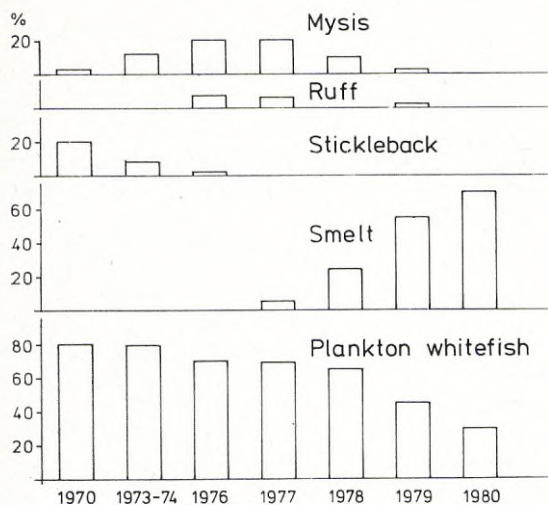
Fig. 3. The food of lake trout (*Salvelinus namaycush*) in Lake Storsjön 1970—80.
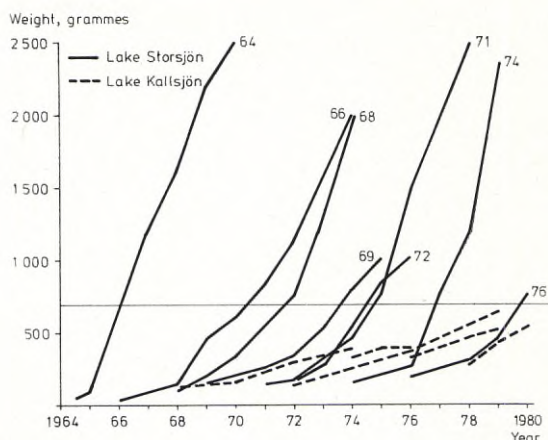
Fig. 4. The growth of tagged lake trout in the Lakes Storsjön and Kallsjön.

elimination of Arctic charr through the introduction of 'älvsik' in a Northern Swedish lake. After the introduction in this lake no catches of charr have been recorded. Recent investigations (NILSSON and PEJLER 1973) have indicated that 'size biased' predation be the fundamental factor in this context.

Vacant niches

The idea to find organisms that fit in with an ecosystem where there possibly is a 'vacant' niche that is not fully exploited by native species should be the main philosophy behind introductions of exotics: a Phoenix.

The search for the Phoenix has in the ligth of History been both troublesome and time-consuming — sometimes even horrid.

Here just one Swedish example is given which involves three aspects of the introduction of exotics, *viz.* two active introductions of food organisms (*Mysis relicta* and smelt) and one predator (*Salvelinus namaycush*) in the same lake. The Lake Storsjön is one of the large lakes of Sweden (surface area 456 km², with a complex fish community, dammed for hydroelectric purposes), which is important both for professional and sport fishery, but has declined as regards Arctic charr and brown trout fishery, mainly because of hydroelectric constructions.

To improve the adversely affected fishery it was decided that the American lake trout (*Salvelinus namaycush*) should be introduced in order to 'convert' the flesh of four species of whitefish into more valuable food as well as sport fishing opportunities (GÖNCZI and NILSSON 1984).

Simultaneously the glacial relict *Mysis relicta* was introduced into the head waters of the lake and soon appeared as a very important member of the plankton community of the lake as well as an important fish food organism.

The growth rate of the lake trout initially was very good (Fig. 3) but after some years the growth declined, possibly because of overgrazing of pelagic food organisms, such as stickleback (*Pungitius pungitius*) and dwarfed coregonids (Fig. 4). At last it was decided that another food organism should be introduced — after much discussion and devoted concern — the smelt (*Osmerus eperlanus*) was introduced in 1974. The population of smelt very rapidly increased, and after only 3—4 years it became the most important food of both lake trout and Arctic charr (close to 100 per cent in 1980).

The Storsjön Story provides a very interesting example of how three exotics (lake trout=predator, *Mysis*=invertebrate prey, and at last smelt=fish prey) interacted in a way that by now looks satisfactory, albeit we certainly have to

study all interrelationships carefully before we are ready to design an ultimate model how to manage a fish community similar to this one.

IV. ACKNOWLEDGMENTS

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The Vertical Distribution of Fish Species in Lake Mjøsa, Norway, as Shown by Gill-net Catches and Echo Sounder

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ABSTRACT

The vertical distribution of fish species in the deep Lake Mjøsa was observed by means of benthic and pelagic gill nets and echo sounder.

The water column was utilized by a significant number of fish of several species down to a depth of 80—100 m, both in the pelagic zone and along the bottom. The dominant species in the benthic catches were smelt, whitefish, roach, perch, ruffe and burbot. Roach was a littoral species. Perch was caught down to nearly 50 m depth, whereas both smelt, whitefish, ruffe and burbot were utilizing most of the bottom profile down to 80 m or more for parts of, or the whole year. The pelagic zone was dominated by vendace, whitefish and smelt. Vendace was caught within 25 m from the surface. Whitefish were common down to approx. 40 m, and smelt down to 80 m in late summer and autumn.

The distribution pattern is discussed in relation to food supply, predation and competition.

I. INTRODUCTION

Information on the horizontal and vertical distribution of fish species is of prime importance in discussions of habitat selection, and possible inter- and intraspecific competition for food and space. Until recently, there has been little systematic information on the vertical distribution of multi-species fish communities in deep Scandinavian lakes (*e.g.* NILSSON 1979). Most of the published information on fish distribution is from relatively shallow lakes (*e.g.* NORTHCOTE and RUNDBERG 1970, HAMRIN 1973, ELORANTA and ELORANTA 1978).

Mjøsa is a deep fjord lake (Fig. 1), which gives an excellent opportunity to study the utilization of the deep water column by a fish community of 20 species (Table 1).

II. STUDY AREA

Mjøsa (Fig. 1) is Norway's largest lake, with a surface area of approx. 365 km², and a maximum depth of 449 m. Since 1912 it has been regulated for hydroelectric power production. The maximum regulation amplitude is 3.6 m, leaving much of the littoral zone dry in late winter. The lake is usually ice covered from the end of January to the beginning of May. In summer the thermocline is established at a depth of 10—20 m, usually by the end of June or in July (HOLTAN *et al.* 1980a). Because of the thermal stratification, and the summer floods, the epilimnic water is theoretically renewed twice during the summer period (HOLTAN *et al.* 1979).

The main inlet is the River Gudbrandsdalslågen, draining large mountaineous areas. The outlet is in the south, the River Vorma.

In the twentieth century, especially after 1950, Lake Mjøsa has been subject to an accellerating cultural eutrophication caused by domestic sewage, agricultural runoff, and industrial wastes (HOLTAN 1981). This development culminated in 1976, with a mass bloom of the blue green algae *Oscillatoria rubescens*, making the water unsuitable for drinking and industrial use. Since 1976, measures taken by the authorities have resulted in a pronounced improvement of the water quality. In 1979—80 the primary production was back to the satisfactory level of the early 1950's (HOLTAN *et al.* 1980a). The eutrophication did never, not even in 1976, reach a level of reducing the oxygen content of the deep waters.

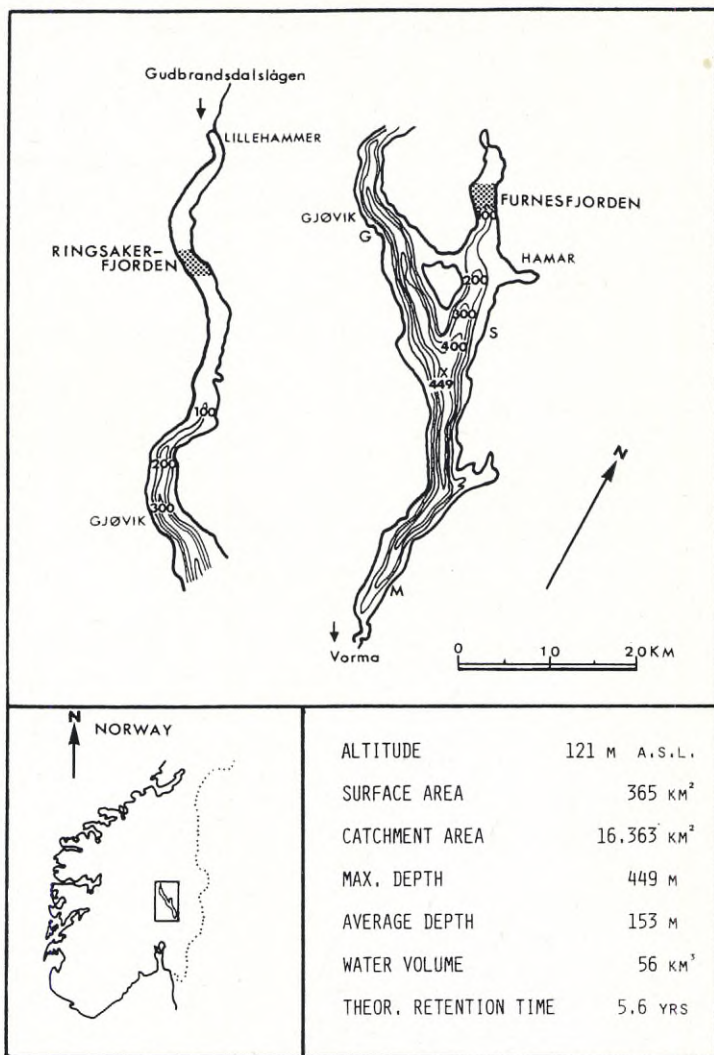The Furnes Fiord is an arm of the lake in direct connection with the deep central basin, whereas

Fig. 1. Lake Mjøsa. The test fishing areas are shaded. G, S, and M are localities for benthic net fishing in deeper water.

The Ringsaker Fiord is isolated by a relatively shallow area (Fig. 1).

The zooplankton community in Lake Mjøsa has an August—September maximum dominated by *Daphnia galeata* (Holtan *et al.* 1980b). The main zooplankton biomass is found in the upper 30 m of the water column. There is also a relatively large population (approx. 150 ind. m^{-2}) of *Mysis relicta* (Kjellberg and Sandlund 1983). The *M. relicta* population lives pelagically, and in the ice-free season occupies the water layers between approx. 25 and 110 m.

The zoobenthos in Lake Mjøsa is dominated by insect larvae (mostly Chironomidae), molluscs, oligochaetes and amphipods. The highest zoobenthos biomass and diversity is found in shallow water, from the lower regulation limit to approx. 25 m. The chironomids, molluscs, and oligochaetes are the dominant benthic fauna in this zone. The amphipods *Pallasea quadrispinosa* and *Gammaracanthus loricatus* are most important in deeper waters, but *P. quadrispinosa* is also found in the littoral zone in summer (Holtan *et al.* 1980b, Næsje *et al.* 1981).

Table 1. *Total catch by gill net sampling in Lake Mjøsa (localities Furnesfjorden and Ringsaker-fjorden, Fig. 1), October 1978—November 1979.* N=number of fish, W=weight of catch (kg), C.P.U.E.=catch per unit effort (number of fish per 100 m² net area per 24 hrs), p.n.=pelagic nets, b.n.=benthic nets. + indicates that the species is rare in gill net catches, — indicates that the species was only caught with other methods.

Species	Total Catches				C.P.U.E.	
	N	%	W	%	p.n.	b.n.
Lamprey *Lampetra fluviatilis* (L.)	—	—	—	—	—	—
Brown trout *Salmo trutta* L.	98	0.7	90	7.0	0.1	+
Vendace *Coregonus albula* (L.)	1194	8.8	84	6.6	0.9	0.1
Whitefish *Coregonus lavaretus* (L.)	1173	8.7	280	21.9	0.4	1.4
Smelt *Osmerus eperlanus* (L.)	5427	40.2	54	4.2	2.4	5.1
Grayling *Thymallus thymallus* (L.)	72	0.5	13	1.0	—	0.1
Pike *Esox lucius* L.	21	0.2	69	5.4	+	+
Roach *Rutilus rutilus* (L.)	1688	12.5	184	14.4	+	3.4
Ide *Leuciscus idus* (L.)	93	0.7	63	4.9	+	0.1
Dace *Leuciscus leuciscus* (L.)	1	+	+	+	+	—
Bream *Abramis brama* (L.)	15	0.1	25	2.0	—	+
Bleak *Alburnus alburnus* (L.)	78	0.6	3	0.2	+	0.2
Minnow *Phoxinus phoxinus* (L.)	—	—	—	—	—	—
Crucian carp *Carassius carassius* (L.)	—	—	—	—	—	—
Perch *Perca fluviatilis* L.	1047	7.7	103	8.1	+	2.1
Ruffe *Gymnocephalus cernua* (L.)	2131	15.8	25	2.0	+	4.3
Burbot *Lota lota* (L.)	439	3.2	284	22.2	—	0.9
Miller's thumb *Cottus poecilopus* Heckel	38	0.3	+	+	—	0.1
Deepwater sculpin *Myoxocephalus quadricornis* (L.)	2	+	+	+	—	+
Stickleback *Pungitius pungitius* (L.)	—	—	—	—	—	—

III. METHODS

The two major localities for gill-net sampling were chosen to cover different levels of eutrophication in Lake Mjøsa (Fig. 1). The investigations by the Norwegian Institute of Water Research (NIVA) indicate clearly that the Furnes Fiord is the most eutrophic, and the Ringsaker Fiord the most oligotrophic part of the lake (Holtan et al. 1980a). This is mainly due to the influence of the main inlet, River Gudbrandsdalslågen, in the Ringsaker Fiord. For practical reasons, the moderate depth (80—100 m) of these two arms of the lake make them suitable for sampling with pelagic gill nets. Echo soundings over the deeper parts of the lake clearly showed that the density of fish in the pelagic zone was very low deeper than 80—90 m (Lindem 1977, 1978). The sampling sites in the Furnes and Ringsaker Fiords are therefore assumed to show the main pattern in the vertical distribution of the pelagic fish species in the lake.

To collect more information on the distribution of benthic fish species in the deeper parts of Lake Mjøsa, benthic nets were used at three additional localities (S, G, and M in Fig. 1).

The sampling was done by gill nets of twelve different mesh sizes (8—50 mm knot to knot). The benthic nets (2 m deep) were mounted in gangs of twelve nets with a fixed succession of mesh sizes (15, 35, 18, 45, 8, 29, 22.5, 50, 10, 39, 12.5, and 26 mm). The nets were set from the shoreline to the deepest part of the sampling station. The exact depth of the nets on the bottom profile was registered by an echosounder (Simrad EL). The nets were fished for 24 hrs, and the sequence of mesh sizes reversed to get the best cover of mesh sizes in each depth zone. The benthic nets were set on two localities in each sampling area, to cover variations in bottom profile and substrate.

The pelagic nets (6 m deep) were mounted in three gangs of four mesh sizes each, and all twelve mesh sizes were set for 24 hrs within each of five different depth zones (0—10, 15—25, 30—40, 50—60, 70—80 m in the Furnes Fiord and 0—10, 15—25, 30—40, 45—55, 60—70 m in the Ringsaker Fiord. The position of the pelagic nets were controlled by echo sounding. The catches were sorted in species and counted. Catch per unit effort (cpue) was calculated as number of fish per

100 m² net area per 24 hrs. This is used as cpue throughout this paper. The methods are described in further detail by SANDLUND *et al.* (1980a).

The test fishing in the Furnes Fiord was performed in October and November 1978, February 1979 (through the ice) and monthly from May through November 1979. In the Ringsaker Fiord, fishing was performed in March 1979 (through the ice) and monthly from May through November 1979.

In localites S, G, and M fishing with benthic nets were performed in September/October 1979. To investigate the distribution of fish in the deeper part of the pelagial zone, fish was registered with an echo sounder system designed for calculating fish density and size distribution (LINDEM 1981a, LINDEM and SANDLUND 1984). During the project period, fishing was also performed with beach seine, pelagic pair trawl, traps etc., and some observations from this sampling will be referred to in this paper.

The selectivity of gill nets is well known (*e.g.* HAMLEY 1975), both in respect to fish species and fish size. By using a wide spectrum of mesh sizes and performing the fishing in exactly the same way in all sampling periods, the errors caused by the selectivity of the gear will be minimized. The results can therefore be used to study qualitative and quantitative changes in distribution (cf. *e.g.* FILIPSSON 1972, NILSSON and NORTHCOTE 1981, HINDAR and JONSSON 1982). As the nets were fished during 24 hrs, the diurnal migrations of pelagic fish in Lake Mjøsa, which have been demonstrated by hydroacoustic methods (LINDEM 1978), were not detected in the net catches.

IV. RESULTS

Species composition of the gill net catches

Sixteen fish species were recorded in the gill-net catches from Lake Mjøsa (Table 1). Approx. 40 % of the total number was smelt. Ruffe and roach constituted approx. 16 and 12 %, and vendace, whitefish and perch 7—8 % each. Burbot were also common in the gill net catches (3 %), whereas nine other species each contributed less than 1 % of the total number of fish caught. Based on the weight of the catches, whitefish and burbot were

Table 2. *Relative fish density (number of fish per 1000 m³) in the central part of Lake Mjøsa between 50 and 120 m depth, calculated from echograms of the Simrad EY-M echosounder.*

Depth (m)	May	June	Sept	Oct	Nov
50— 60	4.53	2.19	3.26	1.81	1.40
60— 70	3.07	0.53	2.49	2.21	0.76
70— 80	0.66	0.39	2.49	2.19	1.08
80— 90	0.08	0.02	1.54	1.20	1.81
90—100	—	—	0.51	0.24	0.71
100—110	—	—	0.13	0.01	0.02
110—120	—	—	0.01	—	0.01

dominating. Roach, vendace, trout and pike were also important in the total catch.

The overall catch per unit effort indicates that only four species were common in the pelagic zone (Table 1). These were smelt, vendace, whitefish and predatory trout. Seven additional species were caught in the pelagic nets on rare occasions. In the benthic net catches, the five species smelt, ruffe, roach, perch, and whitefish were most frequent. There is only one form of whitefish in Mjøsa, with approx. 31 gillrakers (AASS 1972a, NÆSJE 1984).

The spatial distribution of the main species in Lake Mjøsa

Echo soundings in Lake Mjøsa, in the period 1977 through 1981, show that the density of fish is very low in the pelagic zone deeper than 80—100 m (Table 2). Fish schooling greatly influence density estimates by echo sounding (LINDEM and SANDLUND 1984). During the echo soundings in Mjøsa, fish schools were never detected deeper than approx. 40 m. Echograms from waters deeper than 120 m in Mjøsa show very low fish density (less than 0.01 fish per 1000 m³). The density of fish deeper than 70 m increases in autumn (September—November). A typical echo recording from September is shown in Fig. 2.

Smelt were very prominent in the pelagic and benthic gill-net catches in the Furnes and Ringsaker Fiords (Table 1). The size of the catches varied throughout the year, but in the benthic catches, smelt was common in all months (Fig. 3). The benthic catches of smelt in the Furnes Fiord indicated that this species mainly utilizes the
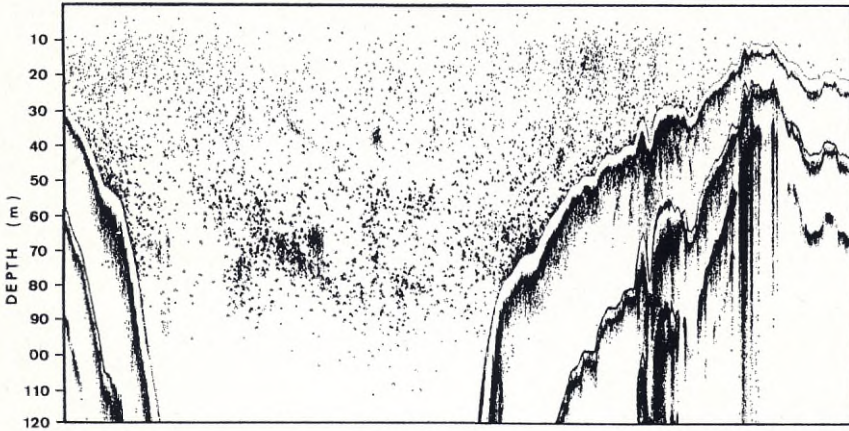
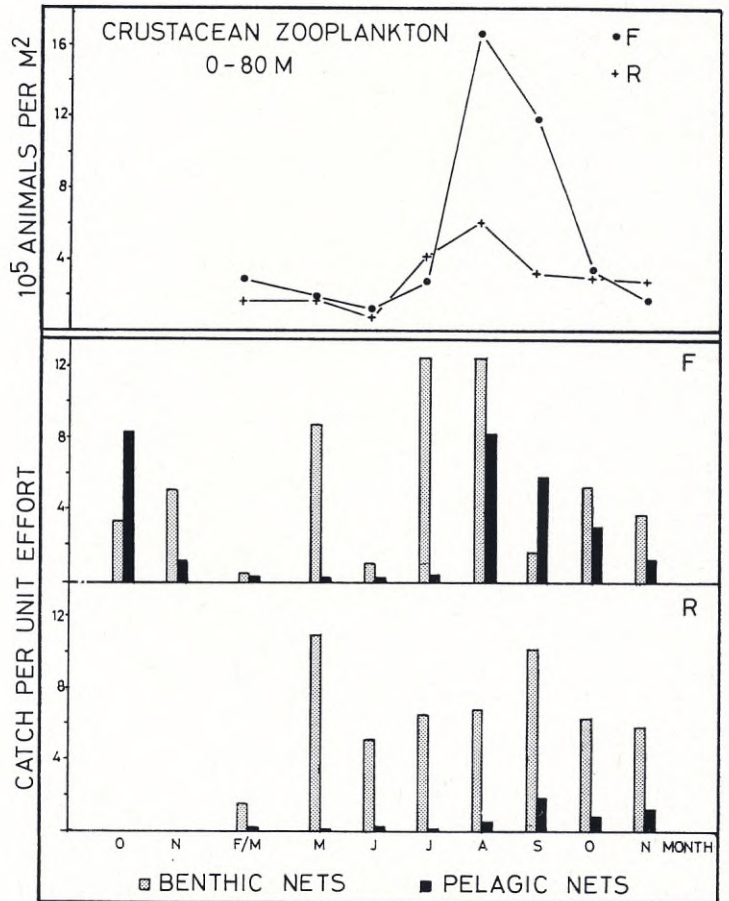Fig. 2. Typical echogram from Lake Mjøsa, recorded at nighttime, September 1979.

Fig. 3. Average catch per unit effort (number of fish per 1000 m² net area per 24 hrs.) in pelagic and benthic nets in Furnesfjorden (F) and Ringsakerfjorden (R), 1978—79, compared with density of crustacean zooplankton in the two areas.
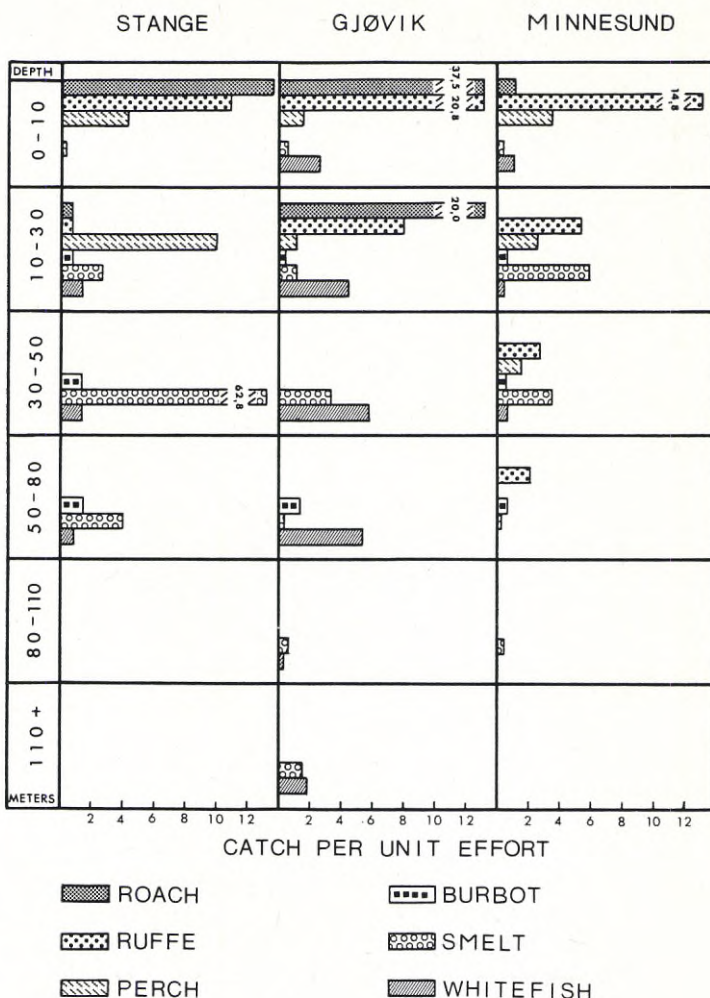
Fig. 4. Catch per unit effort in benthic nets at locality Gjøvik, Stange and Minnesund (G, S, and M in Fig. 1).

bottom profile from 10 to 50 m (Figs. 4 and 5). In the littoral zone (0—10 m), smelt were caught in significant numbers only during spring, close to spawning time. In the 50—80 m zone, smelt were only caught in appreciable numbers during autumn (October—November). Roughly the same pattern was found in the Ringsaker Fiord. In the pelagic nets, smelt were only caught in larger numbers from August to November. This coincides with maximum in the zooplankton biomass (Fig. 3). The pelagic net catches in August indicated that smelt first occupy the upper water strata (Fig. 6). Later, in September—October, smelt were caught in large numbers in all depth strata down to 80 m. There was a reduction in catches in late autumn and winter (November—February).

The distribution of whitefish in Lake Mjøsa shows roughly the same pattern as demonstrated for smelt. Whitefish were caught in both pelagic and benthic nets. It was prominent in the benthic catches throughout the year. In the benthic catches in the Furnes Fiord, whitefish were common in all depth zones down to 80 m, except deeper than 30 m in the winter period (Fig.7). Whitefish were more common than smelt in the littoral zone (0—10 m). It should be noted that a comparatively large proportion of the benthic whitefish in the Furnes Fiord were caught deeper than 50 m. The catches in the Ringsaker Fiord indicate approximately the same pattern. Deeper than 80 m, whitefish were only caught at the locality south of Gjøvik (Fig. 4). Local fishermen know this locality
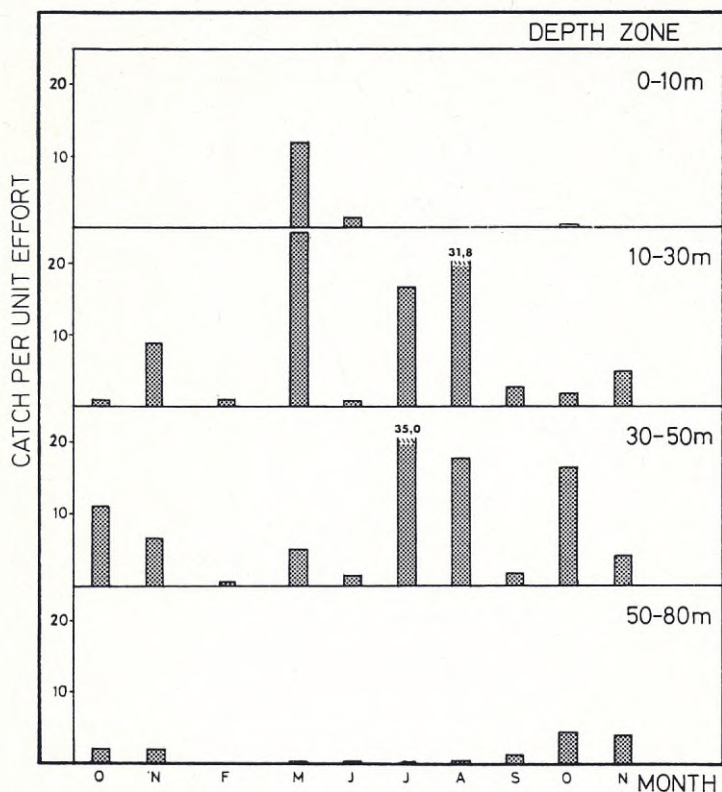
Fig. 5. Catch per unit effort of smelt in benthic nets in four depth zones in Furnesfjorden, 1978—79.

to be the only place in Mjøsa to catch benthic whitefish in deep waters. Whitefish catches in pelagic nets during winter and early summer were small. The catches of pelagic whitefish reached maximum from August to November, similar to smelt (Fig 8). This coincides with the maximum in zooplankton biomass (Fig. 3, and SANDLUND *et al.* 1980a). The pelagic net catches in the Furnes Fiord indicates that pelagic whitefish keep mainly to the upper 40 m of the water masses (Fig. 8). This differs from smelt, which were caught in appreciable numbers down to 80 m.

Vendace is the only species in Lake Mjøsa that was almost completely pelagic. Only on a very few occasions vendace were caught in the benthic habitat during our investigations (Table 1). In late summer and autumn, during the spawning migration towards the main inlet, River Gudbrandslågen, local fishermen catch vendace with floating beach seine. This commercial fishery yield some 50—150 tons (average 136 tons, AASS 1978) of vendace every year. The main catches of

vendace were made in the upper 25 m of the pelagial zone, and only very rarely deeper than 40 m (Fig. 9). In both fishing areas, the catches were low during winter and spring. In the Furnes Fiord, the catches increased from July onwards, and reached a maximum in August—September. In the Ringsaker Fiord, the catches remained low throughout July, and maximum was reached in September—October.

Brown trout and, to a lesser degree, pike are living as pelagic predators in Lake Mjøsa, preying mainly on smelt, and some vendace and whitefish (HUITFELDT-KAAS 1917, SANDLUND *et al.* unpubl. data). Being large predators, however, these species are present in low numbers, and catches are small (Table 1).

Gill-net catches indicate that roach, perch, ruffe and burbot were the most numerous of the benthic fish species in Lake Mjøsa. Roach is a littoral species, rarely caught deeper than 10 m (Fig. 10). Perch were commonly caught down to 30 m, whereas ruffe were common at all depths down to
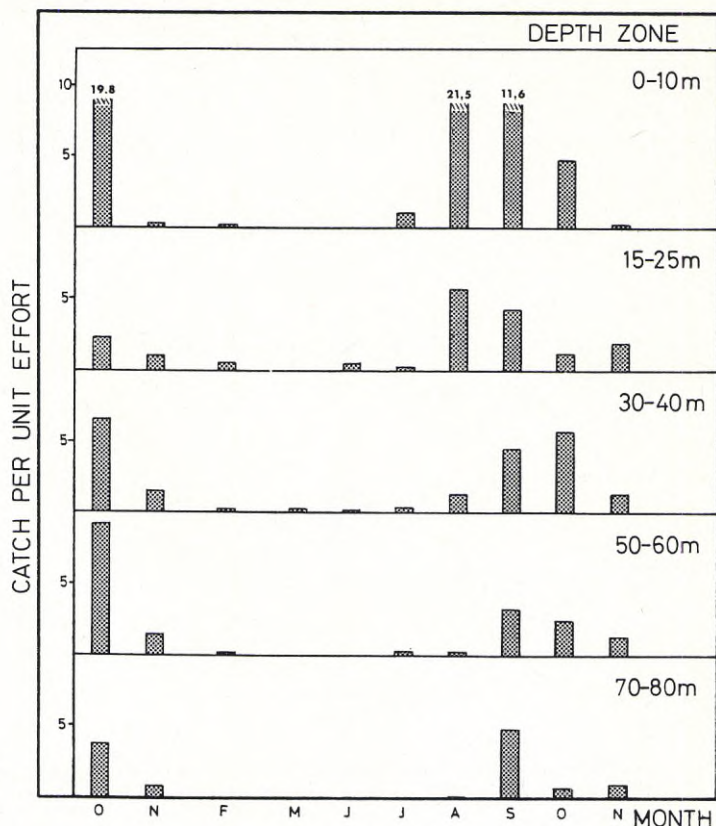
Fig. 6. Catch per unit effort of smelt in pelagic nets in five depth zones in Furnesfjorden, 1978—79.

80 m, exept in summer when most of the population appeared to be living shallower than 30 m (Fig. 10). This might be connected with spawning, which takes place in June. The burbot spawns in winter and early spring, and they were caught above 10 m only at this period (SANDLUND *et al.* 1985). During winter they were not caught in the 50—80 m zone, but at all other seasons, they were common in the bottom net catches from 10 to 80 m (Fig. 10). Neither ruffe nor burbot were caught deeper than 80 m (Fig. 4).

Perch and ruffe have been caught very occasionally in pelagic nets and trawl, whereas burbot appear to live strictly within one metre from the substratum.

Several other species, *e.g.* bream, bleak and ide, were of less importance in our gill-net catches (Table 1), but appear to be quite common in shallow, protected bays of the lake. This is shown both in trap and beach seine catches.

V. DISCUSSION

The spatial distribution of fish species is most often related to food supply, suitable spawning localities, and inter- and intraspecific competition, including predation (NILSSON 1967, KEAST 1977, PYKE *et al.* 1977, WERNER and MITTELBACH 1981).

The fish distribution in Lake Mjøsa appears to be in accordance with earlier investigations in lakes where the large, so called "glacial relict" crustaceans are present (JOHNSON 1975, NILSSON 1979). In Lake Mjøsa, *Mysis relicta* create a hypolimnetic food supply with a vertical distribution from 25 to 110 m (KJELLBERG and SANDLUND 1983), and *Pallasea quadrispinosa* a benthic food supply down to more than 100 m depth (MATHISEN 1953). *Gammaracanthus loricatus* seems to have an intermediate habitat between these two species, being semibenthic down to depths of more than 200 m (NÆSJE *et al.* unpubl. data). *G. loricatus* is more
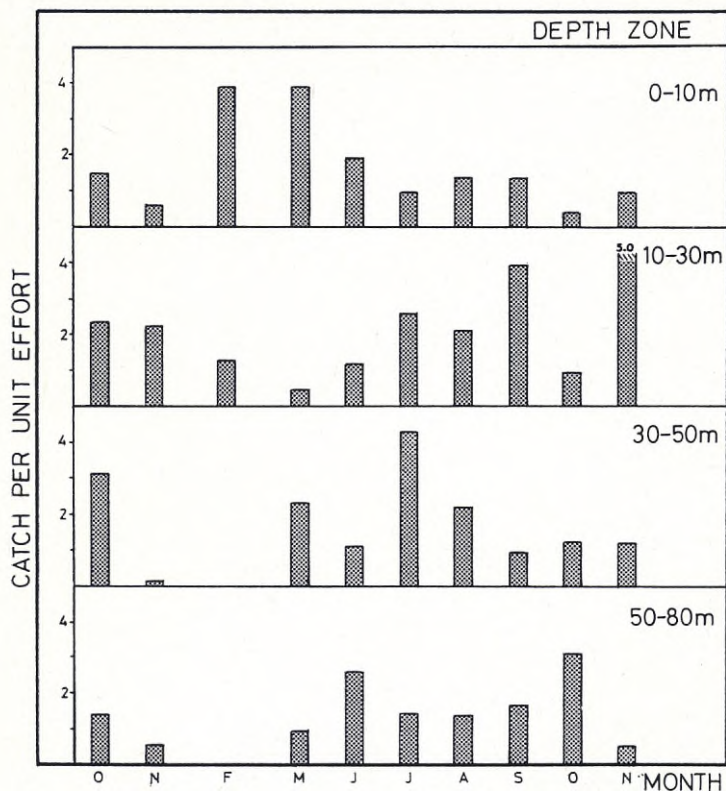
Fig. 7. Catch per unit effort of whitefish in benthic nets in four depth zones in Furnesfjorden, 1978—79.

mobile and swim faster than *P. quadrispinosa*, and is therefore less likely to be eaten by fish (NÆSJE *et al.* 1981).

In Lake Mjøsa, benthic fish density is relatively high down to approx. 80 m depth. In Lake Vänern, where the potential food resources of glacial relicts are similar to that of Lake Mjøsa, several fish species utilize the water column down to at least 85 m, which was the maximum depth in the sampling areas of NILSSON (1979). Similar results are reported from Great Bear Lake, where benthic *M. relicta* was found down to approx. 200 m (JOHNSON 1975). The *Mysis*-eating deepwater sculpin and its predator, lake trout (*Salvelinus namaycush*), were also caught down to this depth, but catches were very low deeper than 80—100 m. In Lake Mjøsa a low number of deepwater sculpin was caught down to at least 150 m, but no predators were caught deeper than approx. 80 m. The catches of smelt and whitefish deeper than 100 m at locality G demonstrate the importance of food supply in determining the distribution of fish. At

this locality industrial effluents containing organic fibers have created a sediment with high organic content down to at least 300 m. This supports an exceptionally high density of oligochaetes (HOLTAN *et al.* 1979), which can be utilized as food by whitefish and smelt.

In oligotrophic lakes where the "glacial relicts" are missing, fish are rarely found in any significant densities deeper than 40—60 m (SANDLUND 1979, LINDEM 1981 a, b, SKURDAL and QVENILD 1982, HINDAR and JONSSON 1982). In eutrophic lakes oxygen depletion may reduce the possibilities for fish to live in deep waters (ANDREASSON and STAKE 1970, BRABRAND *et al.* 1981). The presence of the "glacial relicts" *M. relicta* and *P. quadrispinosa* thus appears to enable the fish to utilize a larger part of the water volume in oligotrophic lakes.

In Lake Mjøsa the upper 30 m of the water volume support the largest fish biomass and the most diverse fish fauna. This is the usual pattern in lakes, and is due to the more abundant food supply of zooplankton, zoobenthos, phytobenthos,
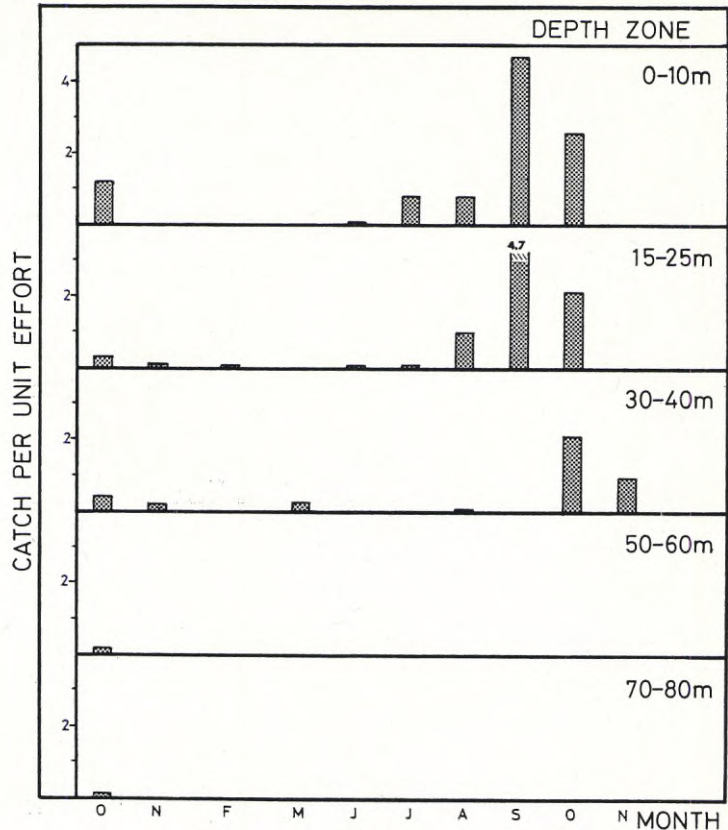
Fig. 8. Catch per unit effort of white-fish in pelagic nets in five depth zones in Furnesfjorden, 1978—79.

and prey fish (JOHNSON 1975, NILSSON 1979, HOLTAN *et al.* 1980 a). The regulation zone appears not to alter this picture, although within the 3.6 m that are left dry in winter, zoobenthos production will be low.

The benthic species

In Lake Mjøsa, roach were dominating in the littoral zone, eating both phyto- and zoobenthos. This is commonly observed in oligo- and meso-trophic lakes (HARTMANN and LÖFFLER 1978). When the lake becomes more eutrophic, other cyprinids, especially bream, become more abundant in the littoral zone (TUUNAINEN 1971, HAKKARI and GRANBERG 1977, HARTMANN and LÖFFLER 1978). The mouth apparatus of bream is specially adapted to catching food organisms buried in the soft sediment found in eutrophic littoral zones (NIKOLSKY 1969, p. 286).

The two most important fish species feeding almost exclusively on zoobenthos are ruffe, and small to medium sized perch. Larger perch also eat fish, mainly smelt. In Lake Mjøsa, perch is restricted to the 0—50 m depth zone, whereas ruffe utilize the bottom profile down to at least 80 m. Ruffe are commonly found in deeper waters than perch (HAMRIN 1973, HANSEN 1978, NILSSON 1979), but due to its small size, ruffe are often missing from gill-net catches done with mesh sizes from approx. 20 mm upwards (*e.g.* NORTHCOTE and RUNDBERG 1970). The different distribution of these two species might be due to differences in their ability to catch various food organisms (NIKOLSKY 1969, p. 286).

The typical distribution of the two benthic predators pike and burbot is that the pike is littoral and the burbot lives in deeper waters (SVÄRDSON 1976). In Lake Mjøsa, large pike also move out into the pelagic zone, preying on smelt and vendace in near-surface waters. The pike is

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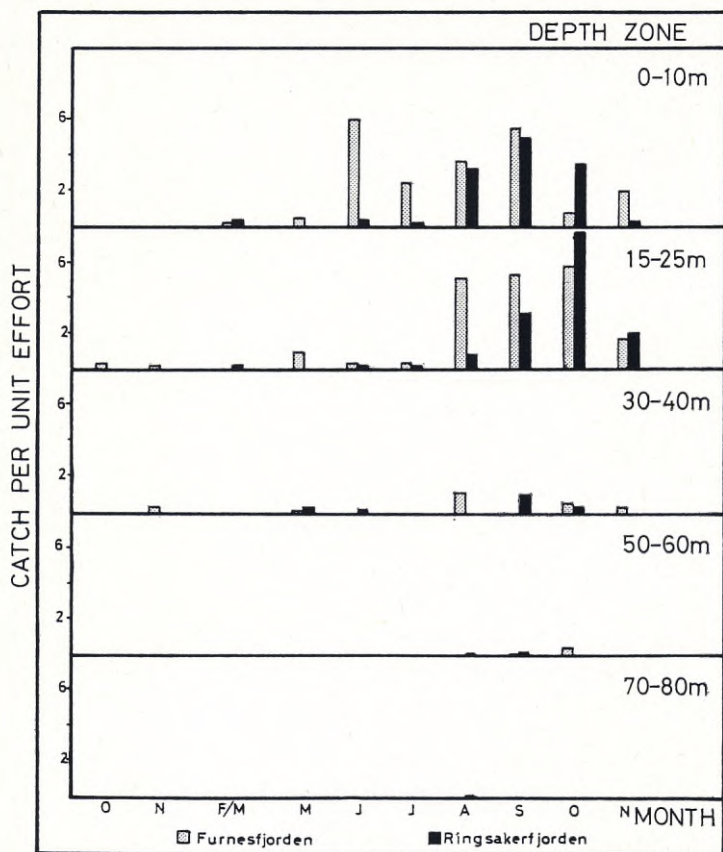
Fig. 9. Catch per unit effort of vendace in pelagic nets in five depth zones in Furnesfjorden (October 1978—November 1979) and Ringsakerfjorden (March—November 1979).

very much depending on sight to catch its prey (NIKOLSKY 1969, p. 264), and must therefore keep close to the surface. The burbot is less dependent on sight, and in Lake Mjøsa it feeds almost exclusively on *P. quadrispinosa* and smelt (HUITFELDT-KAAS 1917, SANDLUND et al. 1985). Its distribution mainly follows that of its prey on the bottom, *i.e.* down to approx. 80 m.

The pelagic species

Vendace is considered the most specialized zooplanktivore in the Scandinavian freshwater fish fauna (SVÄRDSON 1976). It is commonly found in the upper layers of the pelagic zone feeding on crustacean zooplankton (VALLIN 1964, HAMRIN 1979, NILSSON 1979). This is in accordance with the strictly pelagic way of life of the Lake Mjøsa vendace. In some warmer lakes vendace move down into the meta- or hypolimnion in summer when surface water temperature exceeds approx. 20°C (NORTHCOTE and RUNDBERG 1970, HAMRIN 1979). In Lake Mjøsa, surface temperature rarely reach 20°C, and no such downward movement was detected in summer. In Lake Mälaren, NORTHCOTE and RUNDBERG (1970) observed that vendace in summer moved in close to the bottom at midday. In Lake Mjøsa almost no vendace were caught close to the bottom, probably due to the relatively high density of smelt and whitefish, increasing competition in this zone.

In addition to vendace, whitefish and smelt are important in the pelagic catches in late summer and autumn. This dominance of salmonids in the pelagic zone indicates the oligo-mesotrophic state of the lake. With increasing eutrophication other species, particularly roach, have been observed to migrate into the pelagic zone (*e.g.* NORTHCOTE and RUNDBERG 1970, BRENNER 1973, BRABRAND et al. 1981).
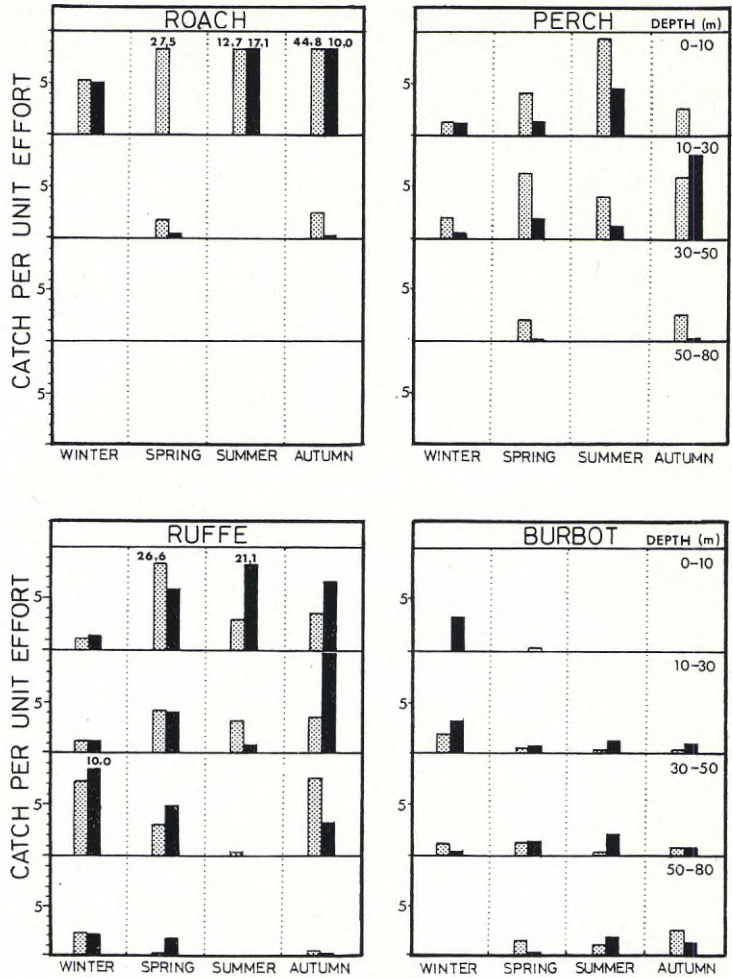
Fig. 10. Catch per unit effort in benthic nets of roach, perch, ruffe and burbot in four depth zones in Furnesfjorden (shaded) and Ringsaker-fjorden (black) in 1979. The four seasons are represented by catches in February/March, May, July and October.

Species utilizing both the benthic and the pelagic habitat

Whitefish and smelt appear to be the most versatile species in Lake Mjøsa, utilizing almost all habitats where fish were found. Both species are commonly found to occupy both the benthic and the pelagic zone (SVÄRDSON 1976, NILSSON 1979, SKURDAL and QVENILD 1982). Whitefish is often found in two or more different "morphs" or semispecies, living sympatrically, but in different habitats (SVÄRDSON 1976, BERGSTRAND 1977). In Lake Mjøsa, however, only one morph of whitefish is found (AASS 1972 a, NÆSJE 1984), and it is only the medium sized part of the population (approx. 30 cm body length) that migrates out into the pelagic zone in late summer. Analyses of

stomach contents show that its main food source is crustacean zooplankton and some surface insects, and that there is no diurnal migration between benthic and pelagic habitat (NÆSJE 1984). The benthic part of the whitefish population had eaten a much greater proportion of zoobenthos, especially *P. quadrispinosa*, than the pelagic part. The same separation of stomach content was found between benthic and pelagic smelt (SANDLUND et al. 1980b). Pelagic smelt utilize crustacean zooplankton, *M. relicta* and smelt fry, while the benthic smelt also eats *P. quadrispinosa*. The reason for the habitat shift in parts of the white-fish and smelt populations in Lake Mjøsa might be as follows: In the benthic habitat, in addition to smelt and whitefish, at least four species (ruffe,

perch, burbot and deepwater sculpin) prey on *P. quadrispinosa.* Both smelt and whitefish are generalists able to utilize both zoobenthos and zooplankton (SVÄRDSON 1976). With a strong competition for food in the benthic habitat, it seems natural for these facultative planktivores to migrate out into the pelagic zone when this habitat offers abundant food, *i.e.* in late summer and autumn. The smelt, being a more effective predator (SVÄRDSON 1976), can utilize the deeper part of the pelagic zone, preying on *M. relicta*, which is living below the thermocline (KJELLBERG and SANDLUND 1983). The reason that the zooplankton specialist, the vendace, does not exclude these two generalists in the pelagic zone might be that the vendace is subject to quite extensive fishing. Fishing mortality of adult vendace is estimated to 40 % (AASS 1972b). Fishing mortality of whitefish in Lake Mjøsa is very low (AASS 1978), and smelt are not fished at all.

As smelt is the main prey of all predators in the lake (HUITFELDT-KAAS 1917), natural mortality of this species is relatively high, approx. 55 % in adult fish (SANDLUND *et al.* 1980b). In adult whitefish, however, natural mortality is apparently very low (NÆSJE 1984). The smelt and whitefish both take other prey in addition to zooplankton, and utilize a larger part of the pelagic zone. In addition, there might exist a more subtle habitat partitioning concerning space, time of feeding etc. than we are able to detect by 24 hrs gill-net fishing. Thus the habitat utilization indicates interactive segregation (*sensu* NILSSON 1967), with smelt and whitefish as the generalist species widening and contracting their niche according to food supply.

VI. ACKNOWLEDGMENTS

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Strategies for Prey-Selection and Anti-Predator Defence in Lake Ecosystems

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ABSTRACT

This paper treats strategies for prey-selection among vertebrate and invertebrate predators in fresh water ecosystems. The predation impact of different categories of predators is discussed under three different headlines: encounter problems *i.e.* the probabilities for encounters between predators with different hunting strategies and prey, anti-predator adaptations such as behavioural modifications and phenotypical adjustments and, finally, predator efficiency *i.e.* conditions for alterations of the prey environment by different types of predators.

I. INTRODUCTION

The aquatic environment has always been an important resource for man. The greater need for protein for a growing human population has led to a more intense use of lakes and rivers, and attempts to increase the yield through manipulations have been made. These manipulations, in general, have been introductions of fish to lakes previously devoid of fish or enhancement of an existing fish population by introductions of new fish species or additional individuals. Professional fishermen, sport fishing people as well as scientists have gathered a great deal of information about the feeding habits of fish. Thus the fact that the vast majority of fish species have predatory feeding habits has been known for a long time. However, very little energy has been expended in synthesizing this information and analysing the relations between different fish predators and the rest of the ecosystem. The remarkable fact is, therefore, that these manipulations with the fish populations, *i.e.* the introductions of new predators, have in the past been undertaken without basic knowledge of their impact on the system. Predictions about the results have of course been difficult to make on these grounds, and the success of many of these manipulations has mostly been a matter of chance.

The older view of the lake ecosystem as a hierarchic system with the structure at any trophic level given by the structure and functions of the level below, was seriously questioned independently in Europe (HRBACEK 1959) and in USA (BROOKS and DODSON 1965) during the late fifties and the sixties. Although flexibility may be a common trait of most predators and hence most fish, it must be underlined that this ability ta feed on a large variety of prey items does not mean that fish feed at random or in proportion to the abundance or even in proportion to the availability of different prey organisms. The major discovery was that fish may well have flexible feeding habits but that they are very selective at the same time, with far reaching consequences for the prey populations. This new knowledge became the starting point for a very considerable increase in research on predator-prey interactions and related problems in fresh water ecosystems.

The purpose of this paper is to discuss aquatic predator-prey relations from a theoretical point of view including prey selection strategies, predator defence strategies etc. illustrated by field study results. Fish to fish interrelations will not be treated.

II. THEORETICAL FRAMEWORK

In a competitive relationship, both species compete for a resource of mutual interest and both species are negatively influenced, for example, in their growth or reproduction. In a predator-prey relationship, on the other hand, one of the species benefits from the interaction. In an evolutionary time scale a selective premium is placed on reducing competitive interference. In the predator-prey relationship, there is a selective advantage for the predator to increase the efficiency in finding,

capturing and handling the prey, while a better ability to escape will be adaptive for the prey.

Vertebrate predators

The dominating group of predators in normal fresh water ecosystems are vertebrates and among these fish is the most important group. With few exceptions, they can only process the prey item in one piece *i.e.* the prey item has to be swallowed whole. Thus, the diameter of the mouth of the predator determines the upper limit for the size of the prey. According to ZARET (1980 a), these predators are "Gape-limited", and defined as predators with a prey electivity curve which shows an increase correlated with properties of the prey which may attract the predator, for example body size (Fig. 1). The electivity curve represents a probability function which implies that the larger the prey is below the level determined by the mouth diameter of the predator, the more probable will it be taken by the predator. This was obvious from early studies in this field. Larger species of zooplankton were more prevalent in the fish stomachs than in the surrounding water (GALBRAITH 1967). STENSON (1976) showed that the numeric relations between the larger *Bosmina coregoni* and the smaller *B. longirostris* in fish stomachs were different from those in corresponding net plankton. *B. coregoni* was more prevalent in the stomachs than *B. longirostris*, whatever the situation in the surrounding water. Furthermore, specimens in the stomachs were significantly larger than in corresponding littoral and limnetic plankton samples. Thus, the electivity for a certain prey type may be predicted from certain properties of the prey which attract the predator *e.g.* body size.

Although fish possess morphological structures, the gill rakers which may be used for filter feeding, very few fish species are true filter feeders. Instead they are particle selectors *i.e.* they locate possible prey items with their eyes. This has been demonstrated by SEGHERS (1974) in his study of the feeding behaviour of the lake whitefish (*Coregonus clupeaformis*). By observing the frequency of feeding "nips", he could show that is was possible for the fish to ingest 0.5—1 daphnids per second. PERSSON (pers. comm.) reported 2 "nips" per second for roach (*Rutilus rutilus*). Thus particle selection may well explain the presence of thou-
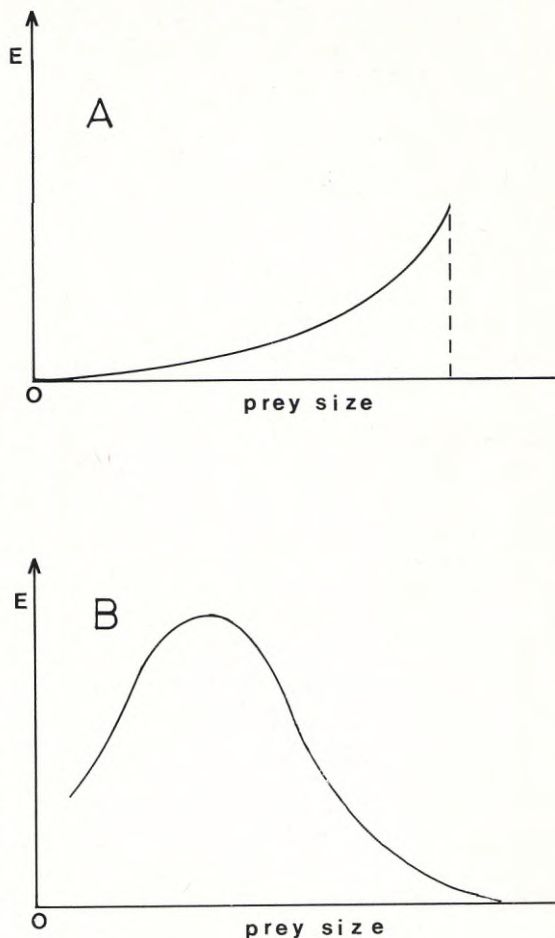
Fig. 1. Electivity curves for *e.g.* fish and salamanders (A) and for invertebrate predators (B). The curves represent probability functions. In A the probability to be caught by the predator increases with increasing prey size up to a limit where the prey is to big to be eaten *i.e.* when the size of the prey exceeds the diameter of the mouth. In B the electivity increases for increasing prey size up to a level where the size or the shape of the prey cause increasing difficulties of handling and the electivity drops.

sands of zooplankton individuals in the stomach of fish. GALBRAITH (1967), was able to show that the gill rakers were not involved in the feeding by comparing the size distribution of zooplankton within the stomachs of fish with the "theoretical" size distribution which would result from using the gill rakers.

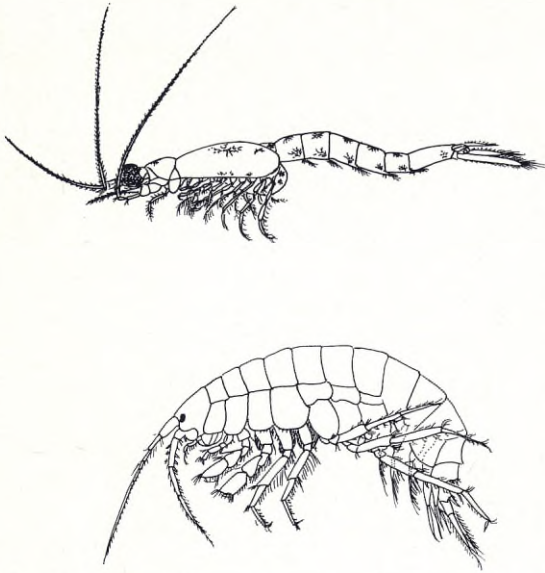The strong visual component in the feeding behaviour of fish implies that the light climate of

Fig. 2. Female of *Mysis relicta* (above), an omnivorous species which feeds on dead organic matter as well as living zooplankton. Male of *Gammarus pulex*, a normally benthic-living species, which under certain circumstances can move out into the pelagic zone where it preys on *e.g.* zooplankton and other invertebrates.

the water is of crucial importance. Consequently, the susceptibility in the prey depends upon the ease with which the predator can discover and capture it. Large animals, brightly coloured animals, animals active during daylight and animals which are active in open unsheltered areas are more likely to be preyed upon.

Invertebrate predators.

The invertebrate predators comprise a very heterogeneous group, not as studied by far as the vertebrate predator category. They belong to several taxonomical groups and have different feeding strategies. However, they all have size dependence in common. They have to manipulate or hold the prey item to be able to ingest it, in pieces or by sucking. The size and shape of the prey, therefore, is critical for the ability to capture and handle it. Consequently, these predators are characterized by a bell-chaped electivity curve (Fig. 1). This means that the electivity increases up to a level where the size or the shape of the prey cause increasing difficulties of handling (ZARET 1980 a).

Freshwater crustaceans include many predatory groups. Some species have been shown to have significant impact on the prey populations. One such example is *Mysis relicta* (Fig. 2), an omnivorous species which feeds on dead organic matter as well as living zooplankton. Its ability to control the prey populations has been demonstrated by GOLDMAN *et al.* (1979). Fluctuations in the zooplankton density could be inversely related to the density of *Mysis* (THRELKELD *et al.* 1980). Studies by ANDERSON and RAASVELT (1974) revealed that one species of *Gammarus* (Fig. 2), which normally is benthic, can move out at times into the pelagic zone and prey on *Chaoborus* and crustacean zooplankton.

The feeding mechanisms seem to be well documented among the smaller crustaceans such as copepods and cladocerans. Copepod predators belong to the orders Cyclopoida (*e.g.* members of the genus *Cyclops*) and Calanoida (*e.g.* the genera *Heterocope* and *Epischura*) (Fig. 3). The copepods do not use their eyes in prey detection. STRICKLER (1975) showed that they can locate prey items from the disturbances in the water produced by the moving prey, by using setae on the first antenna which serve as mechanoreceptors. From the strength of the signal produced by the moving object, it is possible for the copepode predator to judge whether it should attack the object, escape from it or just ignore it. The presence of these mechanoreceptors and the fact that vision is not involved, makes it possible to feed as efficiently during dark conditions as during light, a fact which has been demonstrated for the calanoid copepod *Diaptomus shoshone* (ANDERSON 1967).

There are four species of predatory cladocerans present in Swedish freshwater systems. These are *Leptodora kindti*, *Bythotrephes longimanus*, *B. cederströmii* and *Polyphemus peliculus* (Fig. 4). The bivalve carapace which is a typical morphological structure within the cladoceran group, is reduced in these four species. This reduction is a trait which may give a less efficient shelter against predators, but which may increase the swimming velocity and the manipulative capacity on the positive side. All these species have protuberant, well-developed compound eyes, an eye construction which may give a detailed image of objects which surround the animals. That vision may be used for

Fig. 3. Examples of predatory copepods in freshwater ecosystems. The genera *Cyclops* (left) is represented by a large number of species in Scandinavian lakes. The calanoid copepod genera *Heterocope* (right) although common has only a few representatives in Scandinavian lakes.
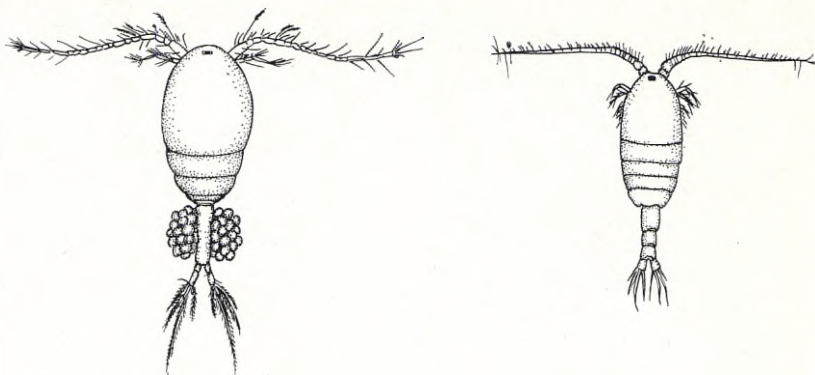
prey detection is indicated in *Polyphemus* (BROOKS 1959). Moreover, it is shown that the related estuarine genera *Podon*, which feeds on ciliates and rotifers, has a light-dependent feeding (BOSCH and TAYLOR 1973 a, b).

One large and important class of freshwater inhabitants are the insects. Some of the species spend their whole life cycle in the water. Others complete their egg and larval development in the water and leave the habitat as adults for some days or weeks in the air. Several of the species are predators active in the pelagic, benthic and littoral zones. Typical species in the pelagic zone are, for example, *Chaoborus* spp. and aquatic hemipterans like *Glaenocorisa propinqua* (Fig. 5). Although larvae of *Chaoborus* have eyes, they are able to feed independently of light (*e.g.* PASTOROK 1980). They obviously use a mechanoreceptive mechanism to locate prey items from the signals produced by the swimming prey. The larva has a large array of different receptors all over the body, which serve as mechano-receptors. The larva is able to maintain its position in the water when feeding or it drifts slowly with a minimum of disturbance, waiting for suitable prey objects to pass. Cyclopoid copepods, *Bosmina* spp. and even smaller individuals of *Daphnia* are reported to be significant prey species of *Chaoborus* spp. (FEDORENKO 1975 a, b; DODSON 1972; PASTOROK 1980; NYMAN *et al.* 1985).

Many aquatic hemipterans are considered to be so-called scrapers *i.e.* they feed on a large variety of food including dead organic matter, bacteria, algae or animals living on objects submerged in the littoral zone (BAY 1974). *Glaenocorisa*, on the other hand, is a true pelagic species with predatory

A

B

C

D
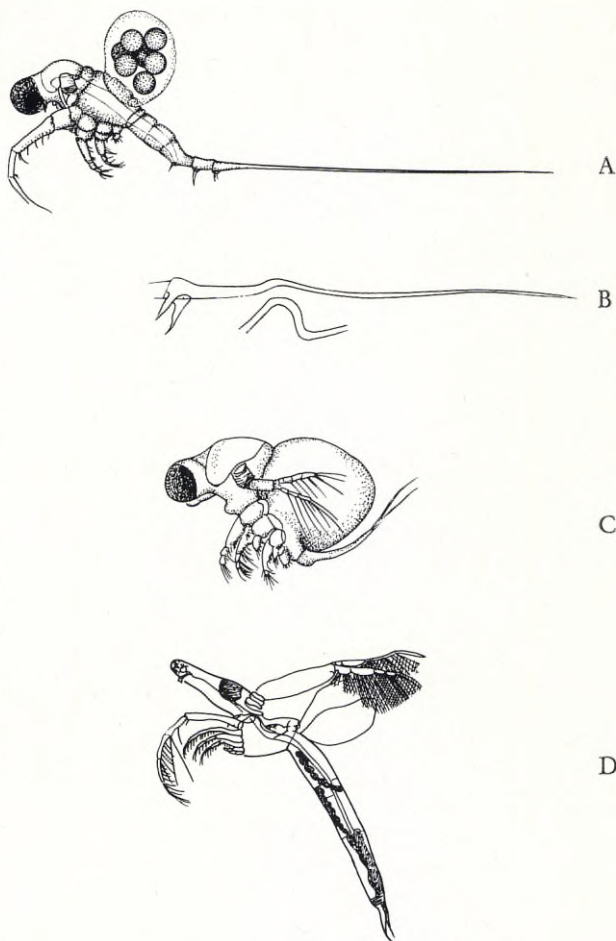
Fig. 4. Predatory cladoceran species in Scandinavian freshwater ecosystems. A: *Bythotrephes longimanus* female; B: the caudal spine of *B. cederströmii*; C: *Polyphemus pediculus* female; D: *Leptodora kindti* female. The bivalve carapace which is a typical morphological structure within the cladoceran group is reduced in these four species.
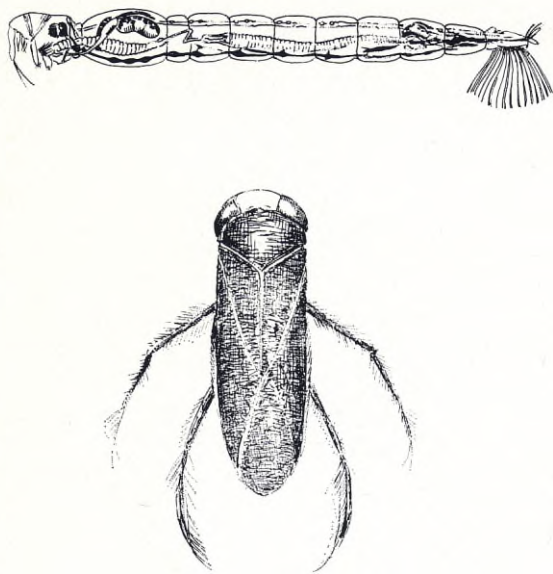
Fig. 5. Predatory insects in the pelagic zones of lakes. The species of the genera *Chaoborus* (above) are typical ambush predators *i.e.* they wait motionless for suitable prey objects to pass *i.e.* they rely on actively-moving prey. The aquatic hemipterans, here represented by *Glaenocorisa propingua*, are in general cruising predators *i.e.* they actively hunt for prey objects.

feeding manners (OSCARSON in press). Visual stimuli are probably important for prey detection. *Glaenocorisa* is able to dive at least to a water depth of 10 m and it seems to be able to locate prey objects from a distance of 2—3 cm. The prey consist of different zooplankton species (NYMAN *et al*. 1985).

Odonate larvae may serve as examples of benthic or littoral predators. They are efficient with a large variety of prey from zooplankton to larger benthic invertebrates and even tadpoles and fish larvae. Different modes of feeding are found within the group. Some species are visually dependent while others rely on tactile stimuli (JOHNSON and CROWLEY 1980).

III. PREDATION IMPACT

The ultimate impact of predation on the different prey populations depends on several factors among which some important like encounter probability, anti-predator adaptations and predator efficiency will be discussed below.

Encounter problems

The amount of food in a water volume available for a certain animal is not simply a function of the number of food objects per litre water. The activities of predators and prey must be considered in order to obtain a reliable estimate of the food situation. The basic thinking in this field for aquatic environments has been done by GERRITSEN and STRICKLER (1977), who developed a three-dimensional model for encounters. The original model assumed that the water volume is homogeneous, a random distribution of organisms, a locomotion in random directions and that the predators have a constant encounter radius within which they can detect and catch possible prey items. According to the model, it could be demonstrated that the encounter rate was affected mainly by three factors, the encounter radius, the swimming speed of the predator and prey, and the density of animals. From the model it is evident that a predator can increase the encounter rate by increasing its swimming velocity and that the prey can reduce the encounter rate by reducing its swimming speed. Changes of the velocity of the fastest moving animal have the largest effect on the encounter rate. This means, for example, that a predator cannot increase the probability of encountering prey until its swimming speed exceeds that of the prey animal. When energetic costs of locomotion were considered versus energetic rewards of prey capture, the model could predict two optimal strategies. Firstly, the "ambush" predator type which relies on fast-moving prey, and secondly the fast-moving "cruising" predator which rely on slower-moving prey (Fig. 5). A related model for predator-prey encounters was presented by GIGUÈRE *et al*. (1982). The different invertebrate predators discussed in the previous chapter all belong to either one of these predator categories regardless of their actual habitat, *i.e.* both littoral and pelagic animals can be defined as either one of these predator types. The predacious copepods and cladocerans discussed above are all cruisers with swimming speeds which exceed approximately 5—15 times the swimming speeds of their prey species among the filtrators. The existence of fast-moving zooplankton is also a condition for the existence of the ambush predator type. The best-documented example of an

planktonic ambush predator is *Chaoborus* spp. which have diets with larger proportions of fast-swimming prey animals SWIFT and FEDORENKO 1975). Copepod copepodits are, for instance, more prevalent in the diet than copepod nauplii because of their higher swimming rate (LEWIS 1977; GERRITSEN 1978).

The occurrence of cruising and ambush predators, respectively, in particular those in the littoral zone, is not only related to the food situation but also to the occurrence of visually dependent predators like fish. The ambush type tends to be more prevalent in lakes with fish than without (JOHNSON and CROWLEY 1980; HENRIKSSON in prep.).

GERRITSEN and STRICKLERS' original model assumed a random swimming pattern. However, it is well-known that locomotion in aquatic animals often has directional components, for example, a diel up-and-down migration pattern, which has definite effects on the encounter rates. GERRITSEN (1980) considered these problems and showed that the best way for a predator to maximize the encounter rate with the prey is to swim at right angles to prey movement. Accordingly, the best way for a prey to cheat the predator is to swim in the same direction as the predator. The adult *Cyclops scutifer* swims more frequently and faster in the horizontal plane than in other planes, which is supposed to be orthogonally to the swimming plane of the prey organisms (GERRITSEN 1980).

Anti-predator adaptations

As fish are visually-dependent predators, adaptations which reduce visibility would be the adequate evolutionary response for the prey. This reduction can be achieved in several ways as vision is light-dependent. One successful trait may be diel up and down migration. Many pelagic species migrate down to the deeper and darker layers of the water at sunrise and return to the upper part at sunset (HUTCHINSON 1967). The adaptive value of this behaviour has been discussed from several points of view. The two major hypotheses, which the discussion has been focused on are the resource hypothesis and the predation hypothesis. The first one suggests energetic advantages in the behaviour to regularly reduce the metabolic rate in the cold

water of the deeper layers (KERFOOT 1970). The second hypothesis has been tested by WRIGHT *et al.* (1980) in a simulation model. The model showed that downward migration leads to better survival despite the probable disadvantageous growth conditions in the cold and dark water layers. Further support for the predation hypothesis is given by another model study by IWASA (1982). There is strong empirical evidence for migration in fact reducing predation losses. ZARET and SUFFERN (1976) showed that larger individuals of *Daphnia parvula i.e.* the most conspicuous specimens and hence the most susceptible to predation from a visually-dependent predator, had a more pronounced migration pattern than the smaller individuals. This is true also for the phantom midge, *Chaoborus flavicans*, whose inclination to migrate increases markedly from the first to the fourth *i.e.* the last larval instar (TERAGUCHI and NORTHCOTE 1966, GOLDSPINK and SCOTT 1971). The reactive distance for fish is closely dependent on the light intensity and it seems probable that some zooplankton species are able to adjust their vertical position to a specific low light intensity in order to decrease the reactive distance for visually-dependent predators like fish (WRIGHT *et al.* 1980).

A second trait, which implies reduced visibility, is reduction of the "visible size" which may be accomplished along two possible evolutionary pathways. Reduction of body size has this effect and since it reduces the reactive distance for visually-dependent predators, it may therefore be an alternative to vertical migration. *Bosmina longirostris* may be an example of a small-sized species that would aquire only minimal benefit from reducing an already short reactive distance. Thus, *B. longirostris* has only a weak tendency to migrate (WRIGHT *et al.* 1980). The next possible way of reducing the reactive distance is to reduce pigmented areas. The size of the compound eye has been shown to be critical for susceptibility to predators. ZARET (1969) showed that fish selected the large-eyed morph of *Ceriodaphnia cornuta* over the small-eyed morph with the same body size. STENSON (1978) showed that the larger eye and the slightly more brownish body colour of *Chaoborus obscuripes* from fishless lakes made them significantly more susceptible to fish predation than *C. flavicans* with smaller eyes and trans-
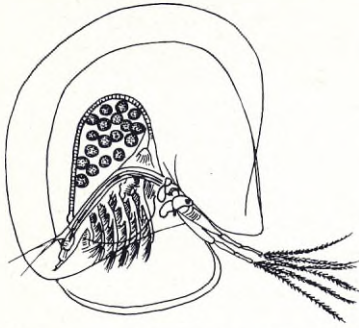
Fig. 6. *Holopedium gibberum*, female with eggs in the brood chamber. Instead of having a bivalve carapace the body is surrounded by a gelatinous capsule which opens ventrally. The relative size of the capsule is variable and the size depends on the density of the populations of invertebrate predators.

parent body, a species that is able to coexist with fish.

Finally, there are examples of larger clearly visible species which do not migrate and which can live together with fish. In these cases they are either species with smooth motion patterns which do not attract fish as much as species with jerky movements (ZARET 1980 b), or species with good escape abilities. Examples of the latter category are found within the copepod group where several species have been shown to resist and escape from the suction attack from fish (SZLAUER 1965).

Vertical migration among prey organisms might also be an adaptive response to certain types of invertebrate predators. FEDORENKO (1975 b) described a probable example of this in the reverse diel migration of *Diaptomus tyrelli*. The reverse type of migration might in this case be a way to minimize the period of spatial overlap with one significant non-visual predator, *Chaoborus trivittatus*, which ascends to the surface layers during night and descends to the bottom layers during daytime.

As mentioned above, vertical migration in most cases takes place between surface layers, where the predation losses may be too high, down to regions of water near the bottom on or in sediment, where the risks of being eaten are significantly lower. However, this kind of migration pattern may be fatal under other circumstances: for example, in lakes where significant predators show another pattern of vertical distribution. In lakes devoid of fish, for example, potent invertebrate predators may occur in dense populations on or in the sediment. The habit of migrating down into the sediment may therefore be selected against. The difference between the two phantom midge species *Chaoborus flavicans* and *C. obscuripes* in diel migration behaviour may be explained by differences in predator distribution in the environments where the two species naturally occur and have evolved. *C. flavicans* live together with fish and have a well-pronounced diel migration while *C. obscuripes* which live in lakes with often dense populations of benthic predators and without fish, do not show a diel up and down migration pattern (STENSON 1981).

All invertebrate predators have to seize and manipulate the prey in order to ingest it. This means that shape — size of the prey is of critical importance. Hence, successful evolutionary responses to the selection pressure from invertebrate predators should be increases in size or additions of morphological structures. These phenotypical changes will make the handling of the prey significantly more difficult for the predators. There seems, however, to be an evolutionary dilemma in this, since counteracting selective forces may be present at the same time. The conflict is between the need to become small in order to minimize the reactive distance for the visually-dependent fish, and the need to become larger in order to increase the difficulties for invertebrate predators. The solution of the problem is rather simple. The increase in body size can be achieved by adding transparent structures. The transparent gelatinous sheet of the cladoceran *Holopedium gibberum* (Fig. 6) makes it difficult for invertebrate predators to seize (ALLAN 1973). Furthermore, the size of the gelatinous capsule is variable and related to the size of the predator population according to studies by STENSON (in press). The trigger for capsule size increase or decrease is some, still unknown, substance released into the water by the predator and which can be detected by *Holopedium*. Another phenotypical specialization, which has the same purpose, is the cyclomorphosis best known from the cladoceran zooplankton. Only smaller species, such as *Daphnia cristata*, *D. cucullata*, *Bosmina coregoni*, show the
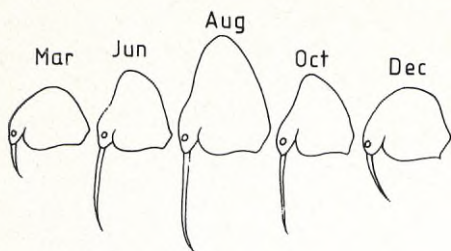
Fig. 7. Cyclomorphosis *i.e.* temporal phenotypical varia-
tion in *Bosmina coregoni*. The most spectacular morph
occurs in August, thus time-correlated to the peak-
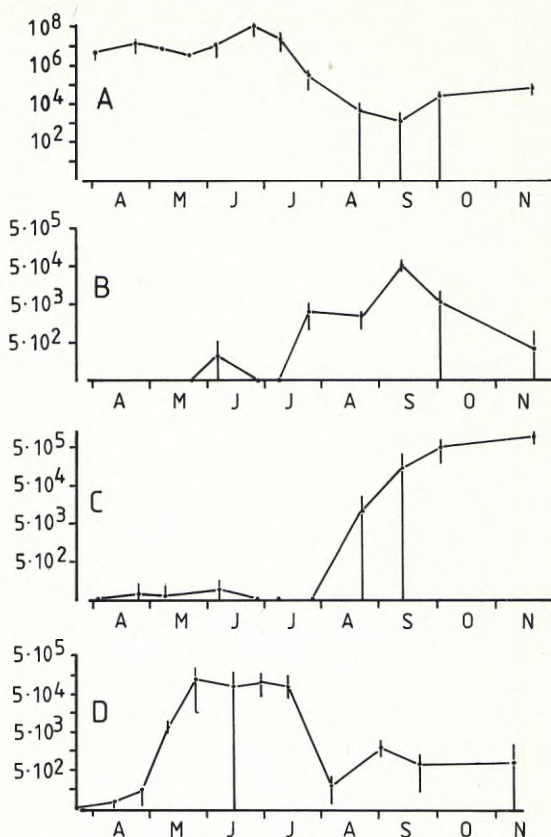occurrence of invertebrate zooplankton predators.

Fig. 8. The temporal development of the populations
of the ciliate *Vasicola lutea* (A) and the rotifers,
Conochilus unicornis (B), *Filinia longiseta* (C) and the
predatory rotifer *Asplanchna priodonta* (D). Note
that the Y-axis is logarithmic.

development of anterior helmets, posterior spines
or hump-backs (Fig. 7). Larger species like *D.
pulex* are big enough to resist most planktonic
invertebrate predators (BROOKS 1965). Comparable
phenotypical adaptations can be shown among
rotifers as well. The most well-known example is
the development of the spines in the herbivorous
Brachionus calyciflorus in the presence of the pre-
dator *Asplanchna brightwelli* (BEAUCHAMP 1952 a,
b). The trigger or the development of spines was
shown to be a substance secreted by *Asplanchna*
(GILBERT 1967). The anti-predator armour of the
cyclomorphotic cladocerans and rotifers is not a
direct response to the stimulus. Instead the stimulus
induces an embryonic development of armour for
the next generation of parthenogenetic females.

The loss of defence structures in response to
decline in predator density suggests some cost in
maintaining these structures. This suggestion was
supported by RIESSEN (1984) who showed that the
armoured morph of *Daphnia retrocurva* has a
poorer reproductive capacity than the unarmoured
morph. STENSON (in press) showed that the need
for a large gelatinous capsule in *Holopedium* post-
poned the start of reproduction.

Predator efficiency

The impact of a predator population very much
depends on the ability of the predator to respond
to increases in the prey population. This can be
achieved in two ways, by an increase of the popu-
lation size *i.e.* a numerical response, or by in-
creasing the food intake *i.e.* a functional response.

Only few predators in Swedish lakes are theo-
retically able to show a numerical response to in-

creases in the prey number. These are, in general,
parthenogenetically reproducing species such as,
for instance, predacious cladocerans and rotifers.
There are few proofs of the significance of this
mechanism in the literature. The rotifer *Asplanch-
na priodonta*, however, is able to follow the in-
crease in the prey population by a rapid numerical
increase. *A. priodonta* was shown to increase to an
extremely dense population when a pelagic ciliate
species had a population peak. Furthermore, the
predator fed exclusively on this ciliate and the
decline of the prey population was interpreted as
mainly an effect by the predator (STENSON 1984)
(Fig. 8).

Other predators like fish, aquatic insects etc.
have discrete sexual reproductive periods, implying

that the availability of prey items when the eggs hatch is crucial for the development and survival of the larval stages and hence the population size. It is evident that the population size of annual species can differ between years because of the food situation for the different larval stages. It follows from this that high prey numbers later in the season (well after reproduction) cannot induce a numerical response in these predator populations.

Fish can be characterized as energy maximizers and as such able to respond functionally to an increase in prey density. In fish, the energy intake can easily be transformed into somatic growth (ELLIOT 1975). This may not be the case with invertebrate predators in general. Many of these, insects and crustaceans, are defined as to the size by their exo-skeletons, which restrict the possibilities of size increase. However, it may be possible to store energy in substances like fat, or they may speed up the rate of larval development. In summary, there seems to be definite differences between fish and invertebrate predators in the ability to show functional responses to numerical increase in the prey populations.

Based on the discussion above it seems probable that fish have the best potential for significant impact on the prey populations. NEILL and PEACOCK (1980) and NEILL (1981) have shown that invertebrate predators with "bottlenecks" in their development had only limited effects on the prey structure. Furthermore, these bottlenecks offered an important mechanism for coexistence between predator and prey species. NEILL (1981) also showed that an experimentally-improved food supply during a developmental bottleneck gave better larval survival and thereby population densities, which had significant impact on the prey community. NEILL made his experiments in enclosures but his results and conclusions have lately been confirmed from a whole lake experiment. STENSON (in press) showed that liming of a previously acidified lake improved the survival of populations of *Chaoborus* spp. to such an extent that the structure of the crustacean community was radically changed.

Thus, the prerequisite condition for a radical change of the structure of the prey "environment" by invertebrate predators with discrete reproductive periods is the widening of a developmental bottleneck. Invertebrate predators of this type may, however, have an important role in structuring *e.g.* the zooplankton community after a change on the top predator level in a lake. NYMAN *et al.* (1985) showed that when fish disappear from a lake ecosystem, invertebrate predators are important for the structure of the prey "environment" before a new balance between predators and prey has been established.

IV. FINAL REMARKS

The conditions in an aquatic ecosystem and the properties of the organisms in the system are not products of any simple cause-effect relationships. This statement is, of course, a truism but nevertheless it concludes the present knowledge about structural and functional interrelations in lake ecosystems. This understanding has developed from an early view of the system characterized by unidirectional relationships to the present picture of complexity or multi-directional relationships. By continuously adding new items of information to those already existing, and by future studies the basis of our knowledge about the complex lake ecosystem will increase. Gains in knowledge will also increase the predictability of the system, a development which is highly beneficial for practical lake management.

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