SWEDISH BOARD OF FISHERIES

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 59

LUND 1981
BLOMS BOKTRYCKERI AB

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Methods of Estimating Total Stock, Smolt Output and Survival of Salmonids Using Electrofishing

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ABSTRACT

Some methods to assess stock parameters of stream-living salmonids by electrofishing are proposed and exemplified. The parameters are stock size, smolt output, and survival. Proposed methods are based on the ZIPPIN/MORAN estimator combined with the theory of finite populations and a "change-in-ratio" method.

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I. INTRODUCTION

Electrofishing is a method well suited to sampling fish populations in fresh waters, and is commonly used when data on stream-living salmonids are required. In spite of the fact that electrofishing has been used extensively during the past decades, and in spite of the fact that several methods of population estimation have been developed, situations often arise in electrofishing investigations which are not easily handled with existing methods. In this paper, an attempt is made to discuss some common cases, including total stock assessment, smolt output, and estimation of survival. Proposed methods are based on the removal method (MORAN 1951, ZIPPIN 1956), combined with theory of finite populations and a "change-in-ratio" method. Examples are provided, and a brief review of the MORAN/ZIPPIN estimator is given as an introduction.

The following notation is used.

Subscript $_i$ refers to conditions in a stream section i.
A 'hat' ($\hat{}$) over a symbol denotes its estimate.
V(symbol) denotes the variance of (symbol).
p = catch probability
$q = 1 - p$
k = number of removal fishings
T = total catch in k removals
N = total number of stream sections in a stream
n = the number of stream sections in a random sample of stream sections.
X = total stock size
x = population size in a stream section
Y, y = same as X and x but at a later time
$Z = X - Y$
$z = x - y$
R_x, R_y, R_z = the fraction of females among X, Y and Z

$S = Y/X$ = finite rate of survival

$\bar{x} = \overset{N}{\Sigma} x_i/N$ = mean number per stream section

$\hat{\bar{x}} = \overset{n}{\Sigma} \hat{x}_i/n$ = the mean of n randomly chosen estimates of x

$V(x) = \overset{N}{\Sigma}(x_i - \bar{x})^2/(N-1)$ = the variance of x among sections

$V(\hat{x}_i)$ = the sampling variance of the estimate $\hat{x}_i$.

x may be substituted by y or z. Some additional symbols are used according to the text.

II. A REVIEW OF THE REMOVAL METHOD

A size estimate of a closed population may be obtained from a series of removal fishings, provided that the catch probability p is equal among individuals and does not change from one fishing to another. MORAN (1951) developed such an estimator, and ZIPPIN (1956) gave a graphical solution to this together with formulas for the computation of sampling variances. SEBER (1973, p. 309—327) reviewed the whole field, including the work of JUNGE and LIBOSVARSKY (1965), SEBER and LE CREN (1967) and SEBER and WHALE (1970), to which the reader is referred for additional information. The following is a short summary of the removal method in the general case of k removal fishings.

The population size x_i in a closed stream section *i* is estimated by

$$\hat{x}_i = \frac{T_i}{1 - \hat{q}_i^{k_i}} \quad (1)$$

with the notation given above. The estimated catch probability $\hat{p}_i$ is usually obtained from the successive catches by the graphical solution of ZIPPIN (1956), from which $\hat{q}_i = 1 - \hat{p}_i$ is calculated and inserted into eq. (1) to obtain the population estimate. It may be noted, however, that a more accurate result can be obtained by an iterative solution of ZIPPIN's eqs. (4) and (8), which are readily programmed into a modern desk calculator, and which give the population size estimate directly. In the examples below, this method is used. In cases when $k_i = 2$ or 3, explicit solutions of $\hat{x}_i$ are derived (*e.g.* SEBER 1973, p. 315—319). For x_i large, the sampling variance $V(\hat{x}_i)$ of $\hat{x}_i$ and $V(\hat{p}_i)$ of $\hat{p}_i$ is estimated as

$$\hat{V}(\hat{x}_i) = \frac{\hat{x}_i(1 - \hat{q}_i^{k_i}) \cdot \hat{q}_i^{k_i}}{(1 - \hat{q}_i^{k_i})^2 - (\hat{p}_i k_i)^2 \cdot \hat{q}_i^{k_i - 1}} \quad (2)$$

and

$$\hat{V}(\hat{p}_i) = \frac{(\hat{q}_i \hat{p}_i)^2 \cdot (1 - \hat{q}_i^{k_i})}{\hat{x}_i \left[\hat{q}_i (1 - \hat{q}_i^{k_i})^2 - (\hat{p}_i k_i)^2 \hat{q}_i^{k_i}\right]}. \quad (3)$$

The approximate 95 % confidence limits about $\hat{x}_i$ are then $\hat{x}_i \pm 2\sqrt{\hat{V}(\hat{x}_i)}$.

The removal method may thus be used to estimate population size in closed stream sections, provided that the population size is large enough. Although knowledge of "local densities" may sometimes be of primary interest in fishery investigations, estimates of total stock or mean density are usually more useful figures in fishery management and in many ecological studies. This is especially true when estimates of smolt output and survival rates are required. In the sections below, some methods of calculating these useful stock parameters are suggested. Further, in most electrofishing surveys several independent estimates of the catch probability p are often available. In cases when p can be assumed constant among stream sections, this can be used to improve the stock parameter estimates, a matter which is also discussed below.

III. IMPROVEMENT OF POPULATION ESTIMATES IN CASES WHEN p IS ASSUMED CONSTANT AMONG STREAM SECTIONS

For given values of p and k, it follows from eq. (2) that the relative precision of population estimates decreases with decreasing population size x_i, and this is one of the drawbacks of the removal method. In cases when p is constant among the stream sections, it follows that some kind of pooling may be used to improve the p estimate and thereby each population estimate. First, however, the consistency of p shold be tested. This may be accomplished by a straight forward χ^2 test of independence of the successive catches among a number of sections.

Testing the consistency of p

Example 1. In 12 50-m sections of a small stream, 3 removal fishings were carried out. The number of I+ brown trout in each catch was:

Section no.	First catch	Second catch	Third catch
1	42	22	5
2	62	27	11
3	50	18	6
4	15	8	2
5	24	11	5
6	13	8	2
7	56	25	16
8	36	11	5
9	52	26	17
10	54	13	5
11	30	10	8
12	48	18	16

In this example, $\chi^2=22.46$, d.f. $=22$. This is not enough to reject the null hypothesis, and it may be accepted that p is the same among the sections.

It should be noted that the test above does not give information as to whether or not the catchability p may considered constant among individuals. Zippin (1956) and Seber and Le Cren (1967) suggest goodness-of-fit calculations to test this kind of consistency. Deviations from the assumption of equal catchability will cause underestimation of x_i (Seber and Whale 1970, Bohlin and Sundström 1977).

Estimating the common p

(i) In cases when the number of removals are constant among sections, the catches may be pooled and the common p estimated *e.g.* using the Zippin graphs or the iterative method mentioned above. For the catches in ex. 1, the pooled catches are 482, 197 and 98. Using the iterative method and eq. (3), the pooled estimate of p is 0.561, and $\hat{V}(\hat{p})=0.000518$.

(ii) In cases when the number of removals are varying, pooling is inconvenient, and a weighted mean may be used (Seber and Le Cren 1967). If the populations are large enough, the weighted mean p_w may be calculated as

$$\hat{p}_w=\frac{\sum\frac{\hat{p}_i}{\hat{V}(\hat{p}_i)}}{\sum\frac{1}{\hat{V}(\hat{p}_i)}} \qquad (4)$$

and

$$\hat{V}(\hat{p}_w)=\frac{1}{\sum\frac{1}{\hat{V}(\hat{p}_i)}} \qquad (5)$$

In eqs. (4) and (5), each $\hat{p}_i$ is computed in the usual way using the Zippin graphs or the iterative method, and each $\hat{V}(\hat{p}_i)$ using eq. (3). The summing is carried out over the n sections.

Example 2. Say that the following catches were obtained, and that we have reason to assume p constant among sections:

Section no.	First catch	Second catch	Third catch	Fourth catch
1	42	22	5	5
2	62	27	11	
3	50	18		

Using the iterative method and eq. (3), the following catch probability estimates are obtained:

$\hat{p}_1=0.557$, $\hat{V}(\hat{p}_1)=0.003481$
$\hat{p}_2=0.578$, $\hat{V}(\hat{p}_2)=0.003806$
$\hat{p}_3=0.640$, $\hat{V}(\hat{p}_3)=0.009790$

Inserting these estimates into eqs. (4) and (5), we get

$$\hat{p}_w=\frac{\frac{0.557}{0.003481}+\frac{0.578}{0.003806}+\frac{0.640}{0.009790}}{\frac{1}{0.003481}+\frac{1}{0.003806}+\frac{1}{0.009790}}=0.578$$

$$\hat{V}(\hat{p}_w)=\frac{1}{\frac{1}{0.003481}+\frac{1}{0.003806}+\frac{1}{0.009790}}=$$

$=0.001533$

Using the common p to improve the population estimates

Given the pooled or weighted estimate of the common p, say p′, including an estimate of its variance, we can now turn to the problem of using this to improve the population estimate $\hat{x}_i$. The point estimate of x is obtained simply by calculating $q'=1-p'$ putting this value into eq. (1) together with the total catch T_i. The variance of this population estimate $\hat{x}_i'$ is found by the delta method (*e.g.* Seber 1973, p. 8, and Appendix 1) as

$$\hat{V}(\hat{x}_i') \cong \frac{\hat{x}_i' \cdot \hat{q}'^{k_i}}{1-\hat{q}'^{k_i}} + \hat{V}(\hat{p}') \left[\frac{x_i' \cdot k \cdot \hat{q}'^{k_i-1}}{1-\hat{q}'^{k_i}} \right]^2 \cdot \qquad (6)$$

Alternate forms of this expression are

$$\hat{V}(\hat{x}_i') \cong (1-\hat{q}'^{k_i})^{-2} \left[\hat{x}_i' \hat{q}'^{k_i} (1-\hat{q}'^{k_i}) + \right.$$

$$\left. + \hat{V}(\hat{p}')(\hat{x}_i' \cdot k_i \hat{q}'^{k_i-1}) \right]^2 \qquad (6')$$

and

$$\hat{V}(\hat{x}_i') \cong (1-\hat{q}'^{k_i})^{-2} \left[T_i \hat{q}'^{k_i} + \hat{V}(p') \right.$$

$$\left. \left(\frac{T_i k_i \hat{q}'^{k_i-1}}{1-\hat{q}'^{k_i}} \right) \right]^2 \cdot \qquad (6'')$$

As an example (*example 3*), the first section in example 1 yielded the three successive catches 42, 22 and 5 trout. Hence, $k_1=3$ and $T_1=69$. The pooled estimate of the catch probability was calculated in example 1 as 0.561 with variance 0.000518. Thus $\hat{p}'=0.561$, $\hat{q}'=1-0.561=0.439$, and $\hat{V}(\hat{p}')=0.000518$. The number of trout present in section 1 is estimated by putting these values of $\hat{q}'$, k_1 and T_1 into eq. (1):

$$\hat{x}_1' = \frac{T_1}{\dfrac{k_1}{1-\hat{q}'}} = \frac{69}{1-0.439^3} = 75.4$$

The estimated variance if this value is (from eq. 6″):

$$\hat{V}(\hat{x}_1') = (1-0.439^3)^{-2} \left[69 \cdot 0.439^3 + 0.000518 \right.$$

$$\left. \frac{69 \cdot 3 \cdot 0.439^2}{1-0.439^3} \right]^2 = 6.99$$

Approximate 95 % confidence limits are thus $75 \pm 2\sqrt{6.99}$ or 70–80.

The magnitude of the gain in precision by using pooled or weighted estimates of the catch probability may be seen by a direct comparison of eqs. (2) and (6). For reasonably large pooled populations, the second term in eq. (6) will be small if the numbers of catches in the pooled population are large. In the extreme case of $V(\hat{p}')=0$, *viz.* if p′ is exactly known, eq. (6) degenerates into

$$V(\hat{x}_i') = \frac{\hat{x}_i' q'^{k_i}}{1-q'^{k_i}} \qquad (7)$$

(which also follows from binomial theory). The maximum gain in precision using pooling compared with the usual method of independent estimation of $V(\hat{x}_i)$ from eq. (2) may be viewed as follows, assuming $p=0.5$, a magnitude common in electrofishing:

k_i	$\frac{V(\hat{x}_i')}{\hat{x}_i'}$ (p known)	$\frac{V(\hat{x}_i)}{\hat{x}_i}$ (p estimated)
1	1.0	—
2	0.33	3.00
3	0.14	0.54
4	0.07	0.15

Using pooled or weighted p estimates, the relative variances will fall somewhere between these extremes. In practice, pooling may greatly improve the population estimates in the event of few removal fishings.

IV. ESTIMATION OF TOTAL STOCK AND MEAN DENSITY USING SIMPLE RANDOM SAMPLING OF STREAM SECTIONS

As stated above, figures of total stock sizes are usually more useful in both basic and applied fishery investigations than are "local densities", since the total stock is the functional unit in most situations, including many ecological, evolutionary and applied problems. It is therefore essential to develop practically useful methods of assessing stock parameters from electrofishing records, as well as the sampling variances of these estimates. In this section, an attempt is made to develop a method for stock assessment, based on simple random sampling of stream sections and applying the removal method to each of these sections.

Frequently, it is not possible to cover the whole area (stream) of interest with electrofishings. To make statements of the total stock in this case, random sampling of stream sections is convenient. The stream is divided into N sections of approximately the same area or length, from which a random sample of n sections is drawn, *e.g.* using a table of random digits. In each of these sections *i*, the population size x_i may be estimated by some of the methods suggested above, using pooling or weighted mean of p if possible, together with estimates of each variance $V(\hat{x}_i)$ from eqs. (2) or (6). To calculate total stock size, mean density, and the sampling variance of these estimates, the following model is used.

$$\begin{array}{l} \;x_1 \qquad x_2 \qquad x_3 \qquad\qquad x_n \qquad\qquad x_N \\ |\!-\!-\!-\!|\!-\!-\!-\!|\!-\!-\!-\!|\;-\;-\;|\!-\!|\;-\;-\;|\!-\!-\!| \\ \underbrace{\;\hat{x}_1 \qquad \hat{x}_2 \qquad \hat{x}_3 \qquad\qquad \hat{x}_n\;} \end{array}$$

a random sample of n sections

In this case, the total stock $X=\sum^{N} x_i$, and the mean density per stream section $\bar{x}=X/N=\sum^{N} x_i/N$. These are the two parameters to be estimated. An estimator of $\bar{x}$ is

$$\hat{\bar{x}}=\bar{\hat{x}}=\frac{\sum^{n}\hat{x}_i}{n} \tag{8}$$

and of X

$$\hat{X}=\hat{\bar{x}}\cdot N. \tag{9}$$

In Appendix 2, the approximate sampling variances of these estimators are derived:

$$\hat{V}(\hat{\bar{x}})\simeq\frac{\hat{V}(\hat{x})\cdot(N-n)+\sum^{n}\hat{V}(\hat{x}_i)}{N\cdot n} \tag{10}$$

and

$$\hat{V}(\hat{X})=\hat{V}(\hat{\bar{x}})\cdot N^2. \tag{11}$$

In eq. (10),

$$\hat{V}(\hat{x})=\frac{\sum^{n}(\hat{x}_i-\hat{\bar{x}})^2}{n-1}. \tag{12}$$

The calculation of the term $\sum^{n}\hat{V}(\hat{x}_i)$ in eq. (10) may deserve some attention. If p can be assumed constant among the sections and if k is the same among the sections, the pooled population estimate $\hat{x}_p$ is used. Thus in this case,

$$\sum^{n}\hat{V}(\hat{x}_i)=\hat{V}(\hat{x}_p). \tag{13}$$

If p can be assumed constant, but the number of removal fishings k varies within the sample of sections, each $\hat{V}(\hat{x}_i)$ may be calculated as $\hat{V}(\hat{x}_i')$ according to eq. (6), using pooled or weighted estimate of p, followed by summing the variances over the n sections. Finally, if p cannot be assumed constant, each $\hat{V}(\hat{x}_i)$ is calculated in the usual way, using eq. (2) and summing over the n sections. (10) and (11) may be used if n is not too small, say $n > 10$. Approximate 95 % confidence limits are $\hat{\bar{x}}\pm 2\sqrt{\hat{V}(\hat{\bar{x}})}$ and $\hat{X}\pm 2\sqrt{\hat{V}(\hat{X})}$ respectively.

Example 4. Consider example 1. In this case n=12. Say that these sections were drawn at random from a stream containing a total of 70 such sections, *viz.* N=70. Further, p can be assumed constant, and the number of removals is the same for all sections. To calculate the population size in each section, pooling may be carried out to estimate the common catch probability, using the Zippin graphs or the iterative method, and inserting this estimate into eq. (1). The pooled catches are 482, 197 and 98, yielding a p estimate of 0.561. Using eq. (1) to obtain the population estimates in each of 12 sections, the result is

Section no.	T_i	$\hat{x}_i$
1	69	75.4
2	100	109.2
3	74	80.8
4	25	27.3
5	40	43.7
6	23	25.1
7	97	106.0
8	52	56.8
9	95	103.8
10	72	78.7
11	48	52.4
12	82	89.6

$\hat{\bar{x}}=70.7$, $\hat{X}=70\cdot 70.7=4{,}949$

$\hat{V}(\hat{x})=871$ (eq. 12).

Thus, mean density per section is 70.7 and total stock 4,949 trout.

To obtain the sampling variances of these estimates according to eqs (10) and (11), the sum of variances in eq. (10) must first be estimated. In this case relation (13) may be used. Using the pooled catches, the pooled population size $\hat{x}_p$ is 849 by the iterative method. As above, the pooled catch probability is 0.561. Inserting these values into eq. (2), the variance of the pooled population size is 178. Thus $\sum^{n}\hat{V}(\hat{x}_i)=\hat{V}(\hat{x}_p)=178$.

The variance of the estimated mean density per section is then, from eq. (10),

$$\hat{V}(\hat{\bar{x}}) = \frac{871(70-12)+178}{70 \cdot 12} = 60.4.$$

Approximate 95 % confidence limits are $70.7 \pm 2\sqrt{60.4}$ or 55 – 86.

The variance of the total stock estimate, (eq. 11), is $\hat{V}(\hat{X}) = 60.4 \cdot 70^2 = 295{,}960$.

Approximate 95 % confidence limits for the total stock estimate are $4949 \pm 2\sqrt{295{,}960}$ or 3861 – 6037.

It may be noted in this example that a very small fraction of the total variance is due to the sum of variances in eq. (10), and that most of the sampling variance of the mean density or total stock comes from large variation of population sizes among the sections. In practice this means that it is probably wiser to include a larger number of sections in the study than to expand the number of removal fishings in each section when estimates of total stock is of primary interest. If p can be assumed constant among sections, and if this p is estimated with reasonable precision, even the one-catch case may be considered, at least in sections with low population density. The formulas above will hold in this case also.

V. A 'DIFFERENCE' METHOD OF ESTIMATING SMOLT OUTPUT USING PAIRED OBSERVATIONS

For migratory stocks, the estimation of smolt output is frequently the most important task in practical management. For brown trout, and some similar species, only a fraction may be migratory, and the rest stationary. Thus, in this case, a total stock estimate prior to the migration season cannot be used alone as an estimate of the smolt run. If the use of traps etc. is inconvenient, the smolt run may be estimated by quantitative electrofishing using the following method or that suggested in the following section.

In each of the N stream sections, x_i is the population size before and y_i the population size after the smolt run. Ignoring mortality during the period, the number of smolt emigrating, Z, is the difference between the total stock size X before and Y after migration:

$$Z = X - Y = \sum^{N} x_i - \sum^{N} y_i = \sum^{N} (x_i - y_i) = \sum^{N} z_i = N \cdot \bar{z}$$

where $z_i = x_i - y_i$. Thus, $Z = N \cdot \bar{z}$, which is the parameter to be estimated. Using a random sample of n sections, of which each section is sampled before and after the smolt run, an estimator of $\bar{z}$ is

$$\hat{\bar{z}} = \frac{\sum^{n} \hat{z}_i}{n} = \hat{\bar{x}} - \hat{\bar{y}} \qquad (14)$$

and of Z

$$\hat{Z} = N \cdot \hat{\bar{z}}. \qquad (15)$$

The sampling variances of these estimates may be derived using a similar approach to that in Appendix 2:

$$\hat{V}(\hat{\bar{z}}) = \frac{(N-n)\left[\hat{V}(\hat{x}) + \hat{V}(\hat{y})\right] + \sum^{n} \hat{V}(\hat{x}_i) + \sum^{n} \hat{V}(\hat{y}_i)}{N \cdot n} - 2 \cdot r\sqrt{\hat{V}(\hat{\bar{x}})\hat{V}(\hat{\bar{y}})} \qquad (16)$$

and

$$\hat{V}(\hat{Z}) = N^2 \hat{V}(\hat{\bar{z}}). \qquad (17)$$

In eq. (16), $\hat{V}(\hat{x})$ and $\hat{V}(\hat{y})$ are calculated according to eq. (12), and $\hat{V}(\hat{\bar{x}})$ and $\hat{V}(\hat{\bar{y}})$ according to eq. (10). r is the estimated coefficient of correlation between the observations $\hat{x}_i$ and y_i, calculated in the usual way.

Approximate 95 % confidence limits are $\hat{\bar{z}} \pm 2\sqrt{\hat{V}(\hat{\bar{z}})}$ and $\hat{Z} \pm 2\sqrt{\hat{V}(\hat{Z})}$.

Example 5. Consider example 4. In this case, the population size in 12 sections was estimated by the removal method. Assume that these fishings were carried out immediately before the smolt run, and that each of the sections was also subject to population estimation after the smolt run, yielding the following result:

Section no.	$\hat{x}_i$	$\hat{y}_i$
1	75.4	22.5
2	109.2	25.0
3	80.8	20.2
4	27.3	12.1

Section no.	$\hat{x}_i$	y_i
5	43.7	16.9
6	25.1	6.6
7	106.0	30.0
8	56.8	17.7
9	103.8	20.7
10	78.7	19.0
11	52.4	15.0
12	89.6	26.3

In example 4, the following estimates were obtained:

$\hat{\bar{x}}=70.7$
$\hat{X}=4949$
$\hat{V}(\hat{x})=871$
$\sum^{n}\hat{V}(\hat{x}_i)=178$
$\hat{V}(\hat{\bar{x}})=60.4.$

Using the same procedure for $\hat{y}_i$ as for $\hat{x}_i$ above, the following result was obtained:

$\hat{\bar{y}}=19.33$
$\hat{Y}=1353$
$\hat{V}(\hat{y})=40.8.$
$\sum^{n}\hat{V}(\hat{y}_i)=48.4$ (To calculate this estimate, the catches must be used as in example 4. This is omitted.)
$\hat{V}(\hat{\bar{y}})=2.97$

To use eq. (16), the correlation coefficient between $\hat{x}_i$ and $\hat{y}_i$ is calculated as $r=0.89$.

Inserting $\hat{\bar{x}}$ and $\hat{\bar{y}}$ into eqs. (14) and (15), the mean smolt output per section is $\hat{\bar{z}}=70.7-19.3=51.4$, and total smolt output thus $\hat{Z}=70\cdot 51.4=3598$. Inserting the variances above into eq. (16), the variance of the mean smolt output is

$$\hat{V}(\hat{\bar{z}})=\frac{(70-12)(871+40.8)+178+48.4}{70\cdot 12}$$

$$-2\cdot 0.89\sqrt{60.4\cdot 2.87}=39.9$$

and using eq. (17),

$$\hat{V}(\hat{Z})=70^2\cdot 39.9=195{,}510.$$

Approximate 95 % confidence limits for the total smolt run are thus $3598\pm 2\sqrt{195{,}510}$ or 2714—4482.

Using the above method to estimate the absolute decrease in population size, it may be noted that a positive correlation between $\hat{x}_i$ and $\hat{y}_i$ will increase the precision of this estimate. Since such a correlation may be expected, pairing of the observations as in the suggested method is to be recommended. If, however, this correlation turns out to be negative, a better approach would be to use independent stream section samples. In practice this means using a "new" random sample in the latter period. If so, the last term in eq. (16) will be zero.

VI. A 'CHANGE-IN-RATIO' METHOD OF ESTIMATING SMOLT OUTPUT

In the class of methods known as "change-in-ratio" or "survey removal" methods, changes in observed proportions of sex, age or marked-to-unmarked animals have been used to estimate population size and related parameters. PAULIK and ROBSON (1969) and SEBER (1973, p. 353—392) cover this topic fully.

The fact that smolt of migratory trout stocks usually have a skewed sex ratio in favour of females compared to the original even sex ratio may be used to estimate the proportion of the population emigrating as smolt. Once this proportion "u" is estimated, the total number of smolt may be calculated after total stock assessment, using *e.g.* the method proposed in section IV.

The basic steps of the calculation of u are given in SEBER (1973, section 9.1.5.), who calls this fraction "exploitation rate". Let the ratio of females to females plus males be

R_x in the population prior to the smolt run,
R_y in the population after the smolt run, and
R_z among smolt.

The ratio (number of smolt)/(initial population) is then estimated as

$$\hat{u}=\frac{\hat{R}_x-\hat{R}_y}{\hat{R}_z-\hat{R}_y} \qquad (18)$$

The sampling variance if this estimate, obtained by the delta method, is given by SEBER (1973, p. 380) as

$$\hat{V}(\hat{u})\cong(\hat{R}_z-\hat{R}_y)^{-4}\Big[(\hat{R}_z-\hat{R}_y)^2\hat{V}(\hat{R}_x)+$$
$$+(\hat{R}_z-\hat{R}_x)^2\hat{V}(\hat{R}_y)+(\hat{R}_x-\hat{R}_y)^2\hat{V}(R_z)\Big] \qquad (19)$$

Assuming binomial sampling, the variances of the sex ratios in this expression are

$$\hat{V}(\hat{R}_x)=\hat{R}_x(1-\hat{R}_x)/n_x \qquad (20)$$

$$\hat{V}(\hat{R}_y)=\hat{R}_y(1-\hat{R}_y)/n_y \qquad (20)$$

$$\hat{V}(\hat{R}_z)=\hat{R}_z(1-\hat{R}_z)/n_z, \qquad (20)$$

where n_x, n_y and n_z are the numbers in each category examined for sex. Sometimes the smolt is made up of a single age class. In this case, $R_x=0.5$ and $V(\hat{R}_x)=0$, since trout is known to have an even sex ratio.

Having an estimate of u by the method above, the total number of smolt Z may be calculated as

$$\hat{Z}=\hat{u}\cdot\hat{X}, \qquad (21)$$

where $\hat{X}$, the total stock prior to smolt migration, is estimated from eq. (9). Following GOODMAN (1960), the sampling variance of $\hat{Z}$ in this case is obtained as

$$\hat{V}(\hat{Z})=\hat{u}^2\cdot\hat{V}(\hat{X})+\hat{X}^2\hat{V}(\hat{u}), \qquad (22)$$

where $\hat{V}(\hat{X})$ follows from eqs. (11) and $\hat{V}(\hat{u})$ from eq. (19).

Example 6. Aging of trout smolt showed that a vast majority migrated at age II and a minor fraction at age III. A sample of II smolt was sexed, yielding 35 females and 20 males. After the smolt run, sex determination of the remaining II population gave 6 females and 34 males. The initial sex ratio was assumed to be one female per male.

Thus

$\hat{R}_x=0.5$ and $\hat{V}(\hat{R}_x)=0$

$\hat{R}_y=6/(6+34)=0.1500$, and $\hat{V}(\hat{R}_y)=0.1500(1-$
$-0.1500)/40=0.003188$

$\hat{R}_z=35/(35+20)=0.6364$, and $\hat{V}(\hat{R}_y)=0.6364(1-$
$-0.6364)/55=0.004207$.

Hence from eq. (18),

$\hat{u}=(0.5000-0.1500)/(0.6364-0.1500)=0.720$

and from eq. (19),

$$\hat{V}(\hat{u})=(0.6364-0.1500)^{-4}\Big[(0.6364-0.1500)^2\cdot 0+ \\ +(0.6364-0.5000)^2\cdot 0.003188+(0.5000- \\ -0.1500)^2\cdot 0.004207\Big]=0.01027.$$

Thus 0.720 of the initial II population is estimated to migrate, and the sampling variance of this is 0.0127. To estimate the total number of II trout emigrating, this $\hat{u}$ value is multiplied by the estimated II stock. Say that the total stock figure in ex. 4 is the size of this age class. If so, $\hat{X}=4949$ with variance $\hat{V}(\hat{X})=295{,}960$ (ex. 4). From eq. (21), the total smolt output of this age class is then $\hat{Z}=0.720\cdot 4949=3563$ smolt, with variance (eq. 22) $\hat{V}(\hat{Z})=0.720^2\cdot 295{,}960+4949^2\cdot$ $\cdot\, 0.01027=404{,}965$. Approximate 95 % confidence limits are then $3563\pm 2\sqrt{404{,}965}$ or $2290-4836$.

It may, finally, be noted that the number of fish for sex determination needed to reach some desired precision of $\hat{u}$ may be roughly calculated if preliminary values of the sex ratios are available. Using the values in ex. 6, a coefficient of variation of 0.1 would require approximately 100 trout of each category.

VII. ESTIMATION OF SURVIVAL USING PAIRED OBSERVATIONS OF STREAM SECTIONS

Estimates of survival S, or mortality $(1-S)$ are of primary interest in a variety of applied and basic fishery problems, and it is therefore important to reduce the bias as well as the sampling error of survival estimates. Since stream-living salmonids normally migrate from shallow "nursery" areas into deeper sections as they grow, it follows that a survival estimate based on measurement of the population change may be biased due to migration. To obtain an unbiased estimate of the true survival of a stock, it is essential that the estimate should be based on a random sample of stream sections. If so, is it also possible to calculate the sampling error of the estimate, *e.g.* by the method below.

Consider an age class of total size X at the beginning of a period, and of size Y at the end of the period. The finite rate of survival is then defined as $S=Y/X$. With the notation above, an estimator of S is

$$\hat{S}=\hat{\hat{y}}/\hat{\hat{x}}, \qquad (23)$$

where $\hat{\hat{y}}$ and $\hat{\hat{x}}$ are calculated using eq. (8). The approximate variance of this estimate may be obtained by the delta method:

$$\hat{V}(\hat{S})\cong\hat{\hat{x}}^{-4}\Big[\hat{V}(\hat{\hat{y}})\cdot\hat{\hat{x}}^2+\hat{V}(\hat{\hat{x}})\cdot\hat{\hat{y}}^2-2\cdot r\cdot \\ \cdot\sqrt{\hat{V}(\hat{\hat{x}})\hat{V}(\hat{\hat{y}})}\cdot\hat{\hat{x}}\cdot\hat{\hat{y}}\Big]. \qquad (24)$$

In this expression, $\hat{V}(\hat{\hat{x}})$ and $\hat{V}(\hat{\hat{y}})$ are from eq.

(10), and r is the coefficient of correlation between the observations $\hat{x}_i$ and $\hat{y}_i$, computed in the usual way. As in section V, it is evident that a positive correlation will improve the precision of the survival estimate. As this is to be expected, pairing of the observations as in section V should normally be used.

Example 7. Consider ex. 5, in which the mean density per section was estimated on two occasions. Assume that the population change is due to mortality (stationary population). The estimated means and their sampling variances are $\hat{\bar{x}}=70.7$, $\hat{V}(\hat{\bar{x}})=60.4$ and $\hat{\bar{y}}=19.3$, $\hat{V}(\hat{\bar{y}})=2.97$. Further, $r=0.89$. Thus $\hat{S}=19.3/70.7=0.273$, and, from eq. (24),

$$\hat{V}(\hat{S})\cong 70.7^{-4}\Big[2.97\cdot 70.7^2+60.4\cdot 19.3^2-2\cdot$$

$$\cdot\, 0.89\sqrt{2.97\cdot 60.4}\cdot 70.7\cdot 19.3\Big]=0.000193.$$

Approximate 95 % confidence limits are $0.273\pm$ $\pm 2\sqrt{0.000193}$ or $0.245-0.301$.

VIII. FINAL REMARKS

Electrofishing is an extremely useful method of fish sampling in shallow fresh waters owing to its efficiency and low selectivity, and the fact that it is seldom harmful to fish. It is therefore widely used in scientific studies as well as in practical management. The extensive use of electrofishing has resulted in a huge pile of data especially on salmonid populations, potentially of great value in the attempts to develop practically useful models of salmonid populations. Unfortunately, however, a large fraction of these data is of limited value owing to improper sampling design: much of it does not represent the stock but some subjectively chosen part of it with unknown relations to the stock. Since stock parameters are usually required, it is essential that the sampling plan should be based on some kind of random selection of stream sections in cases when the whole area is inconvenient to cover.

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APPENDIX 1:

Derivation of eq. (6)

Say that $q=1-p$ is estimated using pooling or weighted mean as $\hat{q}'$.

$$\hat{x}_i=T_i/(1-\hat{q}'^{k_i}). \qquad (1)$$

$\hat{V}(\hat{x}_i')$ is found by the delta method as

$$\hat{V}(\hat{x}_i')\cong\hat{V}(T_i)\left(\frac{\delta\hat{x}_i}{\delta T_i}\right)^2+\hat{V}(\hat{q}')\left(\frac{\delta\hat{x}_i}{\delta\hat{q}'}\right)^2.$$

Assuming binomial sampling of T:

$$V(T_i)=\hat{x}_i'q'^{k_i}(1-\hat{q}'^{k_i})$$

As $V(\hat{q}')=V(1-\hat{p}')=V(\hat{p}')$

and by using (1), this leads to

$$\hat{V}(\hat{x}_i')=\frac{\hat{x}_i'\hat{q}'^{k_i}}{1-\hat{q}'^{k_i}}+\hat{V}(\hat{p}'\left(\frac{\hat{x}_i'k_i\hat{q}'^{k_i-1}}{1-\hat{q}'^{k_i}}\right)^2.$$

APPENDIX 2:

Derivation of eq. (10)

The notation is as above. The model used is

$\hat{x}_i = x_i + \varepsilon_i$

$x_i = \bar{x} + A$

where $\varepsilon_i = N(0, \sigma_i)$ and A is a random variable with mean $= 0$ and variance $= \sigma_A^2$. Thus

$\hat{x}_i = x + A + \varepsilon_i$

The sampling variance of $\hat{\bar{x}} = \bar{\hat{x}} = \frac{\sum^{n} \hat{x}_i}{n}$ is wanted.

Assuming A and ε_i to be independent, this leads to

$$V(\hat{\bar{x}}) = \frac{\sigma_A^2}{n} + \frac{1}{n^2}\sum^{n} \sigma_i^2$$

and with correction for finite number of sections,

$$V(\hat{\bar{x}}) = \frac{\sigma_A^2}{n}\left(1 - \frac{n}{N}\right) + \frac{1}{n^2}\sum^{n} \sigma_i^2.$$

In this expression, not unbiased, the first term contains the sampling variance due to the spatial distribution of fish, and the second to error of measurement in each section. To use the expression, σ_A^2 and σ_i^2 must be estimated. The latter is obtained from the catch data and eqs (2) or (6). The former may be estimated as 'total variance' minus 'measurement variance', viz.

$$\hat{\sigma}_A^2 = \hat{V}(x) = \hat{V}(\hat{x}) - \frac{\sum^{n} \hat{V}(\hat{x}_i)}{n-1},$$

where $\hat{V}(\hat{x}) = \frac{1}{n-1}\sum^{n}(\hat{x}_i - \bar{\hat{x}})^2$.

Inserting this into the expression above,

$$\hat{V}(\hat{\bar{x}}) = \hat{V}(\hat{x})\frac{N-n}{N \cdot n} - \frac{\sum^{n} \hat{V}(\hat{x}_i)}{n(n-1)} + \frac{\sum^{n} \hat{V}(\hat{x}_i)}{N(n-1)} + \frac{1}{n^2}\sum^{n} V(\hat{x}_i).$$

If $N(n-1) \cong N \cdot n$ and $n(n-1) \cong n^2$, the expression is reduced to $\hat{V}(\hat{\bar{x}}) = \frac{\hat{V}(\hat{x})(N-n) + \sum^{n} \hat{V}(\hat{x}_i)}{N \cdot n}$.

Interspecific Food Competition Between the Three Pelagic Zooplanktonfeeders, Cisco (*Coregonus albula* (L.)), Smelt (*Osmerus eperlanus* (L.)) and Herring (*Clupea harengus* L.) in the Norrbotten Part of the Bothnian Bay

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ABSTRACT

The experimental gillnetting of 1975 and 1976 yielded 12,400 fishes of which 28 per cent were cisco, 2 per cent smelt and 39 per cent herring. Cisco, smelt (freshwater fishes) and herring (a saltwater fish) are very rarely found together.

The zooplankton species *Bosmina coregoni*, *Eurytemora* spp and *Limnocalanus grimaldii* were found to be important food items for all three fish species but the smallest of the zooplankton (*B. coregoni*) were most abundant in cisco stomachs and least abundant in smelt stomachs. Large food items like mysids were found in smelt and sometimes in herring but never in cisco.

Usually, the fish species which is best able to feed on small items, in this case the cisco, becomes dominant but it is not so in this ecosystem. Abiotic factors such as the brackish water probably interact, with the result that two species, herring and cisco, are dominant.

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I. INTRODUCTION

The northern part of the Baltic Sea is called the Gulf of Bothnia which can further be divided into the Bothnian Sea and the Bothnian Bay. The Bothnian Bay is characterised by low primary production (Wulff *et al.* 1977, Ackefors *et al.* 1978) rather shallow water, low water temperatures, high oxygen content, salinities ranging from 0—3 per mille (Fonselius 1971) dim light during the summer nights and an ice-cover for 6—7 months of the year.

The water along the Finnish coast is slightly more saline and somewhat more productive (Valtonen *et al.* 1978) than the water on the Swedish (Norrbotten) side.

There are more than twenty fish species which are permanent residents of this brackish water and about ten more occur more or less frequently. Two of these species contribute with more than fifty per cent of the fish biomass. They are the saltwater species herring (*Clupea harengus* L.) and the freshwater species cisco (*Coregonus albula* (L.)). Both are wellknown zooplankton feeders when living in separate areas (Popiel 1951, Vallin 1969, Nilsson 1974, Aneer 1975, Appelberg 1977, Almer 1978, 1979, Hamrin 1979, Sandström 1980) but nothing is known about their interactions when they have to share a resource in brackish water, which is not an environment ideal for either of them.

A third pelagic zooplankton feeder, the freshwater species smelt (*Osmerus eperlanus* (L.)) is also included in the study.

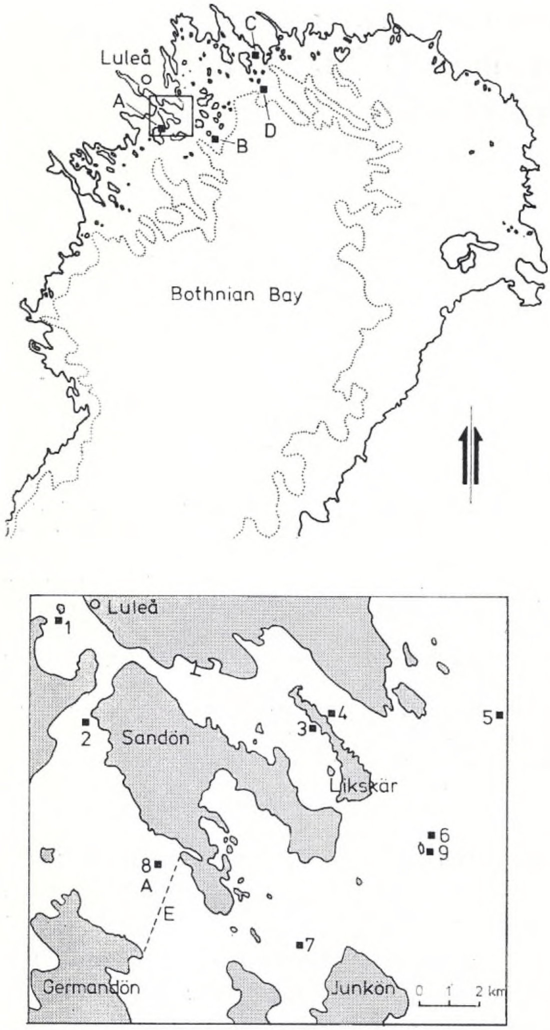

Fig. 1. Map of the Bothnian Bay. 1 to 9 are sampling-stations used in 1975 and A to D are stations used in 1976—78. The dotted line indicates the 25 m depth curve.

II. MATERIAL AND METHODS

Stomachs were collected in 1975 and 1976 during the ice-free season. The ice usually breaks up at the end of May and starts to form again in the beginning of November.

1975

Experimental gillnetting was carried out at stations 1 to 9 (Fig. 1) from June 5 until October 24, by the Fisheries Administration in Luleå. Monofilament-nylon nets with a catch-range of 100 mm and upwards for cisco and herring were used. The nets were set at the bottom at all stations with additional nets at the surface at the deep water stations 5, 6, 7 and 8. Only stomachs from the cisco catch were collected.

1976

In this year the fishing was carried out in co-operation with the Fisheries Administration in Luleå with special reference to cisco, herring and smelt. The stations used were A—D (Fig. 1). The fishing was carried out during five periods; June 14—20, week 25, July 19—25, week 30, August 23—29, week 35, September 27—October 3, week 40, and October 26—31, week 44. Three six metre high series of monofilament-nylon nets were set to cover the surface, midwater and the bottom. The depth was 20 m at stations A and B and 16 m at stations C and D. Each net series consisted of four nets with meshsize 21.5, 16.5, 12.5 and 10 mm from knot to knot respectively. The catch-range for such a series is from 100 to 250 mm for cisco and herring.

In both 1975 and 1976 the nets were set in the evening and lifted in the morning.

The fish were measured (mm) and weighed (g) before the stomach was removed and preserved in 10 per cent formalin.

Laboratory work

Sampling has been necessary in some cases and care has then been taken to choose stomachs from all size-groups.

The contents of each full or half-full stomach were classified according to group or species and these were estimated as percentages of the total volume, which was then measured to the nearest 1/50th of a ml.

III. RESULTS

The stations used in 1975 (1—9) and 1976 (A—D) are indicated on the map in Fig. 1.

The experimental gillnetting in 1975 yielded more than 9,000 fishes. Of these, 25 per cent by number were cisco, 37 per cent herring and 1 per cent smelt.

The aim of the 1976 fishing was to catch pelagic species and this gave 3,400 fishes, of which

Table 1. *The stomach contents and parasitism in per cent for cisco in 1975 and cisco (C), herring (H) and smelt (S) in 1976.*

Year	1975					1976														
Week						25			30			35			40			44		
Date or month	June	July	Aug.	Sep.	Oct.	June 14—20			July 19—25			Aug. 23—29			Sep. 27—Oct. 3			Oct. 26—31		
Species of fish	Cisco					C	H	S	C	H	S	C	H	S	C	H	S	C	H	S
Number	23	30	179	214	207	17	29	2	41	73	27	83	139	36	85	110	32	145	21	21
Bosmia coregoni maritima	+	6	90	94	67	3	3		49	22	18	73	39	14	51	30	14	38	23	15
Daphnia cristata					4				1			+	+		1	2		6	21	11
Evadne sp.									14	3		+	+							
Podon sp.			+						1	+		1	+		+					
Cladocera eggs			+	+	23				+			1	+		3	14		2	24	+
Eurytemora sp.	41	5	1	1	4	44	34	60	22	34	25	4	8	1	28	8	9	34	27	21
Limnocalanus grimaldii	33	89	3	1	2	43	57	25	6	31	50	8	47	28	15	43	35	+	+	
Calanoida copepodits							4					+		+						
Cyclops spp.					+				+				+		+	+	+		+	1
Cyclopoida copepodits										+		+		+		+				
Copepoda eggs	3	+	2	2	+	1	2	15	3	4		2	6	2	2	1		14	2	22
Mysis sp.													+	25		1	38		2	30
Pontoporeia sp.																			1	
Gammarus sp.													+			1				
Chironomidae larvae									+	1	7		+		+			+		+
Chironomidae pupa													+							
Terrestrial insects	23		4	2		9			4	1		11	+	20			+			
Roe from cisco					+													6		
Roe from herring										4										
Fish fry														10						
Parasitism of the stomach																				5
Cestoda	13	13	8	9	5	6	—		7			14								
Acanthocephala														14	11		4	12		
Stomach empty or nearly empty	74	17	41	30	74	35	20	50	54	69	89	23	18	44	65	30	34	41	20	48

+ = Found in many stomachs but in very small quantities.

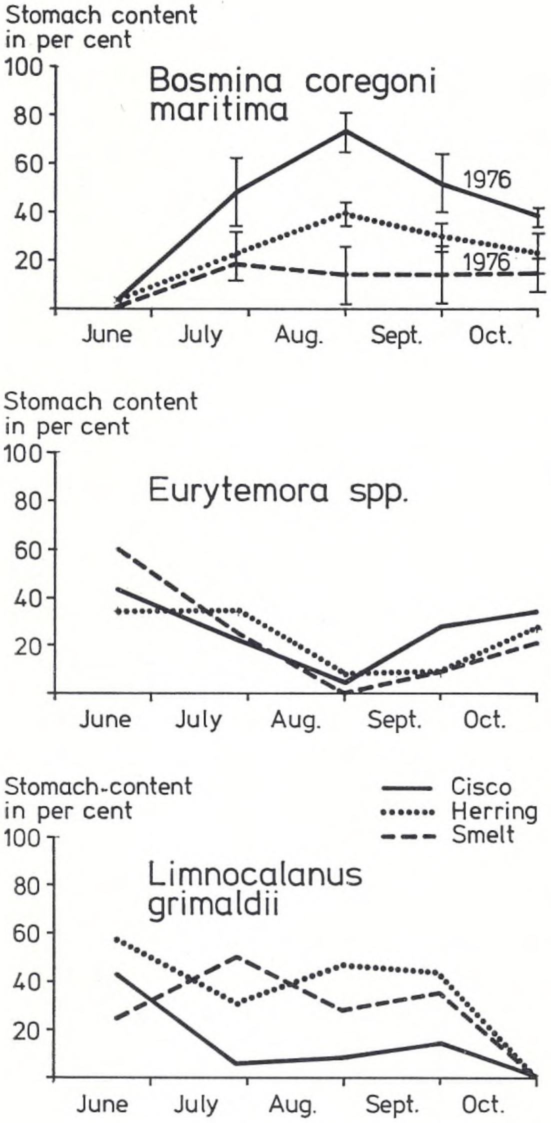

Fig. 2. The percentage of stomach contents composed of *B. coregoni maritima*, *Eurytemora* spp and *L. grimaldii* in cisco, herring and smelt, as a function of time (1976). A 95 per cent confidence interval for the percentage of *B. coregoni maritima* is indicated by vertical bars in the top figure.

36 per cent by number were cisco, 46 per cent herring and 6 per cent smelt.

The percentage composition of stomach contents from the 1975 cisco catch and the 1976 cisco, herring and smelt catch is shown in Table 1, as well as the percentage of stomachs with parasites inside or attached to them.

The material did not reveal any tendency for fish size to be correlated to any type of food except as regards smelt, which tended to become a fish feeder as its size increased.

The size-range for the total length is 100—230 mm for cisco and herring and 120—260 mm for smelt.

The parasitation on the stomachs was in no case severe. The species of parasites have not been determined but the tapeworms *Diphyllobothrium osmeri* and *Proteocephalus* spp are reported to infest cisco in the area (Petersson 1971) and the hookworm *Metechinorhynchus salmonis* with *Pontoporeia affinis* as the intermediate host was found by Valtonen on the Finnish side of the Bothnian Bay (Valtonen 1970).

The three most important zooplankton species found in the stomachs are *Bosmina coregoni maritima* (P. E. Muller), *Eurytemora* spp and *Limnocalanus grimaldii* (de Guerne). The percentages of these three found in the stomachs of the respective fish species are shown in Fig. 2. The smallest of the zooplankton preyed upon, *Bosmina*, is clearly most abundant in cisco stomachs.

IV. DISCUSSION

A zooplankton community not subjected to grazing consists of large forms. When in contact with fish, large forms are grazed upon and will be replaced by smaller forms. The tremendous impact the fish actually have, was not fully realised until the work of Brooks and Dodson (1965), Hrbáček and Novotná-Dvořáková (1965).

The balance between the zooplankton feeders and the zooplankton size structure that appears after some time can easily be disturbed by the introduction of an even more efficient zooplankton feeder. The new result should be that the zooplankton community is replaced by even smaller forms and that the previously dominant (that is to say most numerous) planktivore is either eliminated or has to look for another source of food. That this actually has happened in many Swedish lakes is shown by Nilsson and Pejler (1973). The reason could be that the fish graze on the zooplankton as far as the limits of their vision will allow. The species with the "best vision", in the sense of the highest resolving power, should then be dominant as everything big enough for the other fish species to see, is already eaten, if food is not super-abundant.

The Bothnian Bay is a stable ecosystem with endemic fish species. The zooplankton found, especially the Cladocera, are small forms. (An exception is the cold stenothermal *Limnocalanus grimaldii.*) This is indicative of heavy and efficient predation and both cisco and herring are known to be efficient planktivores. According to the previous arguments the fish with the "best vision" should be dominant (that is to say most common). The smallest food item is the *Bosmina*, which is found in the highest percentage in the cisco stomachs. Cisco should therefore be considered as the fish species with the "best vision" (Fig. 2) and the dominant zooplankton feeder. In oligotrophic lakes cisco is found to be the dominating species (SVÄRDSON 1976), but the experimental gillnetting showed herring in the Bothnian Bay to be slightly more numerous than cisco. This unusual situation of having two planktivorous species in about equal proportions is probably due to the brackish water. JÄRVI (1950) found that cisco was not present in large numbers in water with a salinity greater than 2—3 per mille. The salinity prohibits the expansion of cisco and at the same time provides a refuge area for the herring.

Smelt, the third pelagic planktivore, is found in relatively small numbers and has a very small biomass. Smelt is dominated by cisco in oligotrophic lakes (SVÄRDSON 1976) which fits in well with the finding that it is this species which has the smallest amounts of *Bosmina* in its stomach. (Only in mesotrophic lakes is smelt found to dominate over cisco [HAMRIN 1979].)

In order to survive the smelt has to feed on other organisms such as *Mysis* sp (Table 1) which is not utilized by cisco and only to a small extent by herring and/or become a fish fry predator. (The parasitation by Acanthocephala found in smelt stomachs indicates a *Pontoporeia* sp diet, probably during the winter as none were found in the stomachs.)

Smelt is much more capable of coping with the salinity in the Gulf of Bothnia than cisco is, and as a result, the area in which smelt is found is much greater. In these areas where cisco is absent and smelt competes only with herring, it is far more abundant. On the Finnish side of the Gulf of Bothnia 822 tonnes (1976) of cisco but hardly any smelt were caught in the northern part. Further south in the more saline water, 510 tonnes (1976) of smelt, but hardly any cisco were caught (LEHTONEN 1978). (It should be noted that smelt is not fished for but is only a by-product of fishing for other species.)

V. SUMMARY

The situation in the Bothnian Bay is unusual, with two species of efficient zooplankton feeders in about equal numbers balanced by abiotic factors. The third zooplankton feeding fish species—the smelt—is less efficient and dominated by the others but mostly by cisco, which is probably the most competative pelagic planktivore in the system.

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When, Where, What and How Much Does the Adult Cisco, *Coregonus albula* (L.) Eat in the Bothnian Bay During the Ice-free Season

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ABSTRACT

The cisco breakfast between 6 and 9 a.m. in midwater, on its way down to the bottom. Breakfast consists of *Limnocalanus grimaldii.* Lunch is not eaten except in October when the ciscoes have a brunch (breakfast-lunch) consisting of *Bosmina coregoni maritima*, *Eurytemora* spp and *Daphnia cristata.* Dinner is eaten on the way to and at the surface (the time varies with the season, but is usually between 3 and 9 p.m.) and consists mostly of *Bosmina* and *Eurytemora.* A supper of terrestrial insects trapped at the surface is sometimes eaten in the evenings when the weather is good.

The amount consumed during 24 hours varies considerably, being about 1 per cent of the body weight in the beginning of June and in mid October, 30 per cent at the end of July and about 10 per cent in the beginning of September. There is no direct correlation between the zooplankton species present and those which are consumed. My explanation for this is that the zooplankton are invisible to the cisco for most of the time, but when visible zooplankton are abundant the fish prey heavily upon them. A rapid gastric evacuation rate enables them to take advantage of these occasions.

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I. INTRODUCTION

The cisco in the Norrbotten part of the Bothnian Bay is at present the commercially most important fish species. The yearly catch has increased drastically since trawling was introduced in the beginning of 1960 (ENDERLEIN 1978). Due to fears of overfishing a research program was initiated in late 1975 to deal with the entire biology of the cisco in the Bothnian Bay. This paper is one in a series and attempts to answer the questions: When, where, what and how much does the cisco eat during the ice-free season.

It also suggests an explanation for the fact that the cisco is the second most numerous species in this region (ENDERLEIN 1980), despite low primary production levels and competition from about thirty fish species, in brackish water environment which is not favourable for the cisco (JÄRVI 1950).

II. MATERIAL AND METHODS

A diel fishing was conducted at station A (Fig. 1) in 1977 on three occasions (May 26—27, week 21, July 23—24, week 29, and October 3—4, week 40).

Two net series were used with one series at the surface and one at the bottom (20 m). A series consisted of four 6 m high monofilament nets with meshsize 21.5, 16.5, 12.5 and 10 mm between knots. The nets were set at 12 a.m. and thereafter

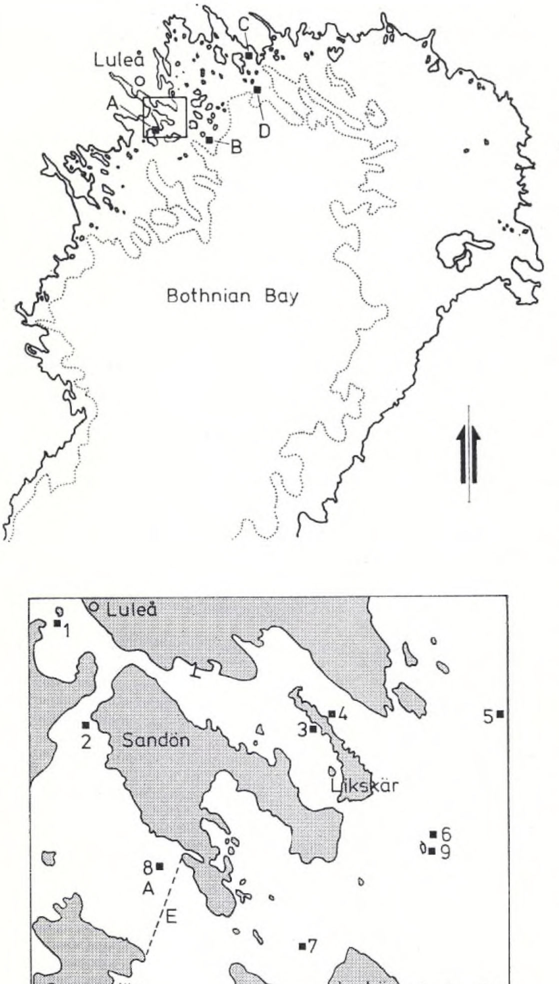

Fig. 1. Map of the Bothnian bay. Numbers 1 to 9 are sampling-stations used in 1975, number 8 was even used 1976—78 as well as transect E. (Dotted line indicates the 25 m depth curve.)

lifted up to the side of the boat every third hour and the catch collected repeatedly during 24 hours.

The stomachs were immediately removed from the fish and preserved in 10 per cent formalin. Weight and total length were recorded at the same time.

After the collection of each catch echosounding was carried out along transect E (Fig. 1). An Atlas Echograph 420 with a frequency of 100 kHz was used with a depth range from 0—25 m.

The diel fishing was repeated in 1978 on four occasions (June 8—9, week 23, July 22—23, week 29, September 4—5, week 36 and October 10—15, week 41) at the same station (A) as in 1977. Dynamite (Dynamex 22) was used instead of nets. Each charge (100 or 200 g) was suspended from the surface by a float and made to detonate at 15 m depth by means of an ordinary fuse, every third hour. At least 10 ciscoes were required per sampling occasion. If this amount was not collected after the first detonation a new charge was exploded. Due to a limited amount of dynamite a maximum of three attempts could be made on each occasion. Only fish floating on the surface were collected. Seagulls competed successfully with us.

Zooplankton was also collected every third hour at 1, 5, 10, 15 and 19.5 m depth at a spot where the maximum depth was 20 m. A 5 l Rodhe sample was used. In October (week 41) zooplankton was even collected at the surface. The zooplankton was preserved in Lugol's solution. The fish analyses and the echosounding were performed as in 1977.

Laboratory work

The contents of each stomach with a measurable volume (more than 0.02 ml) were determined to genus or species and these were estimated as percentages of the total volume. The contents of 30 randomly chosen stomachs were, after measurement of the volumes, dried for 48 hours at 65°C and weighed separately.

The total number of individuals of each species present in the zooplankton samples was transformed into mg per m^3 with the conversion factors used by the Askö Laboratory in their Luleå investigation (Wulff *et al.* 1977).

Calculations.

The feeding rate was estimated using the new method for constant rate of consumption between samplings (Elliott and Persson 1978), given by the equation:

$$C_t = \frac{(S_t - S_0 \cdot e^{-R \cdot t})R \cdot t}{1 - e^{-R \cdot t}}$$

Where C_t is the actual amount of food consumed in t hours. S_0 and S_t are the relative stomach

Table 1. *Numbers of cisco, herring and smelt caught per net series during three hours in six metre high nets. Surface (S) set net series at 0—6 metres depth. Bottom (B) set net series standing on the bottom at 20 metres depth.*

Date	Species	Nets	Hour of the day when collecting catch							
			03	06	09	12	15	18	21	24
May 26—27, 1977	Cisco	S								—
		B								1
	Herring	S								1
		B								—
	Smelt	S	—	—	—	—	—	—	—	—
		B	16	1	4	—	11	4	—	5
July 23—24, 1977	Cisco	S	8	—	—	—	—	—	3	5
		B	—	3	3	6	2	—	—	—
	Herring	S		—						2
		B		1						—
	Smelt	S	—	—	—					1
		B	2	3	1					—
Oct. 3—4, 1977	Cisco	S	20	14	—	—	—	3	16	17
		B	131	108	53	36	34	46	85	90
	Herring	S	17	4	—	2	1	1	15	15
		B	2	5	5	2	9	—	1	1
	Smelt	S	—	—	—	—	—	—	—	—
		B	1	6	—	—	2	6	3	4

contents at the beginning and the end of the interval. R is the evacuation rate, which is assumed to be exponential.

III. RESULTS

The fishing station A and the transect E are shown in Fig. 1.

The net fishing carried out in 1977 was not a success. The number of ciscoes caught was 1, 30 and 653 on the three different occasions (Table 1). This was either too many fishes or too few. In addition, Table 1 indicates vertical migration by the fish, which is also shown in the echograms from 1978 (Figs. 2, 3).

The vertical distribution of *Bosmina coregoni maritima* (P. E. MULLER), *Daphnia cristata* (G. O. SARS), *Eurytemora* spp., *Limnocalanus grimaldii* (DE GUERNE) and *Cyclops* spp. on each sampling occasion during the four 24 hour fishing periods in 1978, together with the cisco stomach contents are shown in Figs. 4—7.

The zooplankton also show a vertical migration, with *Bosmina*, *Daphnia* and *Eurytemora* moving up to the surface in the evening and down again into deeper water in the morning. *Limnocalanus*, a cold stenothermal species, also migrates upwards in the evening but has not been found at depths less than 5 m from the surface.

The *Cyclops* group probably represents species, as on the Finnish side of the Bothnian Bay (VALTONEN *et al.* 1978) and consists of both warm and cold stenothermal species. The distribution of this group does not clearly indicate migrations, as can be seen.

Figs. 4—7 also give a hint of the biomass variation within and between species.

The variations in stomach content with time, for each one of the 24 hour fishing periods are presented in Fig. 8.

To estimate the gastric evacuation rate, the stomach contents of a species or a genus are followed (Fig. 8) from one sampling occasion to the next as soon as the amount starts to decrease. The value of 100 per cent is when the amount is at its greatest and thereafter, contents are expressed as percentages of the starting amount. The resulting plot is found in Fig. 9. The gastric evacuation rate is then used to calculate the consumption.

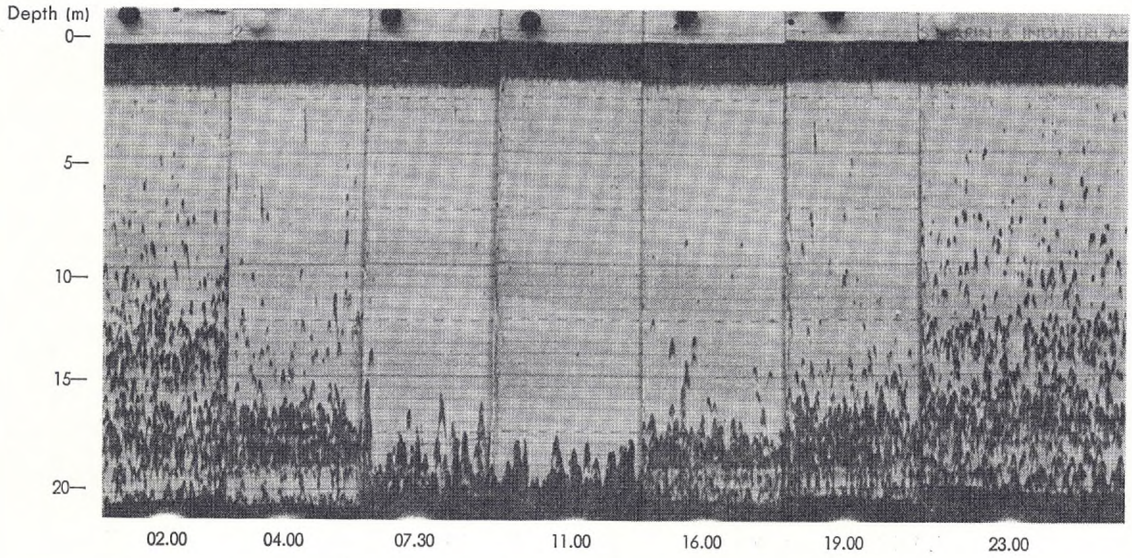

Fig. 2. Echo sounder tracings at different hours along transect E, week 36, 1978.

The consumption of different types of zooplankton is compared with the amounts of the respective zooplankton species present in Fig. 10.

The total consumption during 24 hours in per cent of the fish weight is shown in Fig. 11. Both values are given in terms of dry weight, which is for cisco assumed to be 25 per cent of the wet weight (*Coregonus artedii* varies between 37.4—18.7 per cent, SIDWELL *et al.* 1974). In reality, this varies with time. The corresponding value for zooplankton was observed to have a mean of 12 per cent ($\bar{x}=11.7$, S.E. 0.84).

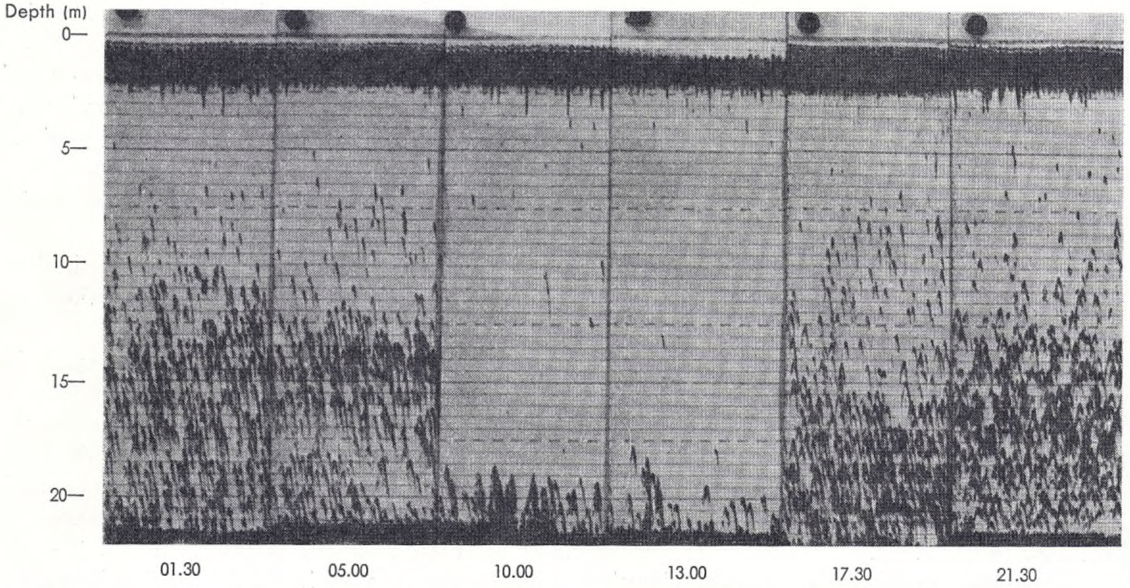

Fig. 3. Echo sounder tracings at different hours along transect E, week 41, 1978.

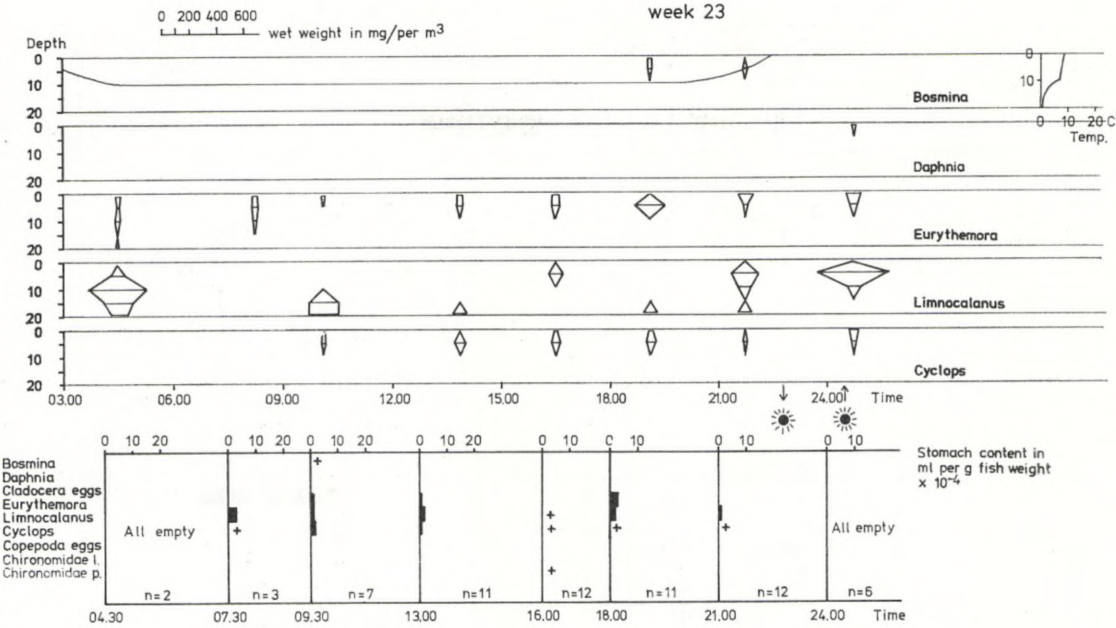

Fig. 4. The vertical distribution of adult zooplankton in mg per m³ and the stomach content of cisco in ml per g fish weight · 10⁻⁴ on each sampling occasion during June 8—9, 1979. The vertical distribution of cisco as inhabiting the area below the solid line in the "*Bosmina*" diagram is given as well as the temperature profile and the times of sunset and sunrise.

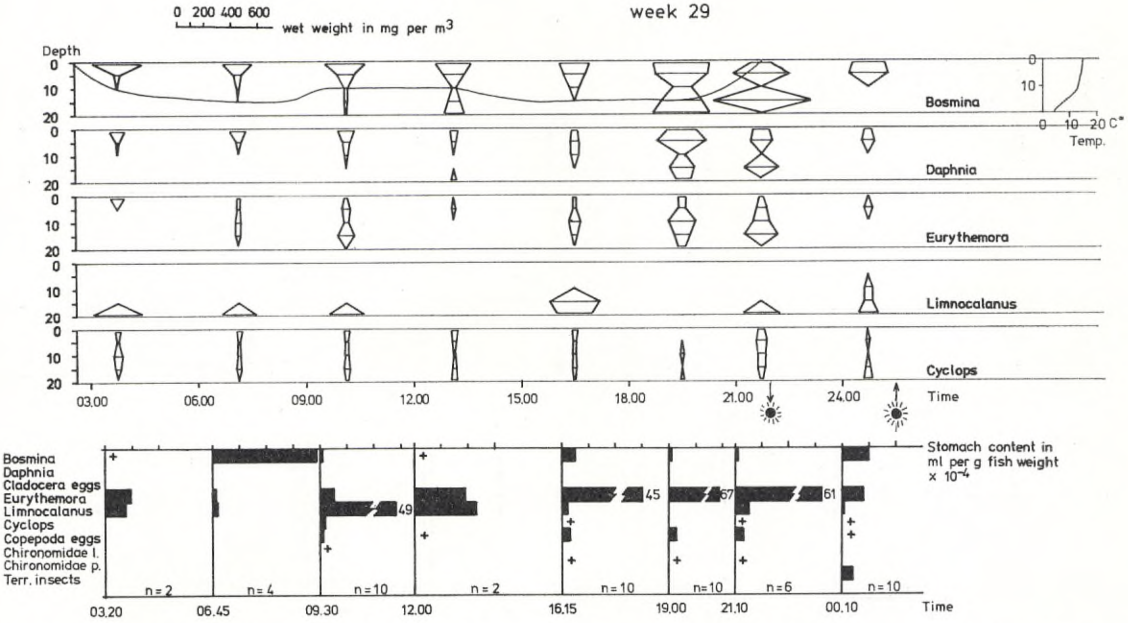

Fig. 5. The vertical distribution of adult zooplankton in mg per m³ and the stomach content of cisco in ml per g fish weight · 10⁻⁴ on each sampling occasion during July 22—23, 1978. The vertical distribution of cisco as inhabiting the area below the solid line in the "*Bosmina*" diagram is given as well as the temperature profile and the times of sunset and sunrise.

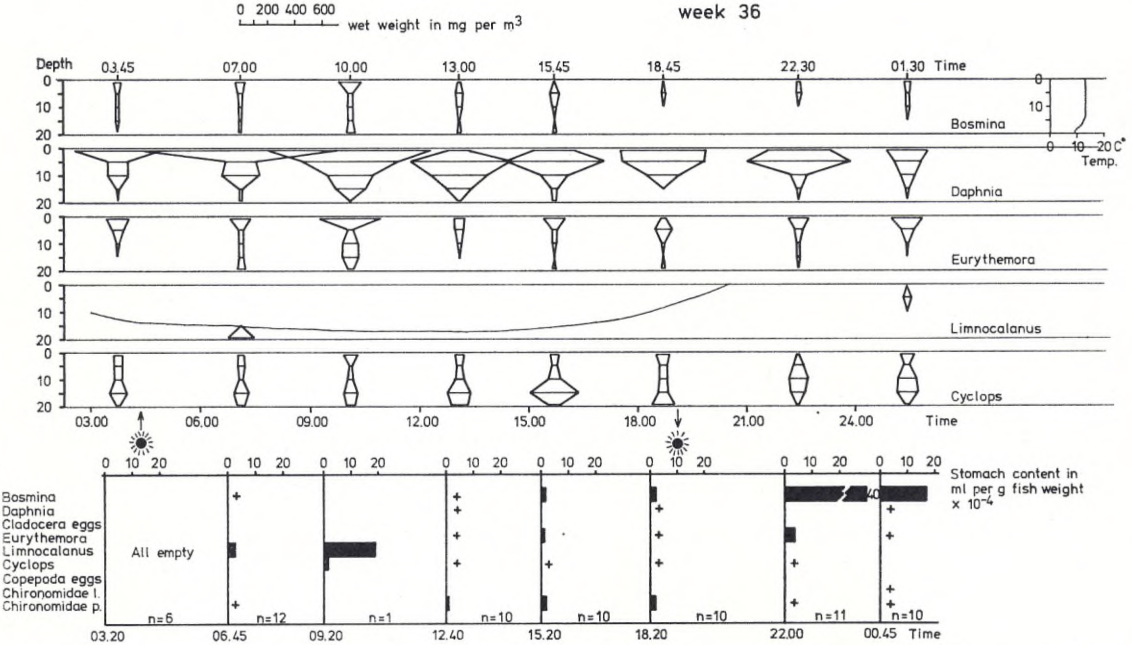

Fig. 6. The vertical distribution of adult zooplankton in mg per m³ and the stomach content of cisco in ml per g fish weight · 10⁻⁴ on each sampling occasion during September 4—5, 1978. The vertical distribution of cisco as inhabiting the area below the solid line in the "*Limnocalanus*" diagram is given as well as the temperature profile and times of sunset and sunrise.

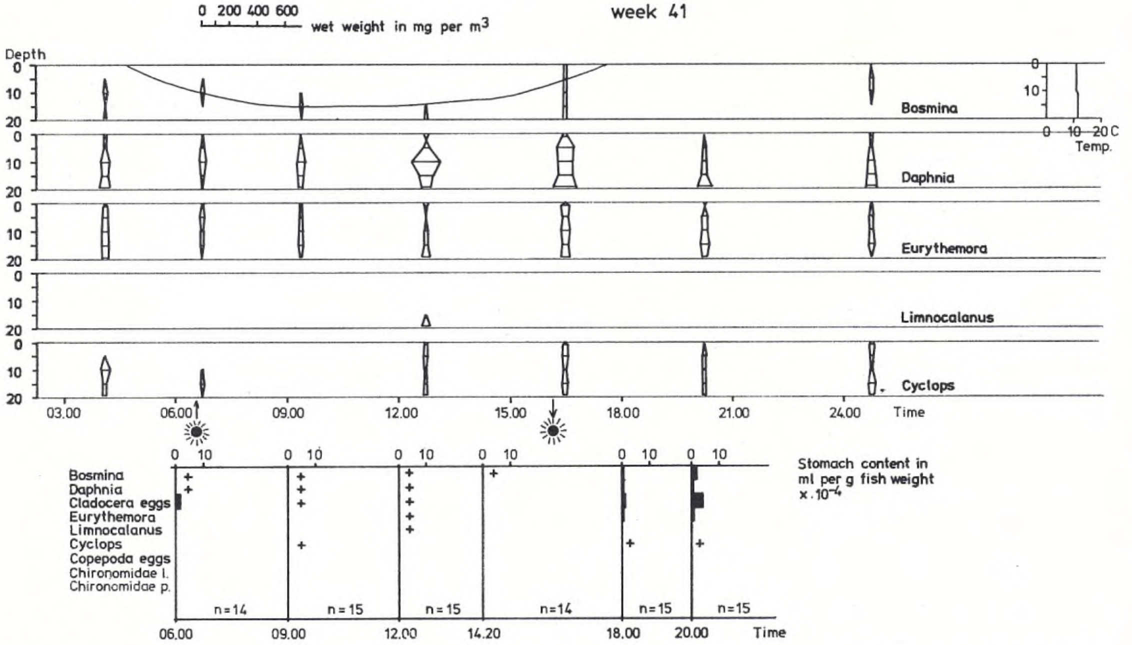

Fig. 7. The vertical distribution of adult zooplankton in mg per m³ and the stomach content of cisco in ml per g fish weight · 10⁻⁴ on each sampling occasion during October 10—15, 1978. The vertical distribution of cisco as inhabiting the area below the solid line in the "*Bosmina*" diagram is given as well as the temperature profile and the times of sunset and sunrise.

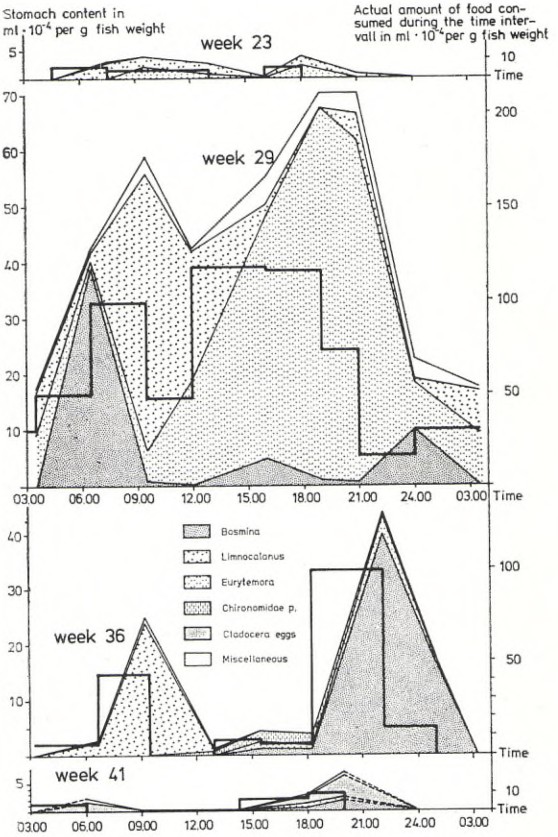

Fig. 8. The diel variation in stomach content and composition in ml $\cdot 10^{-4}$ per g fish weight and the food consumption (solid horisontal or vertical line) during the time interval in ml $\cdot 10^{-4}$ per g fish weight.

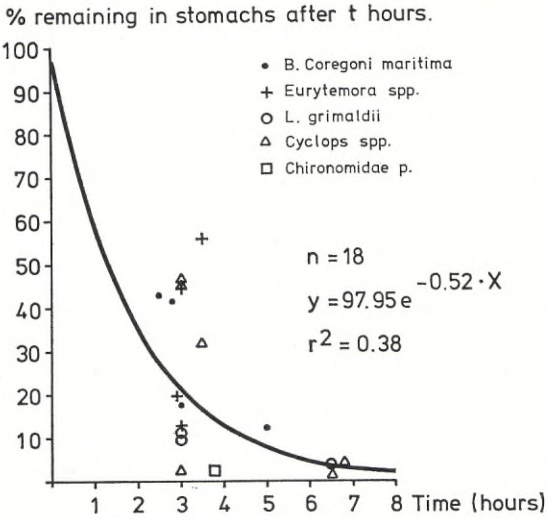

Fig. 9. The decrease in the amounts of different food items in stomachs of cisco has been followed during a period of time and plotted to give the gastric evacuation rate. An exponential curve has then been fitted to the data. The equation for the curve together with the coefficient of determination are also given.

IV. DISCUSSION

When and where

As early as 1919 it was suggested (Järvi 1919) that the migration by cisco up to the surface of lakes during the evening was connected with the zooplankton migration.

That cisco undertake diel vertical migrations from deep waters up to the surface in the evening and back again in the morning is shown in many Swedish lakes (Northcote and Rundberg 1970, Almer and Larsson 1974, Nilsson 1974, Almer 1978, Hamrin 1979). Table 1 and Figs. 2—3 suggest that the cisco in the Bothnian Bay have similar habits during the ice-free season.

The diel vertical movements of zooplankton are also well documented (Hutchinson 1967) and Figs. 4—7 show that the migration by zooplankton in the Bothnian Bay is no exception. If these migration observations are used to put together a model it should be the following: The cisco and *Limnocalanus* leave the bottom at about the same time in the afternoon or evening, probably triggered by the light conditions. On the way up to the surface the cisco eats a few *Limnocalanus*. When the fish reaches the waters just beneath the surface the zooplankton groups *Bosmina*, *Daphnia* and *Eurytemora* are already concentrated there. The cisco can with a minimum of effort feed on this concentration as well as on terrestrial insects caught at the surface, as long as there is sufficient light. In the morning, as light levels increase, the fish starts to migrate downwards again with the zooplankton. On the way down, the cisco meets *Limnocalanus*, which, liking cold water, has stayed in or under the thermocline. The cisco feeds on *Limnocalanus* as they both continue on their way down to the bottom.

During the day the cisco stays close to the bottom, while *Limnocalanus* is even closer to

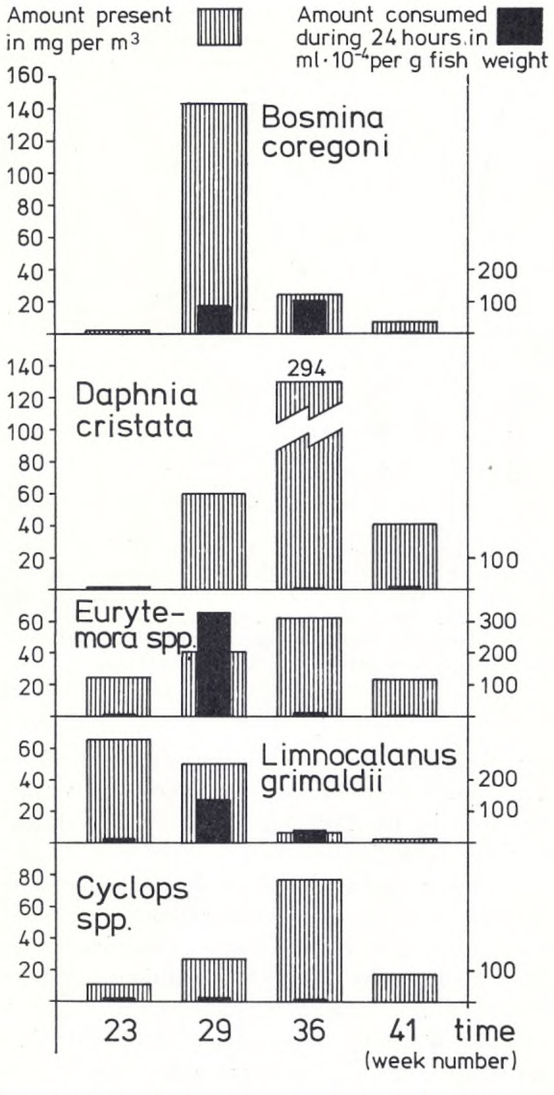

Fig. 10. The amounts of five types of zooplankton present in mg per m³ (striped bars) and the amounts of the respective zooplankton type consumed during 24 hours as ml · 10⁻⁴ per g fish weight (black bars).

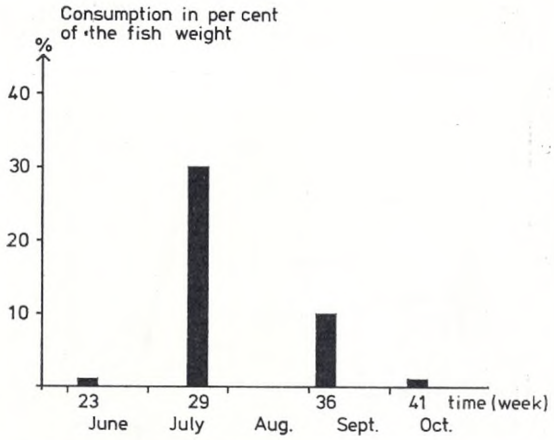

Fig. 11. The food consumption (dry weight) in per cent of the fish weight (dry weight) during 24 hours.

the bottom and out of view of the cisco. In cisco the best visual acuity is found in the ventro-temporal part of the retina (AHLBERT 1969). The other zooplankton groups, *Bosmina, Eurytemora* and *Daphnia*, are now so dispersed in the entire water column that it is not economical for the cisco to go hunting. When not feeding, the most economical behaviour for a fish is to remain stationary in the coldest water (BRETT and HIGGS 1970).

Before looking at the results in Fig. 8, the critique of field methodology for determining fish feeding periodicity by JENKINS and GREEN (1977) must be discussed, in order to verify the validity of the model.

They stress the need to test the results statistically with a one way analysis of covariance. The reason is that the variation in mean stomach content (as in Fig. 8) is often not a true variation, due to a large standard deviation.

Table 2. *The result of a one way analysis of covariance whether or not the variation in stomach content of the three main food items from sampling to sampling are true (significant) or not.*

1978 Week		*Limnocalanus* sp.	*Eurytemora* spp.	*Bosmina* sp.
23	F(7.55 df) =	3.15***	3.35***	—
29	F(7.45 df) =	4.00***	3.35***	1.79
36	F(7.61 df) =	12.42***	—	10.82***

The result of the statistical analysis (one way analysis of covariance) of the material in Fig. 8 for each main species shows that the feeding activity can be considered to be discontinuous with time, except for *Bosmina* during week 29 (Table 2).

The results shown in Fig. 8 can then be said to verify the model of the cisco's diel feeding and can be summarized for weeks 23, 29 and 36 as: Breakfast consisting of *Limnocalanus*, no lunch, dinner at the surface consisting mostly of *Eurytemora* and *Bosmina* and sometimes when the weather is good, supper composed of terrestrial insects (Fig. 8).

The pattern is also repeated for week 41 in 1978 (Fig. 8) but is not in correspondence with the results from week 40 in 1977 when the fish fed from 6 a.m. to 3 p.m., that is to say, they had a brunch (breakfast-lunch). My explanation for this discrepancy is that the fish had difficulties in feeding during the bad weather that forced us to make a break for a few days. When it became calm again, late in the evening a few days later, the fish were starved. With the help of a bright full moon they could start feeding again at the same time as we restarted our dynamite fishing. The light of a full moon is reported to be sufficient for herring to feed in (JOHNSSON 1939) and obviously this is even so for cisco.

The feeding pattern given in Fig. 8 for week 41 in 1978 is therefore probably an exception and the 1977 result with a brunch is the normal pattern in October when the daylight period is short.

The patterns for week 29 in 1977 and 1978 are very similar both as regards foodtype and feeding time.

What

The cisco in the Bothnian Bay feeds mainly on *Bosmina*, *Eurytemora* and *Limnocalanus*. The presence of these zooplankton as well as *Daphnia* and *Cyclops* and the amounts of the respective species or groups of species consumed are presented in Fig. 10. The picture is confusing. If IVLEV's electivity index (IVLEV 1961) applies a food species can be avoided one week and at other times highly selected.

Comments have been made on IVLEV's electivity index for different reasons (O'BRIEN and VINYARD 1974, STRAUSS 1979). I should like to say that in the stable ecosystem of the Bothnian Bay there is no electivity.

It is well documented (NILSSON 1978) that a fish species introduced into a fish-free lake or the introduction of a more "efficient" zooplankton eater will upset the entire zooplankton community. Large forms will be grazed down and eradicated and replaced by new smaller ones. It is also known that in similar stable ecosystems the zooplankton community has a different species composition according to which species of planktivorous fish are present.

Why does eradication stop at a certain level? Why is not all zooplankton consumed? I think that it is because zooplankton is grazed down to a visibility limit. Which level the system ends up at is dependent on the vision of the predator. The reason that the fish does not then starve to death when all the visible forms are consumed is that it is important for the zooplankton to be as large as possible (HALL and THRELKELD 1976).

It is advantageous to be large but not to be eaten. In a stable system the zooplankton balances on the edge of the predator's vision and when they are found in the predator's stomachs it is because they have made the mistake of being visible and not because they were "elected".

Many factors influence the visibility of zooplankton to fish. As we do not know what the fish sees it is difficult to evaluate these factors. ZARET and KERFOOT (1975) showed that the pigmented parts of *Bosmina* and *Ceriodaphnia* rather than the size of their bodies influenced their mortality. Habitat and prey movements are also important factors.

Eurytemora is heavily preyed upon in week 29 (Fig. 12) but otherwise it manages to avoid predation quite well. What happened during this week was that females carrying egg sacs were found in the cisco stomachs.

Egg sacs, eggs and ephippiae are reported to increase the vulnerability of zooplankton tremendously (VALLIN 1969, SANDSTRÖM 1979). The factors behind this could be either the increased pigmentation or lowered mobility. SANDSTRÖM reports that a very common observation when studying zooplankton in the northern region of the Baltic is that there are more male than female *Eurytemora*. The transparent *Daphnia cristata*, the smallest species of *Daphnia* in Sweden, is hardly ever found in the stomachs except when they are carrying ephippiae, as in week 41.

Limnocalanus, a large zooplankton, probably avoids eradication because of the habitat it occupies.

Bosmina is eaten most of the time but it is the large adult animals which are found in the stomachs. These are probably animals that have already served their purpose in the *Bosmina* community and are on their way out (Fig. 8).

The *Cyclops*' species are known to jump out of the binocular field of the predator (LINDSTRÖM 1955). They obviously manage to do so very well.

There are two more zooplankton species that can sometimes be found in plankton samples as well as in cisco stomachs, namely *Podon* sp. and *Evadne nordmanni* (LOVÉN). Both have strikingly large eyes. But their small numbers do not necessarily mean that they are too visible, as it may also be that the water is not saline enough for their liking.

The cisco in the Bothnian Bay inhabit a stable ecosystem. The organisms in it have adapted themselves to each other over a long period of time. I cannot believe that the ciscoes move around choosing or selecting their food items. Instead, they have to eat whatever they can see as fast as they can.

Life is tough for a cisco!

How much

The gastric evacuation rate, necessary for the estimation of food consumption has been difficult to determine. There are many methods (WINDELL 1978) both for field and laboratory use. The most accurate measurements are made in laboratories but they are, on the other hand, difficult to translate into values which apply to the fish in natural conditions. The method used here is carried out under natural conditions but has two important drawbacks. The first one is that it is assumed that the fishes have stopped eating particular food item after the sampling occasion when the amount in the stomachs was set at 100 per cent. The second one is that different fishes are used each time and as the number of fishes on each sampling occasion is small, the individual variation in stomach content causes the results to be biased.

There are many more factors affecting the gastric evacuation rate, such as temperature, fish size, meal size, meal successions, food particle size, food digestibility and fat concentration.

These factors are not considered here as my intention was only to obtain a rough mean value for natural conditions.

The gastric evacuation rate is exponential for a number of species (ELLIOTT and PERSSON 1978). This type of curve is also the one that fits my data best (exponential $r=0.62$, linear $r=0.52$, logaritmis $r=0.52$). The calculated value for the gastric evacuation rate (R) will thus be 0.52 or in other words: 50 per cent of the food consumed has left the stomach after 1 hour and 20 minutes. This is a very fast rate. The fastest similar figure for adult fish is given by WINDELL (1978) as 3 hours for Pacific mackerel (*Scomber japonicus*). However, this is not very fast compared to rates for fry feeding on zooplankton (NOBLE 1973).

I have only found two values for the gastric evacuation rate in cisco in the literature. One is given by HAKKARI (1978) who recorded a much slower rate, but our values are not directly comparable as we have used different methods. The other is from HAMRIN (1979) who says: "After about 6 hours at 8°C only 5 per cent of the foodorganisms remained". This is very similar to my findings.

The conclusion is that the gastric evacuation rate for cisco is very rapid and probably facilitated by the food type used (small items provide a large surface area) and the necessity of taking advantage of the few occasions on which visible food is superabundant. As the estimation of the daily rates of food consumption (Fig. 11) is based on the gastric evacuation rate the same reservations must be made as to the validity of the values.

The results of the estimation is that the consumption during 24 hours is very low in weeks 23 and 41, about 1 per cent of the body weight (Fig. 11). The value is probably even lower as the water temperature at this time was lower than that used when estimating the evacuation rate.

Values from week 29, show a tremendous consumption of about 30 per cent of the cisco's body weight in 24 hours. The presence of numerous *Eurytemora* sp. carrying egg sacs and an optimum water temperature are probably the reasons.

The water temperature in week 36 is similar to that in week 29, but the amounts of visible zooplankton present are probably smaller and the consumption is only about 10 per cent of the body weight.

HAKKARI (1978) gives the daily food consumption of cisco during the summer in Keitele as 1.9 per cent of the body weight, but with different gastric evacuation rates it is natural that the consumption figures also should differ.

My figures are more in accordance with the mean food intake of young herring, which varied between 8.1 and 12.6 per cent of the body weight at 14.5°C and between 3.5 and 5.0 per cent at 6.5°C (DE SILVA and BALBONTIN 1974).

The explanation for why the cisco is so successful, that was promised in the introduction, is that the cisco is highly specialized. It is planktivorous all of its life and its entire morphology is specialized so as to make it an efficient zooplankton eater. Its vision and its ability to take advantage of the few occasions on which visible food items are numerous with the help of a rapid gastric evacuation rate are especially well developed.

The price the cisco has to pay is that it cannot be a large fish. In the Bothnian Bay the total length of the cisco rarely exceeds 200 mm.

V. SUMMARY

The populations of zooplankton found in a stable ecosystem are populations that the fishes in the same system only utilize to a certain extent or not at all, because the zooplankton are, entirely or for most of their lifes, invisible to the fish. There are many strategies for staying invisible, such as being small, having a high transparency, choosing a suitable habitat, migrating or jumping out of the predators field of vision.

Zooplankton easily spotted by the fish are rapidly eliminated from the system and those left are zooplankton that for reasons to do with interspecific competition have to be as large as possible in order to be successful but at the same time invisible to their predators.

Sometimes the zooplankton fail in this balancing act and it is at these times that the fish can feed on them. As these occasions are sometimes brief and usually occur at certain periods, a successful zooplankton eating fish must have the ability to utilize these abundances of food to a maximum. One way of doing so is to have a very rapid and efficient digestive system, which I think the cisco has.

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Results of Introductions of New Fish Food Organisms into Swedish Lakes

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ABSTRACT

Mysis relicta was introduced to 61 lakes in Sweden. 50 new populations have been established and there are several developing populations in downstream waters. The most common reason for failure was acidified lakes. Several studies have been published about the impact on the ecosystem and especially on fish.

Pallasea quadrispinosa was introduced on 25 occasions of which 16 were successful. The main reason for failure was that lakes were probably stocked with too few animals. These experiments started later than those with *Mysis*. The effects on fish seem to be generally more positive than if *Mysis* had been used but it is yet too early to make any final conclusions.

Reproduction has been recorded in 3 lakes with introduced *Gammaracanthus lacustris* but a population has been established in only one of them. In this particular lake there is no *Mysis* population but there are dense populations in the other two.

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I. INTRODUCTION

Experiments to introduce some indigenous crustacean fish food organisms into new localities started in 1954 but were discussed already as early as 1947 (RUNNSTRÖM 1949). Most early attempts were unsuccessful and functional methods were not developed until 1964. The first successful introductions were undertaken in 1966 (FÜRST 1967). In the same year a new law was instituted which restricted free introductions but despite this the water courts have prescribed several introductions while at the same time declaring a decision to impound and regulate the water level of the lake. In many cases the court was influenced by the positive effect on fish in other lakes.

Permission for introductions is very restrictively given by the National Swedish Board of Fisheries. These restrictions, however, have not been enough to inhibit a few private introductions but it is to be hoped that so far most of them have been recorded. Permission is still only given for experimental purposes. Sufficient time must elapse before the full effects of the various introduced animals on the different types of ecosystems can be studied.

The purpose of most attempts to introduce new fish food organisms is described earlier in detail (FÜRST 1965, 1972 a). In these cases the lakes were impounded and the water level was allowed to be regulated within greater ranges than normal. This entailed damage to the littoral bottom fauna with a resulting reaction on the fish populations. *Mysis relicta* LOVÉN, *Pallasea quadrispinosa* G. O. SARS and *Gammaracanthus lacustris* G. O. SARS 1861 were used in these experiments. *Limnocalanus macrurus* G. O. SARS was used unsuccessfully in one case and *Lepidurus arcticus* PALLAS successfully in another. There are plans to experimentally introduce *Pontoporeia affinis* LINDSTRÖM.

Other experiments in natural lakes are in progress. There is always a public demand for "improvements" in such lakes. Common problems, however, are *e.g.* slow growth, stunted popula-

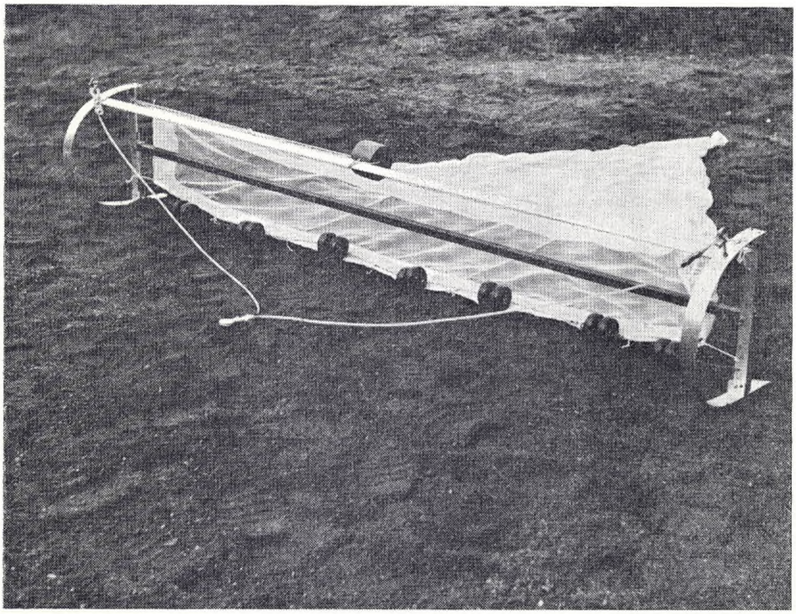

Fig. 1. Beam trawl, two metres wide used for catching *Mysis* and *Pallasea* or *Gammaracanthus*. Weight about 6,000 gram (modified after FÜRST 1965).

tions, low condition and bad meat quality or high frequencies of parasites. Fish species are usually brown trout (*Salmo trutta* L.) or Arctic char (*Salvelinus alpinus* L.). Food organisms in these lakes are *Mysis* or *Pallasea. Gammarcanthus* has been introduced in one unsuccessful case.

The natural distribution of the crustacean "glacial relicts" *Mysis*, *Pallasea*, *Gammaracanthus*, *Pontoporeia* and *Limnocalanus* is limited to the area below the highest shoreline of the former Baltic Sea (about 10,000—4,000 B.C.) (Fig. 2). It is normal to find one or several species of glacial relicts in almost any lake below the highest shoreline. On only one occasion was a population (*Pallasea*) recorded above this line (NYBELIN 1931). In that particular case the animals had been able to swim against the very slow current.

Lepidurus is originally found only in lakes in the high mountains in the northwest. The local distribution seems to be patchy.

II. MATERIAL AND METHODS

Mysis and *Pallasea* were collected using a beam trawl (Fig. 1 modified after FÜRST 1965). It was towed on the bottom during daylight to catch *Mysis* and at night to catch *Pallasea* which leaves the bottom at night and swims just above it. *Gammaracanthus* was collected by professional fishermen. The animals attach themselves to balls of *Chara* or *Nitella* which roll on the bottom and become stuck in the gill nets.

Transportation of *Mysis* was undertaken in plastic bags containing both water and oxygen and at a density of about one thousand individuals per litre of water. Temperature and duration of transport were strongly related to survival. If possible temperatures should not exceed 12° C. *Pallasea* and *Gammaracanthus* were transported in heat insulated bags on layers of moist sack-cloth tightly supported by frames. As a rule 50,000—100,000 *Mysis* or 20,000 *Pallasea* or *Gammaracanthus* were stocked in one lake.

The donor lakes (Fig. 2) were chosen as close as possible to the receivers. The electrolyte contents of the lakes cannot be too different otherwise acclimatization of *Mysis* has to be undertaken. The other species are less sensitive in this respect.

Collections were made in autumn when temperatures had decreased and before the fish spawning period began in order to avoid introductions of undesired fry or fish-eggs. In many cases "new"

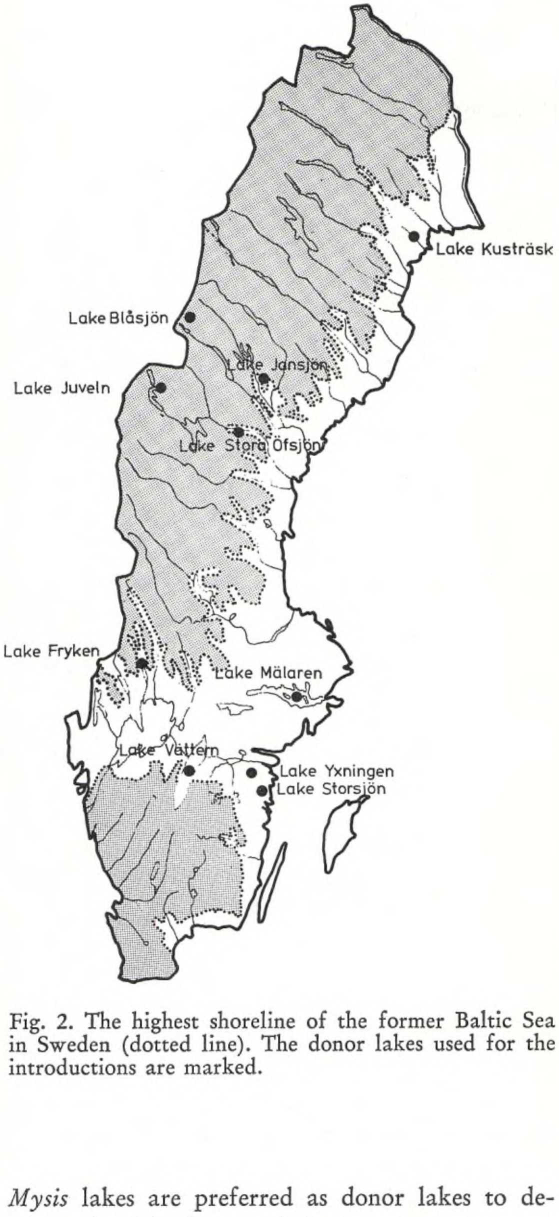

Fig. 2. The highest shoreline of the former Baltic Sea in Sweden (dotted line). The donor lakes used for the introductions are marked.

Mysis lakes are preferred as donor lakes to decrease the risk of transmitting parasites.

Inventories were made two years or later after stocking with *Mysis*. A small beam trawl was towed by boat or a drifting aircraft. It is important to feel from the towing line that the trawl maintains continuous contact with the bottom. Stomachs of Arctic char or burbot (*Lota lota* L.) collected in winter were especially suitable for inventories of *Mysis*. Traps with bait were occasionally used to catch *Pallasea*.

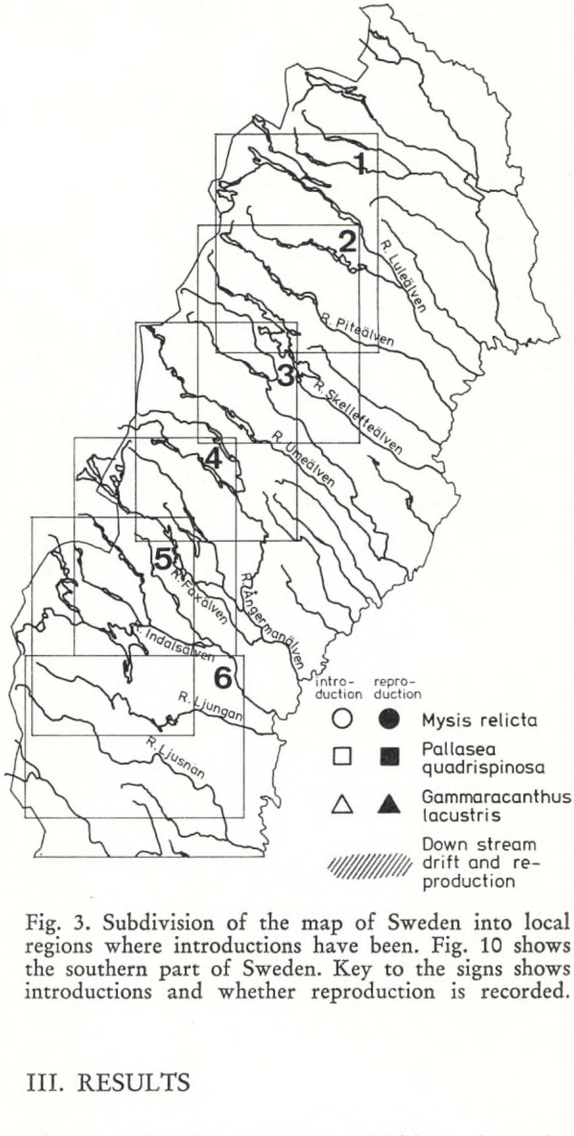

Fig. 3. Subdivision of the map of Sweden into local regions where introductions have been. Fig. 10 shows the southern part of Sweden. Key to the signs shows introductions and whether reproduction is recorded.

III. RESULTS

The maps in Figs. 3—10 and Table 1 show the introductions in Sweden up to 1981. Table 2 gives data about the lakes and Table 3 about fish species in the same lakes.

Mysis relicta was introduced to 61 lakes and has established new populations in 50. In two cases the inventories were insufficient to draw any conclusions (Lakes Övre Oldsjön and Tjärn at point 591) but nine cases were definitely unsuccessful. The reasons for the failures are not known in three cases (Lakes Vaimok, Gardejaure and Lillsjougden) but in another two cases the stocking was insufficient (Lakes Storsjön in Härjedalen and Glim-

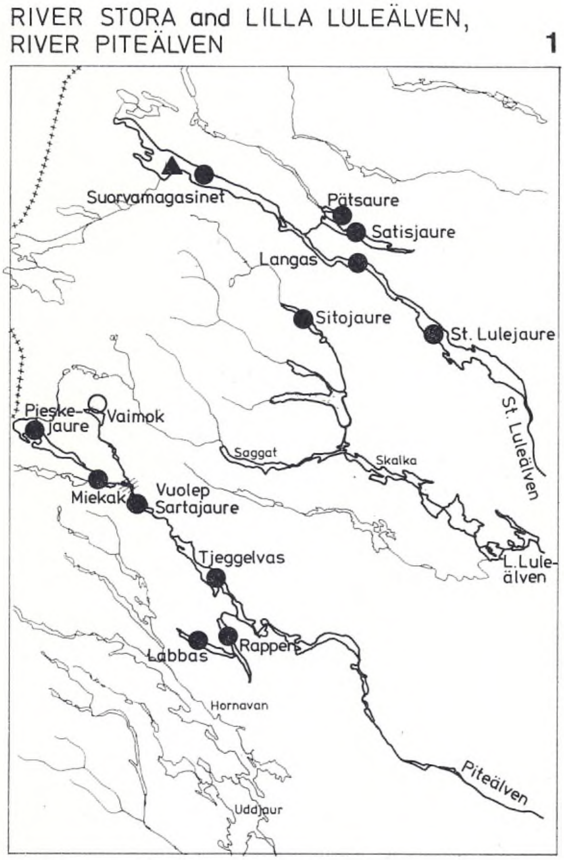

Fig. 4. Introductions in Rivers Stora and Lilla Luleälven and in River Piteälven. Reproduction of *Gammaracanthus* was recorded in Lake Suorvamagasinet but in all only two specimens were found. All recorded *Mysis* populations are very dense. In Lake Pieskejaure a population of *Lepidurus arcticus* has now been established.

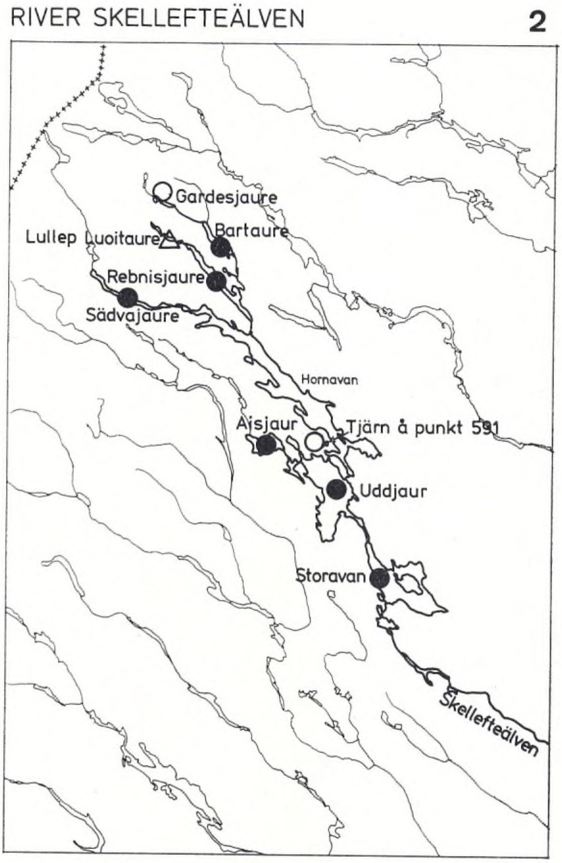

Fig. 5. Introductions in River Skellefteälven.

mingen). The pH was probably too low in the following three lakes:

Lake Stora Mjölkvattnet: An exception among many lakes in the area in that no *Daphnia* species are found (*Lötmarker* 1965). The lake was originally slightly acid. pH was 5.8 on August 8, 1934 (Lundqvist 1936).

Lake Glensjön: During most of the year this lake has a sufficient pH but there is probably a decrease when snow is melting.

Lake Östra Nedsjön: This lake became acidified during the period following the introduction of *Mysis* which never became established. pH was 6.1 (November 26, 1968) and 5.5 (December 17, 1970) respectively.

Another lake, Glimmingen was used in a special experiment. Eggbearing females of a summer breeding *Mysis* population from Lake Yxningen were introduced in an effort to prove whether summer breeding is a genetically fixed phenomenon (Fürst 1972 b, c). Only 1,500 females were introduced and this number was probably too low.

In several rivers *Mysis* has drifted downstream and successively established new populations. This is obvious in the Rivers Fjällsjöälven, Faxälven and Indalsälven (Figs. 7 and 8). In the Faxälven river, *Mysis* was introduced for the first time in Lake Blåsjön in 1964 (Fürst 1972 a). Since then it has spread considerably. In the Indalsälven river it was first introduced in 1957 in Lake Torrön and

RIVER UMEÄLVEN, RIVER ÅNGERMANÄLVEN **3**

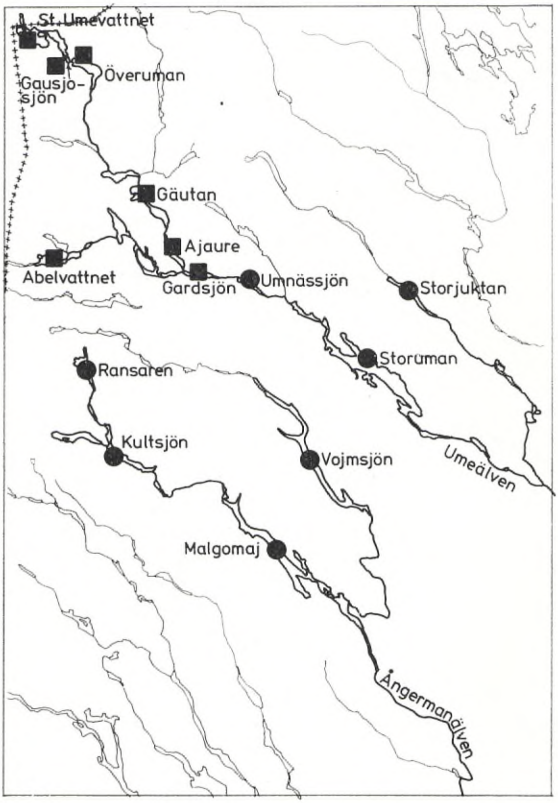

Fig. 6. Introductions in River Umeälven and River Ångermanälven.

by about 1975 had spread down to the highest situated original *Mysis* population below the highest shoreline. No inventories have yet been made in the other rivers but it seems only a matter of time before *Mysis* will have spread down through all of them.

Pallasea quadrispinosa was introduced to 25 lakes and populations have been established in 16. In two of the cases where stocking failed the reason seemed to be that too few animals were used (Lakes Torrön and Näckten). In another two cases the lakes were not suitable in the respect that the water was almost completely drained once a year (Lakes Höljesmagasinet and Stora Stensjön). The reasons for the failure in three other lakes are not, however, known (Lakes Rörvattnet, Östra Rörtjärn and Storrörmyrtjärn and the inventories are insufficient in Lake Bolmen).

RIVER FJÄLLSJÖÄLVEN, RIVER FAXÄLVEN **4**

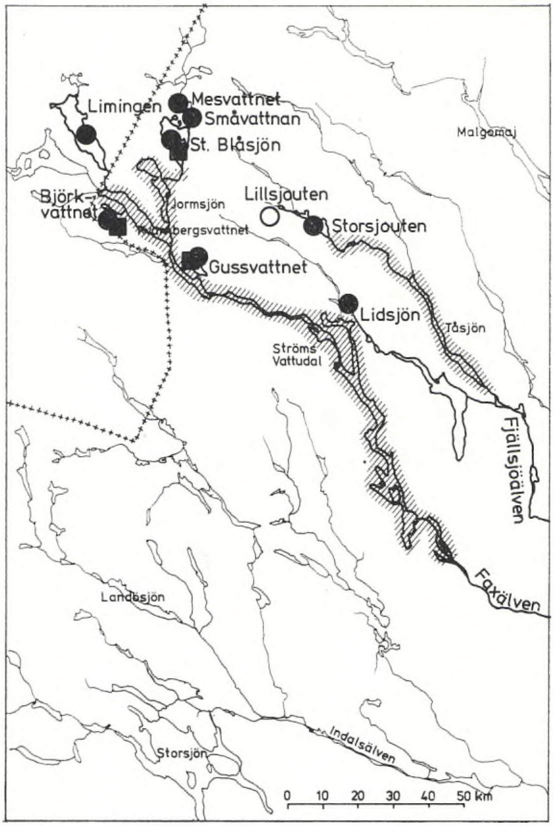

Fig. 7. Introductions in River Fjällsjöälven and River Faxälven. An introduction of *Limnocalanus macrurus* in Lake Kvarnbergsvattnet failed.

There has not been any study of the downstream distribution of *Pallasea*. The introduction of this species started later than the *Mysis* introductions and the development of the populations also seems to be slower.

Gammaracanthus lacustris was introduced in five lakes and reproduction was recorded in three of them (Lakes Suorva, Kultsjön and Håckren). One lake (Höljesmagasinet) was drained almost completely every year and this could explain why no findings were made. One case of failure cannot, however, be explained (Lake Lullep Luoitaure).

In Lake Håckren a population was well established parallel to a new *Pallasea* population. *Mysis* was not introduced here. In Lake Kultsjön reproduction was recorded but in the years fol-

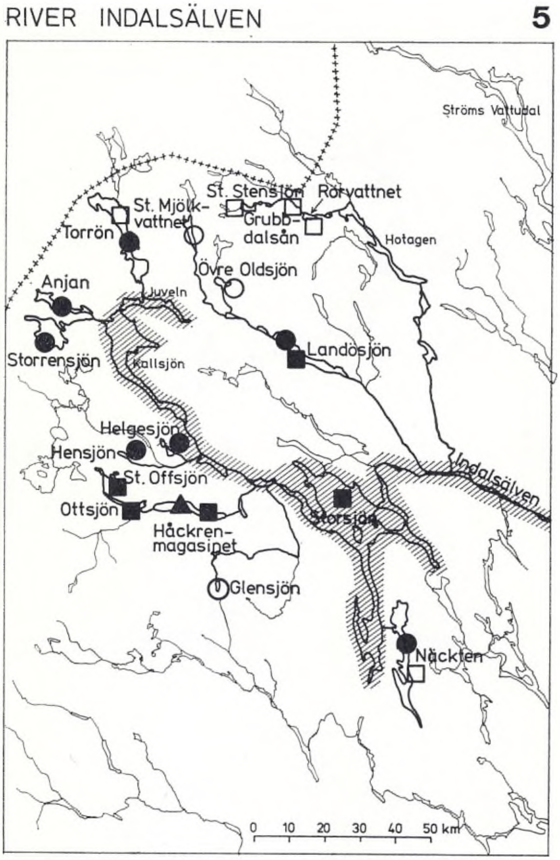

Fig. 8. Introductions in River Indalsälven. *Gammaracanthus* has established a dense population in Lake Håckrenmagasinet and has spread down to Lake Storsjön. In the former lake there is no *Mysis* population but *Pallasea* is present.

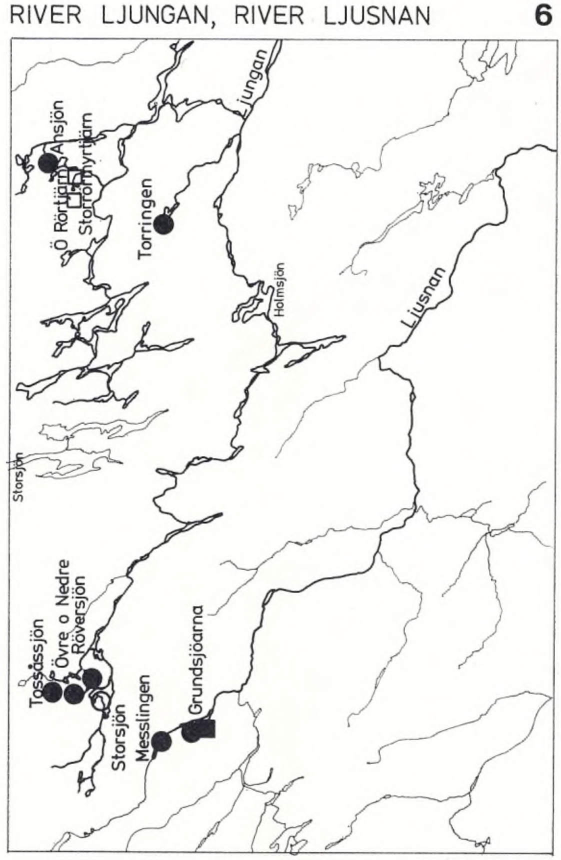

Fig. 9. Introductions in River Ljungan and River Ljusnan.

lowing the introduction only one single small *Gammaracanthus* has been found. In spite of several later inventories made by trawling or trapping or by studying fish stomachs, no more findings were made. In this lake a very dense *Mysis* population has developed. The same has occurred in Lake Sourva where two *Gammaracanthus* specimens were found in a fish stomach six years after the initial introduction. Since then more than a thousand fish stomachs have been examined without any new finding. *Mysis* has developed a dense population in this lake also.

Limnocalanus macrurus was introduced to Lake Kvarnbergsvattnet in the Faxälven river on one occasion after a catch of about 8 million adults was made at a water purification station pumping water from Lake Mälaren. This copepode is known to be an important fish food especially during winter. In impounded and regulated lakes there is a food deficit during winter. The introduction unfortunately failed and will not be repeated.

IV. STUDIES OF THE IMPACT ON FISH AND OTHER ORGANISMS

A number of years must pass before the ecosystem has stabilized to such an extent that it is possible to assess the changes at all trophic levels. The speed of the changes depends *e.g.* on the area or volume of the lake and the number of fish species which are predators and have a restricting effect on the

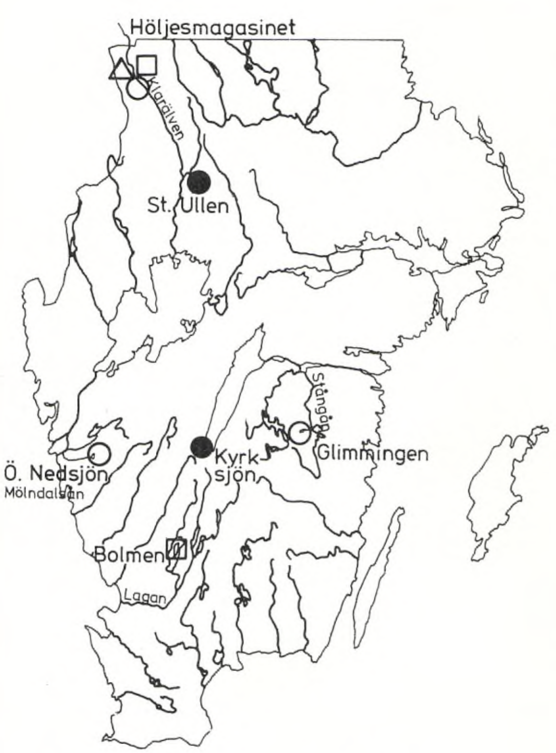

Fig. 10. Introductions in southern Sweden.

population development. If the studies concern fish populations, several generations of a fish species must evolve before any conclusions can be drawn. As yet in fact it is impossible to predict how many years must elapse before a new relatively stable situation has been established. In one of the Swedish lakes where *Mysis* was introduced in 1957 there were still changes in frequencies between fish species as late as 1979. One difficulty directly caused by the long-term run is that the intensity and kind of fishery often changes because the quality of fish generally improves considerably as a first evident result of the introductions. This induces a renewed interest in fishing which changes the basic conditions for studying the specific effect of *Mysis*.

A study was made of the impact of *Mysis* on plankton in two small lakes which were not influenced by any other known changes (KINSTEN and OLSÉN 1981). The fish populations of brown trout and char in these lakes has also been studied (OLSÉN 1980).

A report was published (FÜRST 1972 a) about some effects caused by *Mysis* in the impounded Lake Blåsjön during the first period of development. A series of reports have later been published about stages in the development which are thought to approach an equilibrium level. They concern the impact of *Mysis* on different combinations of fish species.

1) Brown trout and two species of Arctic char (FÜRST *et al.* 1978).
2) Brown trout, one species of arctic char, grayling and burbot (FÜRST *et al.* 1981).
3) Brown trout, grayling, three species of whitefish, burbot, pike and perch (FÜRST *et al.* 1980).

In general, fish species which prefer feeding on bottom living organisms to zooplankton seem to benefit from the new fish food species. The effect on pelagic zooplankton-feeding fish is more complicated to deduce and requires further investigation. *Mysis* appears to affect the zoo-plankton differently depending on the number of fish species influencing the density of the *Mysis* population.

The introduction of *Pallasea* started later than those of *Mysis* and the results of the studies of the effect on fish and other organisms will therefore be published somewhat later.

In Lake Blåsjön the *Mysis* population developed rapidly and the *Pallasea* population very slowly. One reason could be the interaction between the two species or a heavier fish predation on *Pallasea*. The birth rate of *Pallasea* is higher than that of *Mysis*. This time lapse afforded the opportunity of first studying the effect of *Mysis* alone and then of the combination of both *Mysis* and *Pallasea* (FÜRST *et al.* 1978).

The results obtained and the experience gained during the present work on the feeding habits of fish indicate that the introduction of *Pallasea* seems to be more favourable than *Mysis* in several respects, at least as an improvement in impounded lakes. It probably also has a less pronounced influence on the plankton community.

Studies on the introduction of *Gammaracanthus* have just started and as yet there is unfortunately not even a satisfying picture of the population development of the single successful introduction.

Mysis seems to be an extremely powerful and

Table 1. *Data on introduction and results of stock taking. In case of no recapture the year of stock taking is marked within parentheses.*

Lake	Donor lakes	Species	Number	Year	Recapture
River Stora and Lilla Lule älv					
Suorvamagasinet	Kusträsk	*Mysis*	150,000	1970	1974
	Vättern	*Gammaracanthus*	24,000	1972	1980
Pätsaure	Kusträsk	*Mysis*	75,000	1971	1974
Satisjaure	Kusträsk	*Mysis*	125,000	1971	1974
Langas	Kusträsk	*Mysis*	75,000	1971	(1972) 1974
St. Lulejaure	Kusträsk	*Mysis*	150,000	1971	1974
Sitojaure	Kusträsk	*Mysis*	75,000	1971	1974
River Pite älv					
Pieskejaure	Kusträsk	*Mysis*	75,000	1972	1976
		Lepidurus	200	1972	1980
Miekakjaure	Kusträsk	*Mysis*	150,000	1972	1976
Vaimok	Kusträsk	*Mysis*	75,000	1972	(1976, 1980)
Vuolep Sartajaure	Kusträsk	*Mysis*	75,000	1972	1976
Tjeggelvas	Kusträsk	*Mysis*	75,000	1972	1976
Rappen	Kusträsk	*Mysis*	75,000	1972	1976
Labbas	Kusträsk	*Mysis*	75,000	1972	1976
River Skellefteälv					
Gardejaure	Kusträsk	*Mysis*	75,000	1971	(1974, 1976, 1980)
Bartaure	Kusträsk	*Mysis*	75,000	1971	(1974) 1976
Lullep Luoitaure	Vättern	*Gammaracanthus*	5,600	1971	(1976, 1980)
Rebnisjaure	Kusträsk	*Mysis*	100,000	1973	1976
Sädvajaure	Kusträsk	*Mysis*	125,000	1971	1974
Tjärn å ptk 591	Kusträsk	*Mysis*	20,000	1971	—
Aisjaure	Kusträsk	*Mysis*	50,000	1973	1977
Uddjaure	Kusträsk	*Mysis*	50,000	1973	1977
Storavan	Kusträsk	*Mysis*	100,000	1973	(1977) 1980
River Ume älv					
St. Umevattnet	St. Öfsjön	*Pallasea*	18,000	1971	(1976) 1978
Gausjosjön	St. Öfsjön	*Pallasea*	8,000	1971	1976
Överuman	St. Öfsjön	*Pallasea*	15,000	1971	(1976) 1978
Gäutan	St. Öfsjön	*Pallasea*	27,000	1971	(1976) 1977
		Pallasea	50,000	1977	
Ajaure	St. Öfsjön	*Pallasea*	17,000	1971	1976
Gardiken	St. Öfsjön	*Pallasea*	15,000	1971	(1976) 1978
Abelvattnet	St. Öfsjön	*Pallasea*	30,000	1971	1976
Umnässjön	Jansjön	*Mysis*	110,000	1966	1969
Storuman	Jansjön	*Mysis*	122,000	1966	1969
Storjuktan	Juveln	*Mysis*	40,000	1968	1980
River Ångermanälven					
Ransaren	Blåsjön	*Mysis*	100,000	1972	1975
Kultsjön	Blåsjön	*Mysis*	100,000	1972	1975
Malgomaj	Vättern	*Gammaracanthus*	2,000	1968/69	1973 (1978)
	Juveln	*Mysis*	40,000	1968	1972
	Blåsjön	*Mysis*	100,000	1969	
Vojmsjön	Jansjön	*Mysis*	100,000	1967	1969
		Pallasea	75	1967	(1971, 1977)
Lidsjön	Blåsjön	*Mysis*	50,000	1975	(1978) 1979
River Fjällsjöälven					
Lillsjouten	Blåsjön	*Mysis*	75,000	1976	(1978)
Storsjouten	Blåsjön	*Mysis*	100,000	1970	1975
River Faxälven					
Blåsjön	Jansjön	*Mysis*	1,300,000	1964	1966

Table 1. Continued.

Lakes	Donor lakes	Species	Number	Year	Recapture
	Gesunden	*Mysis*	350,000	1964	1966
	Gesunden	*Pallasea*	100,000	1964	1970
	Gesunden	*Pontoporeia*	2,000	1964	
Mesvattnet	Blåsjön	*Mysis*		1971	1972
Småvattnet	Blåsjön	*Mysis*		1971	1972
Björkvattnet	Blåsjön	*Mysis*	50,000	1973	1978
		Pallasea		1973	1978
Gussvattnet	Blåsjön	*Mysis*	50,000	1973	1978
		Pallasea		1973	1978
Kvarnbergsvattnet	Mälaren	*Limnocalanus*	5,000,000	1961	(1975, 1977)
River Indalsälven					
Torrön	Vättern	*Mysis*	20,000	1957	
	Gesunden	*Mysis*	100,000	1965	1966
	Gesunden	*Pallasea*	4,000	1965	(1966—79)
Anjan	Vättern	*Mysis*	25,000	1959	
	Vättern	*Pallasea*	2,000	1959	(1968, 1972, 1975, 1976)
	Vättern	*Gammaracanthus*			
	Vättern	*Mysis*	500,000	1961	(1968, 1975)
	Juveln	*Mysis*	100,000	1968	(1972, 1975) 1976
St. Rensjön	Blåsjön	*Mysis*	80,000	1972	1976
Helgesjön	Juveln	*Mysis*	50,000	1968	1971
Hensjön	Juveln	*Mysis*	50,000	1968	1971
St. Offsjön	St. Öfsjön	*Pallasea*	20,000	1972	1978
Ottsjön	St. Öfsjön	*Pallasea*	16,000	1970	(1972, 1978) 1981
Håckren	Vättern	*Gammaracanthus*	27,500	1968—71	(1972) 1978
	St. Öfsjön	*Pallasea*	40,000	1969—70	(1972) 1978
Glensjön	Juveln	*Mysis*	80,000	1968	
	Juveln	*Mysis*	70,000	1971	(1974, 1978)
Storsjön	St. Öfsjön	*Pallasea*	50,000	1972	1978
Näckten	Jansjön	*Mysis*	40,000	1965	1970
	Jansjön	*Pallasea*	400	1965	(1970)
St. Stensjön	St. Öfsjön	*Pallasea*	20,000	1971	(1975, 1978, 1980)
River Grubbdalsån	St. Öfsjön	*Pallasea*	6,000	1972	(1975, 1978, 1980)
Rörvattnet	St. Öfsjön	*Pallasea*	15,000	1971	
	St. Öfsjön	*Pallasea*	6,000	1972	(1975, 1978, 1980)
St. Mjölkvattnet	Blåsjön	*Mysis*	150,000	1972	(1974, 1978)
Övre Oldsjön	Blåsjön	*Mysis*	50,000	1972	
Landösjön	Jansjön	*Mysis*	60,000	1965	1967
	Jansjön	*Pallasea*	16,000	1965	1967
River Ljungan					
Torringen	Blåsjön	*Mysis*	100,000	1971	(1974) 1978
Tossåssjön	Blåsjön	*Mysis*		1973	1979
Övre Röversjön	Blåsjön	*Mysis*		1973	1979
Nedre Röversjön	Blåsjön	*Mysis*		1973	1979
Storsjön	Mälaren	*Mysis*	200	1954	(1972)
Storrörmyrtjärn	St. Öfsjön	*Pallasea*	4,000	1972	(1980)
Östra Rörtjärn	St. Öfsjön	*Pallasea*	4,000	1972	(1980)
Ansjön	Juveln	*Mysis*		1968	1970
River Ljusnan					
Messlingen	Blåsjön	*Mysis*		1973	1978
Grundsjöarna	Blåsjön	*Mysis*		1973	1978
	St. Öfsjön	*Pallasea*		1973	1978
Lakes in Southern Sweden					
Höljesmagasinet	Fryken	*Mysis*	417,000	1965	
		Pallasea	66,000	1965	
		Gammaracanthus	51,000	1965	
St. Ullen	Rådasjön	*Mysis*	40,000	1966	1972
Glimmingen	Åsunden	*Mysis*	500	1966	(1968, 1970)
	Yxningen	*Mysis*	1,500		
Östra Nedsjön	Vättern	*Mysis*	50,000	1968	(1971)
Bolmen	Storsjön	*Pallasea*	40,000	1974	
Kyrksjön	Vättern	*Mysis*		1959	1961

Table 2. *Data about lakes with introduced fish food organisms. In some cases (Figs. 7 and 8) the organisms have spread down to other lakes Data about total water level amplitude indicates an artificial amplitude.*

Lakes	Metres above sea level	Area in km^2	Maximum depth	Impoundment, m	Draw down limit, m	Total water level amplitude, m	Year of first impondment	Year of final impondment
River Stora and Lilla Lule älv								
Suorvamagasinet	453.0	270.0	> 100.0	29.8	0.2	30.0	1927	1977
Pätsaure	647.0	5.7	> 60.0			—		
Satisjaure	457.0	85.0		19.8		19.0	1965	1966
Langas	375.0	55.0	73.0			—		
St. Lulejaure	372.0	183.0	28.0	2.5	0.6	3.1	1914	1975
Sitojaure	634.0	6.34	c 25.0			—		
River Pite älv								
Pieskejaure	577.8	59.0	89.0			1.75	1940	
Miekakjaure	490.0	1.8	33.0			—		
Vaimok	818.0	11.4	> 50.0			—		
Vuolep Sartajaure	485.0	1.35	19.5			—		
Tjeggelvas	453.0	59.0	c 50.0			—		
Rappen	488.67	25.7	c 40.0			1.42	1937	
Labbas	488.67	21.7	c 40.0			1.42	1937	
River Skellefteälv								
Gardejaure	695.0	5.2	50.5			—		
Bartaure	623.0	17.4	48.0			—		
Lullep Luoitaure	536.0	3.2	28.0			—		
Rebnisjaure	513.0	70.0	38.0	11.0	1.5	13.5	1973	1974
Sädvajaure	467.0	35.8	c 100.0	5.0	0.5	6.3	1942	1953
Tjärn å pkt 591	c 425.0	0.4	17.0			—		
Aisjaure	420.0	51.4	22.0	1.2	0.3	2.0	1935	1959
Uddjaure	420.0	200.6	16.0	1.2	0.3	2.0	1935	1959
Storavan	420.0	173.0	23.0	1.5	0.0	2.0	1935	1959
River Ume älv								
St. Umevattnet	524.6	87.5	c 60.0	3.35	1.05	4.4	1965	1965
Gausjosjön								
Överuman	524.6		83.4	3.4	1.0	4.4	1965	1965
Gäutan	c 441.2	49.0	35.0	2.35	0.0	c 2.35	1967	1967
Ajaure	440.5		37.2	19.2	0.3	19.5	1967	1967
Gardiken	395.0	84.0	80.0	17.42	2.58	20.0	1961	1961
Abelvattnet	667.6	34.0	73.8	12.8	2.8	15.6	1969	1969
Umnässjön	c 354.9	30.0	c 40.0	3.1	5.0	c 8.1	1958	1958
Storuman	352.0	150.7	135.0	3.05	3.95	7.0	1958	1958
Storjuktan	411.66	69.0	45.3	12.97	1.03	14.0	1962	1962
River Ångermanälven								
Ransaren	594.73	29.5	60.0	11.6	6.4	18.0	1956	1956
Kultsjön	542.21	59.0	140.0	2.07	2.93	5.0	1959	1959
Malgomaj	343.5	105.0	116.0	2.23	4.27	6.5	1958	1958
Vojmsjön	417.0	79.0	130.0	3.68	4.32	8.0	1948	1950
Lidsjön	c 300.0	1.3	40.0			—		
River Fjällsjöälven								
Lillsjouten	481.0		30.0			—		
Storsjouten	452.23	31.0	60.0	7.84	3.16	11.0	1948	1950
River Faxälven								
Blåsjön	436.0	43.0	145.0	2.16	11.14	13.3	1949	1958
Mesvattnet	492.0	1.38	49.0			—		
Småvattnet	495.0	0.76	28.0			—		

Table 2. Continued.

Lakes	Metres above sea level	Area in km^2	Maximum depth	Impoundment, m	Draw down limit, m	Total water level amplitude, m	Year of first impoundment	Year of final impoundment
Kvarnbergsvattnet	312.0	68.0	98.0	0.95	9.05	10.0	1940	1949
Björkvattnet	398.0	2.18	20.0			—		
Gussvattnet	313.0	9.9	60.0			—		
River Indalsälven								
Torrön	417.46	106.0	122.5	7.2	5.65	12.85	1936	1940
Anjan	423.5	30.0	56.5	3.77	5.43	9.2	1940	1941
St. Rensjön	502.85	49.0	136.0	1.76	0.34	2.1	1940	1941
Helgesjön	429.0	5.8	17.5			2.2	1916	1916
Hensjön	557.0	2.8	28.0			—		
St. Offsjön	680.0	1.1	25.0			—		
Ottsjön	492.0	15.4	30.2			—		
Håckren	492.9	43.0	54.4	23.95	2.95	26.9	1966	1966
Glensjön	786.0	2.9				—		
Storsjön	293.25	456.0	91.0	1.35	1.4	2.75	1940	1940
Näckten	324.52	83.0	45.0	0.35	0.92	1.27	1940	1944
St. Stensjön	677.7	10.0	50.0	10.6	11.9	22.5	1968	1979
River Grubbdalsån								
Rörvattnet	365.0	5.5	18.0	2.4	0.0	2.4	1969	1969
St. Mjölkvattnet	554.38	14.0	> 55.0	10.91	0.49	11.4	1942	1942
Övre Oldsjön	596.0	11.0		14.5	0.5	15.0	1974	1974
Landösjön	319.6	49.0	78.6	1.28	2.32	3.6	1944	1956
River Ljungan								
Torringen	393.0	6.9	> 20.0	0.3	0.5	0.8	1886	1962
Tossåssjön	700.0	0.99	40.0			—		
Övre Röversjön	c 643.0	0.94	c 30.0			—		
Yttre Röversjön	616.0	2.45	c 20.0			—		
Storsjön	566.0	30.0	c 20.0	1.0	3.4	4.4	1965	1965
Storrörmyrtjärn	449.0	0.08	20.5			—		
Östra Rörtjärn	446.0	0.1	7.5			—		
Ansjön	287.9	10.2	34.4			—		
River Ljusnan								
Messlingen	684.0	3.4	50.0			—		
Grundsjöarna	653.5	20.6	25.5	10.5	13.0	23.5	1972	1972
Lakes in Southern Sweden								
Höljesmagasinet	304.0	27.0	65.0	59.0	0.0	34.0		1962
St. Ullen	233.0	6.7	71.0			3.0		
Glimmingen	145.0	1.7	40.0			—		
Östra Nedsjön	121.0	10.7	67.0			3.15	1910	
Bolmen	141.0	183.0	37.0			1.4	1940	
Kyrksjön	c 220.0	0.16	9.6			—		

dominating species in the ecosystem. In lakes with few fish species *Mysis* increases to such an extent that it almost resembles a "monoculture". Such populations run the risk of being subject to heavy parasite infestations or stages of periodic food deficit resulting in population oscillations. Because of this phenomenon a mixture of several of the fish food species would perhaps be preferable.

The introductions of the new fish food organisms afforded unique opportunities for the understanding of the impact of each of them on both other organisms and on the entire ecosystem. Interactions between two or several introduced organisms could also be followed. One example of this is that despite a recorded reproduction, *Gammaracanthus* has not been able to establish populations in two cases where dense *Mysis* populations were present. The *Mysis* populations in these lakes are

Table 3. *Distribution of fish species in lakes with introduced fish food organisms.*

Lakes	Fish food organisms	*Salmo trutta* L.	*Salvelinus alpinus* (L.) species complex	*Thymallus thymallus* (L.)	*Coregonus*, whitefish species complex	*Salvelinus namaycush* (W.)	*Lota lota* (L.)	*Esox lucius* L.	*Perca fluviatilis* L.	*Gymnocephalus cernua* (L.)	*Rutilus rutilus* (L.)	*Phoxinus phoxinus* (L.)	*Pungitius pungitius* (L.)	*Cottus gobio* L.	*Cottus poecilopus* H.	Other fish species
River Stora and Lilla Lule älv																
Suorvamagasinet	MG	×	× 3	—	× 1	—	×	—	—	—	—	—	—			
Pätsaure	M	—	× 2	—	—	—	×	—	—	—	—	—	—			
Satisjaure	M	×	× 1	×	—	—	×	×	×	—	—		—		×	
Langas	M	×	× 3	×	× 3	×	×	—	—	—		×	×		×	
St. Lulejaure	M	×	—	×	× 3	×	×	×	×	—	×	×	×			
Sitojaure	M	×	× 2	—	—	—	×	—	—	—	—	×	—			
River Pite älv																
Pieskejaure	M Le	×	× 1	—	—	—	—	—	—	—	—	—	—	×	—	
Miekakjaure	M	×	× 1	—	—	—	—	—	—	—	—	—	—	×	—	
Vaimok	(M)	×	×	—	—	—	—	—	—	—	—	—	—			
Vuolep Sartajaure	M	×	×	×	—	—	×	—	—	—	—	—	—	×		
Tjeggelvas	M	×	×	×	× 2	—	×	×	(×)	—	—	—	—	×		
Rappen	M	×	×	×	× 2	—	×	×	×	—	—	×	—			
Labbas	M	×	×	×	× 2	—	×	×	×	—	—	×	—			
River Skellefteälv																
Gardejaure	(M)	×	×	—	—	—	—	—	—	—	—	—	—			
Bartaure	M	×	×	—	—	—	×	×	—	—	—		—			
Lullep Luoitaure	(G)	×	×	—	—	—	—	—	—	—	—	—	—			
Rebnisjaure	M	×	× 2	—	(×)	—	×	×	×	—	—	×	—			
Sädvajaure	M	×	× 2	—	—	—	—	—	—	—	—		—			
Tjärn å pkt 591	M	×	×	—	—	—	—	—	—	—	—	—		—	—	
Aisjaure	M	×	—	×	× 1	(×)	×	×	×	—	—	×	×			
Uddjaure	M	×	—	×	× 5	(×)	×	×	×	—	—	×	×			
Storavan	M	×	—	×	× 5	(×)	×	×	×	—	(×)	×	×			
River Ume älv																
St. Umevattnet	P	×	× 2	—	—	—	—	—	—	—	—		—		—	
Gausjosjön	P	×	× 2	—	--	—	—	—	—	—	—		—		—	
Överuman	P	×	× 2	—	—	—	—	—	—	—	—		—		—	
Gäutan	P	×	× 2	—	× 1	(×)	—	—	—	—	—	×	×		—	
Ajaure	P	×	× 2	—	× 1	(×)	—	—	—	—	—	×	×		—	
Gardiken	P	×	× 2	—	× 1	(×)	—	—	×	—		×	—		—	
Abelvattnet	P	×	—	—	—	—	—	—	—	—	—		—		—	
Umnässjön	M	×	×	×	× 2	(×)	×	×	×	—	—	×			—	
Storuman	M	×	×	×	× 2	(×)	×	×	×	—	—	×			—	
Storjuktan	M	×	(×)	(×)	× 2	×	×	×	×	×	×				—	
River Ångermanälven																
Ransaren	M	×	× 1	—	—	—	×	—	—	—	—		—		—	
Kultsjön	MG	×	× 2	—	—	—	×	—	—	—	—	×	—		—	
Malgomaj	M	×	(×)	×	× 3	(×)	×	×	×			×	—	×	—	
Vojmsjön	M	×	(×)	×	× 3	×	×	×	×	—	(×)	×			—	
Lidsjön	M	×	×	—	—	—	×	×	×	—	×	×				

Table 3. Continued.

Lakes	Fish food organisms	*Salmo trutta* L.	*Salvelinus alpinus* (L.) species complex	*Thymallus thymallus* (L.)	*Coregonus*, whitefish species complex	*Salvelinus namaycush* (W.)	*Lota lota* (L.)	*Esox lucius* L.	*Perca fluviatilis* L.	*Gymnocephalus cernua* (L.)	*Rutilus rutilus* (L.)	*Phoxinus phoxinus* (L.)	*Pungitius pungitius* (L.)	*Cottus gobio* L.	*Cottus poecilopus* H.	Other fish species
River Fjällsjöälven																
Lillsjouten	(M)	×	× 1	—	—	—	—	—	—	—	—	×	—	×	—	
Storsjouten	M	×	× 2	—	—	—	—	—	—	—	—	×	—	×	—	
River Faxälven																
Blåsjön	MP	×	× 2	—	—	—	—	—	—	—	—	—	—			
Mesvattnet	M	×	× 2	—	—	—	—	—	—	—	—	—	—			
Småvattnet	M	×	× 1	—	—	—	—	—	—	—	—	—	—			
Kvarnbergsvattnet	(L)	×	× 2	—	—	—	(×)	—	—	—	—	×	×			
Björkvattnet	MP	×	×	—	—	—	—	—	—	—	—	×	—			
Gussvattnet	MP	×	×	×	—	—	×	—	—	—	—	×	—			
River Indalsälven																
Torrön	M (P)	×	× 2	×	—	—	×	—	—	—	—	×	—			
Anjan	M	×	× 2	×	—	—	×	—	—	—	—	×	—			
St. Rensjön	M	×	× 1	—	—	—	×	—	—	—	—		—			
Helgesjön	M	×	(×)	×	× 1	—	×	×	—	—	—	×	—	—	—	
Hensjön	M	×	×	—	—	—	—	—	—	—	—	×	—			
St. Otfsjön	P	×	×	—	—	—	—	—	—	—	—	×	—			
Ottsjön	P	×	× 1	×	—	—	×	—	—	—	—	×	—			
Håckren	PG	×	× 1	×	—	—	×	×	×	—	—	×	—			
Glensjön	(M)	×	× 1	—	—	—	×	—	—	—	—		—			
Storsjön	P	×	×	×	× 5	×	×	×	×	×	×	×	×	—	×	a, e, (f)
Näckten	M (P)	×	× 1	×	× 3	—	×	×	×		×	×	×	—	×	
St. Stensjön	(P)	×	×	—	—	—	—	—	—	—	—	×	—	—	×	
River Grubbdalsån	(P)	×	(×)	×	—	—	×	—	—	—	—	×	—	—	×	
Rörvattnet	(P)	×	×	×	—	—	×	—	—	—	—	×	—	—	×	
St. Mjölkvattnet	(M)	×	×	—	—	—	×	—	—	—	—	—	—			
Övre Oldsjön	(M)	×	× 1	—	—	—	×	—	—	—	—		—			
Landösjön	MP	×	(×) 1	×	× 3	×	×	×	×		×	×	—	×	×	
River Ljungan																
Torringen	M	×	×	—	× 1	—	—	—	×	—	—	—	—			
Tossåssjön	M	×	×	—	—	—	×	—	—	—	—	—	—	—	—	
Övre Röversjön	M	×	×	—	—	—	×	—	—	—	—		—			
Yttre Röversjön	M	×	×	×	—	—	×	—	—	—	—		—			
Storsjön	(M)	×	×	×	× 2	—	×	×	×	—	—	×	—			
Storrörmyrtjärn	(P)		×	—	—	—	—	—	—	—	—	—	—	—	—	
Östra Rörtjärn	(P)		×	—	—	—	—	—	—	—	—	×	—	—	—	
Ansjön	M	×	—	—	× 3	—	×	×	×	—	×	×	×	×	—	c
River Ljusnan																
Messlingen	M	×	× 2	×	—	—	×	—	×	—	—	×	—			
Grundsjöarna	MP	×	× 1	×		—	×	—	×	—	—	×	—			

Table 3. Continued.

Lakes	Fish food organisms	*Salmo trutta* L.	*Salvelinus alpinus* (L.) species complex	*Thymallus thymallus* (L.)	*Coregonus*, whitefish species complex	*Salvelinus namaycush* (W.)	*Lota lota* (L.)	*Esox lucius* L.	*Perca fluviatilis* L.	*Gymnocephalus cernua* (L.)	*Rutilus rutilus* (L.)	*Phoxinus phoxinus* (L.)	*Pungitius pungitius* (L.)	*Cottus gobio* L.	*Cottus poecilopus* H.	Other fish species
Lakes in Southern Sweden																
Höljesmagasinet	(MGP)	×	—	×	×	—	×	×	×	—	×	×	—	×	—	i, j
St. Ullen	M	(×)	× 1	—	× 1	—	×	×	×	—	—		—			a
Glimmingen	(M)	—	—	—	—	—	×	×	×	×	×					b
Östra Nedsjön	(M)	×	× 1	—	—	—	—	×	×	—	×	×	—	×	—	c, f
Bolmen	P	(×)	—	—	× 2	—	×	×	×	×	×	×		—	×	b, c, d, f, g, h, i
Kyrksjön	M	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

Key to the signs:

Fish food organisms

M = *Mysis relicta*
P = *Pallasea quadrispinosa*
G = *Gammaracanthus lacustris*
L = *Limnocalanus macrurus*
Le = *Lepidurus arcticus*
( ) = Population not established

Fish species

× = The species is common
× 1—5 = Number of species within the species complex
(×) = The species is rarely found
— = The species does not exist
No sign = No knowledge

Other fish species

a	*Osmerus eperlanus* (L)
b	*Coregonus albula* (L.)
c	*Anguilla anguilla* (L.)
d	*Stizostedion lucioperca* (L.)
e	*Carassius carassius* (L.)
f	*Tinca tinca* (L.)
g	*Abramis brama* (L.)
h	*Scardinius erythrophthalmus* (L.)
i	*Alburnus alburnus* (L.)
j	*Salmo salar* L.

probably much denser due to moderate predation pressure by fewer fish species than in lakes where the two species are naturally sympatric. Up to a certain point a heavier fish predation on *Mysis* by a more diversied fish community seems to allow the survival of a *Gammaracanthus* population. This could explain why *Gammaracanthus* is a very rare species when living sympatrically with *Mysis*.

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First-year Growth of Perch (*Perca fluviatilis* L.) and Roach (*Rutilus rutilus* (L.)) in a Heated Baltic Bay

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ABSTRACT

Studies were made on the first year of life of the year-classes 1971—76 with regard to length, growth, length distribution, condition and abundance. About 16,000 fry of perch and about 18,000 of roach were collected by means of underwater detonations in two Baltic bays, one of which receives heated water from a nuclear power station. Growth occurred to the highest temperatures observed, 30—31° C. Under natural conditions there is no growth after October, but in heated water a length increment occurs in the winter. It is small, however, which is suggested to be due to the short daylength. There was a positive relationship between the growth rate and the inter-year variations in temperature between ca 10 and 20—25° C, which can be described by a straight line or an exponential function. Size-dependent mortality during the winter was not observed. Condition was demonstrated to be better in warm years than in cold. It varies seasonally in a similar way for perch and roach, with good condition in the summer and poor in the winter. Inter-year variations in abundance of fry appear to be positively correlated to the temperature during the summer and early part of the autumn. The reasons for this are discussed, especially as regards the importance of condition.

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I. INTRODUCTION

The importance of growth rate during the first year of life for the survival and, consequently, the size of the year-class in fish, has been discussed by many authors. Hot summers have been found to give both better growth as well as larger year-classes than cold summers among both perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* (L.)). A correlation of this nature has been demonstrated in Scandinavian waters for the first-year growth of perch by Segerstråle (1933) and Agnedal (1968), and for roach by Kempe (1962). Their investigations were conducted by means of measuring the length of the fry at the end of the first growth season. By studying the age distribution in catches of older fish, Neuman (1976) demonstrated a positive correlation between year-class size of perch and summer temperature, whereas Kempe (1962) found the corresponding correlation for roach.

In the present report, first-year growth of perch and roach in a Baltic bay was related to the temperature conditions. During most of the period of investigation, cooling-water from a nuclear power station was discharged into the bay which enabled effects of increased temperatures to be studied. Variations in growth under natural conditions were investigated before the start of the power station and also in a neighbouring, uninfluenced bay. In addition to length increment, the condition has also been estimated and attempts have been made to compare the abundance of fry in different years. The material was collected by means of

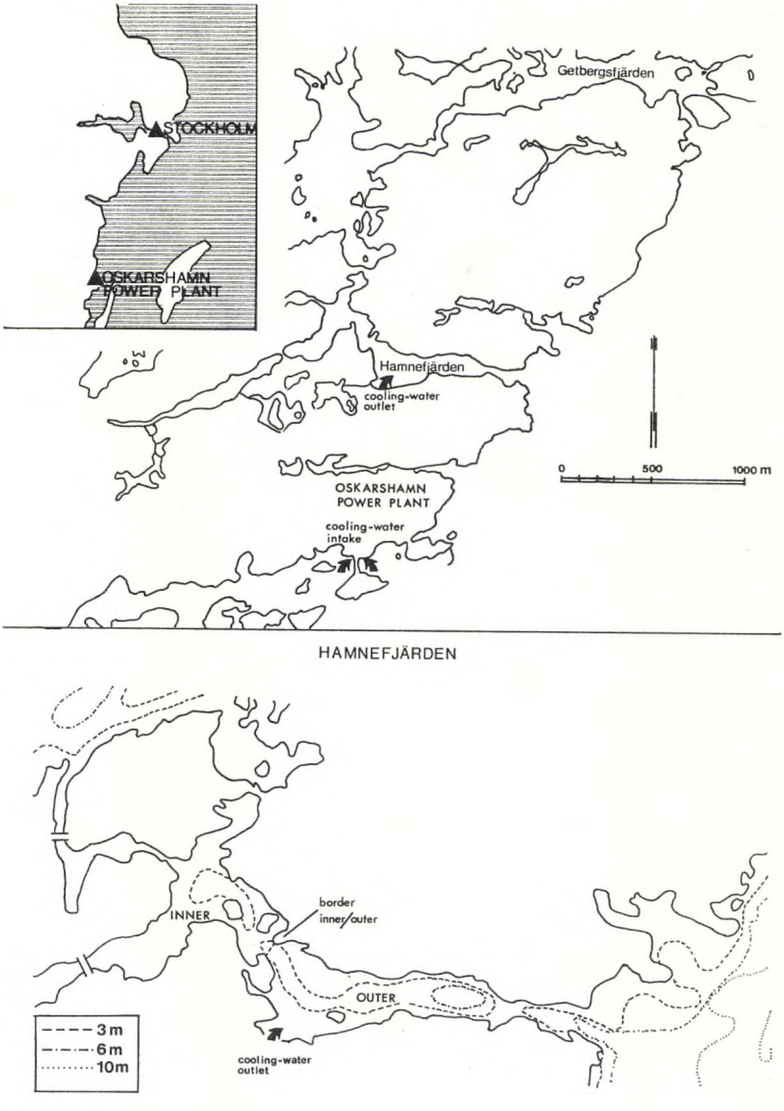


Fig. 1. The investigation area.

detonations. The investigation is part of a larger project concerning the effects of the heated discharge in the area (NEUMAN 1979 a).

Perch and roach normally spawn in the area during May. Their fry biology can be studied in, *e.g.*, ALM (1922), MUUS and DAHLSTRÖM (1968) and FORNEY (1971). FORNEY's observations are made on the American species *Perca flavescens* (MITCHILL), which is closely related to the European perch. Following hatching the perch fry live dispersed in the pelagic zone until the end of July or early August, when they start to congregate in shallow water. Roach fry live in shallow water throughout all this period. In late autumn both species move towards deeper water.

II. INVESTIGATION AREA

The investigation was carried out in the bay Hamnefjärden, which is the recipient for heated discharge from the nuclear power plant Oskarshamnsverket, and in the neighbouring uninfluenced bay Getbergsfjärden (Fig. 1). The power plant is

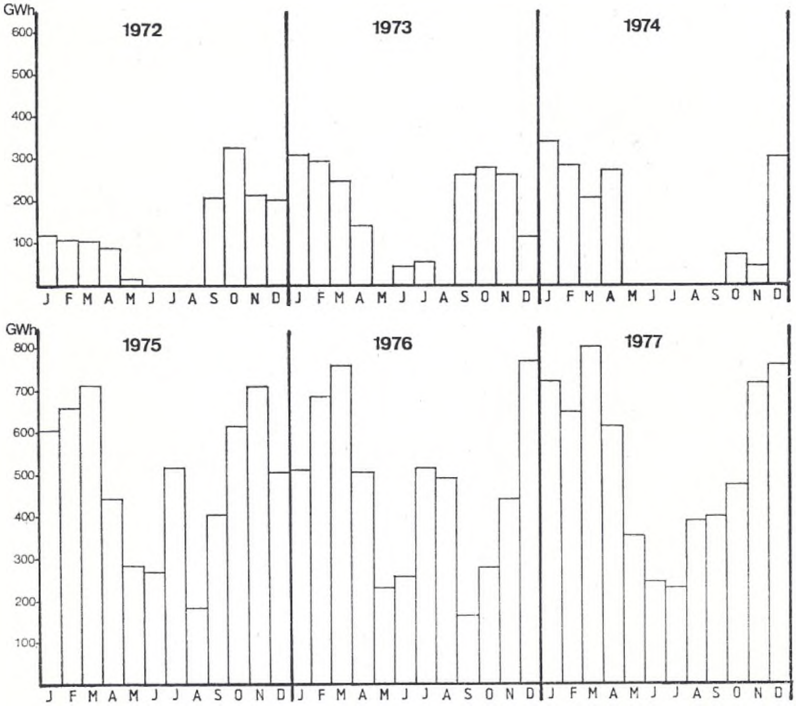


Fig. 2. Production of electricity (GWh).

situated on the Baltic coast 20 km northeast of Oskarshamn. The first reactor, producing 460 MW electric effect, was brought into operation at the beginning of 1972, and a second reactor producing 580 MW was started in late 1974. The production of the power plant during the investigation (1971—77) is shown in Fig. 2. Together, both reactors require ca 50 m^3 cooling-water per second, which is heated about 10° C. During spring and summer the shallow and sheltered investigation areas are warmer than the open sea. The cooling-water used by the power station is taken from the open sea. For that reason the temperature difference between Hamnefjärden and Getbergsfjärden during the period mentioned is considerably less than 10° C.

Hamnefjärden's only link with the sea is through a narrow channel, which opens into a three kilometres long stretch of open coastline. When the power plant is working at full capacity the flow of cooling-water in the channel has a velocity of ca 1 m/s; there is no counter-current into the bay. Inside the bay the depths are generally between two and five metres. Soft bottoms dominate whereas the shores consist mainly of rocks and stones. The inner part of Hamnefjärden constitutes a backwater with a fairly low water turnover and the character of an inland lake, whereas the outer part has a more exposed character on account of the flow of cooling-water. The salinity in the bay and along the coast outside is generally slightly more than 7 $^{0}/_{00}$.

In the inner part of Hamnefjärden there are rich stands of *Myriophyllum* and *Potamogeton* species and also small but dense stands of *Phragmites.* In the outer part the higher vegetation is very scarce, but periphyton, mainly *Enteromorpha* sp., are considerably denser here than inside the outlet (Andersson and Karås 1979). The fish fauna of the bay are dominated completely by freshwater fish, mainly perch and roach (Neuman 1979 b). These two species spawn in the bay, which appears to serve as breeding place also for fish from the open coast outside. Migration into the bay for spawning has decreased strongly since the power station came into operation (Neuman 1979 b and c).

III. MATERIAL AND METHODS

The fry were stunned or killed by means of detonations and thereafter collected by dip-net. The method is simpler and less selective than most other ways of collecting small fish. Dynamite charges, ca 25 g, were thrown 5—10 m from the boat and detonated electrically immediately after impact. The detonation occurred approximately midway between the surface and the bottom. The fish will then either rise to the surface, float freely in the water, or sink, depending on species and the depth at which the fish is present at the time of the detonation. Perch often sink whereas roach generally rise to the surface. All available dead or stunned fish were collected. At depths of between one and two metres, which was the case at most of the detonation stations, the fry within a radius of ca 3—5 m are stunned. The number of fry collected from one detonation has been used as a measure of abundance. The somewhat varying area effected and the difficulties in collecting all of the sinking fish are factors that introduce errors in comparisons of abundances. Each individual fry was measured for length (total length, mm) and for each detonation the total weight of fry of each species was noted. The weighing was done after all excess water had been allowed to run off but before the skin surface had started to dry.

Normally the detonations were done once a fortnight in Hamnefjärden. On account of the different environmental conditions mentioned earlier, the catches were registered as coming from the inner or the outer part (Fig. 1). Reference material was collected in the autumn and spring from the neighbouring bay Getbergsfjärden. The fry were studied from the month of July until June in the start of their second year of life. In Hamnefjärden the detonations were done at a number of permanent stations, usually five in the inner and five in the outer part of the bay. The bottom temperature was measured once a week at one locality in inner and one in outer Hamnefjärden.

The length values presented here are calculated as a mean value of all individuals from all detonations on one occasion. Values based on less than ten individuals have been omitted. Length estimates were continuously made on new fishes, which may account for the individual variation resulting in negative growth occurring between samples close to each other in time.

For each sampling day and area the condition value has been calculated according to the formula $\frac{100 \times \text{weight}}{\text{length}^n}$, where the weight is given as the total weight in grams with one decimal and the length as the sum of all lengths in cm with one decimal. The exponent n for most fish is between 2.5 and 4 (HILE 1936 and MARTIN 1949). In the present investigation 3 has been chosen, which is the most commonly used value for fish of the actual type. No relationship between length and condition that could be considered to influence the condition values was observed. A control of the importance of the amount of stomach contents for the condition value gave the result that the influence is marginal—only a few per cent.

IV. RESULTS

Altogether about 16,000 fry of perch and 18,000 of roach were collected following about 1,500 detonations. As mentioned above perch and roach dominate the fish fauna of Hamnefjärden. In the fry stage the dominance is even more noticeable. Of the collected fry material other species, primarily bleak (*Alburnus alburnus* (L.)) and silver bream (*Blicca bjoerkna* (L.)), make up less than 1 per cent.

Henceforth, when mention is made of a certain year's fry it generally refers to the entire first year of the year-class. For example, year-class 1971 extends over both 1971 and 1972 but is regarded throughout as "1971 fry".

Abundance

The whereabouts of perch and roach during their first year are described in the introduction. This description has been confirmed in the present investigation. In the summer perch stay at deeper localities and roach at shallower than those represented by the sampling stations. In August both species move towards the sampled habitats, where they mainly stay during the autumn. The catches from the period September—December have been used for comparing abundances in different years.

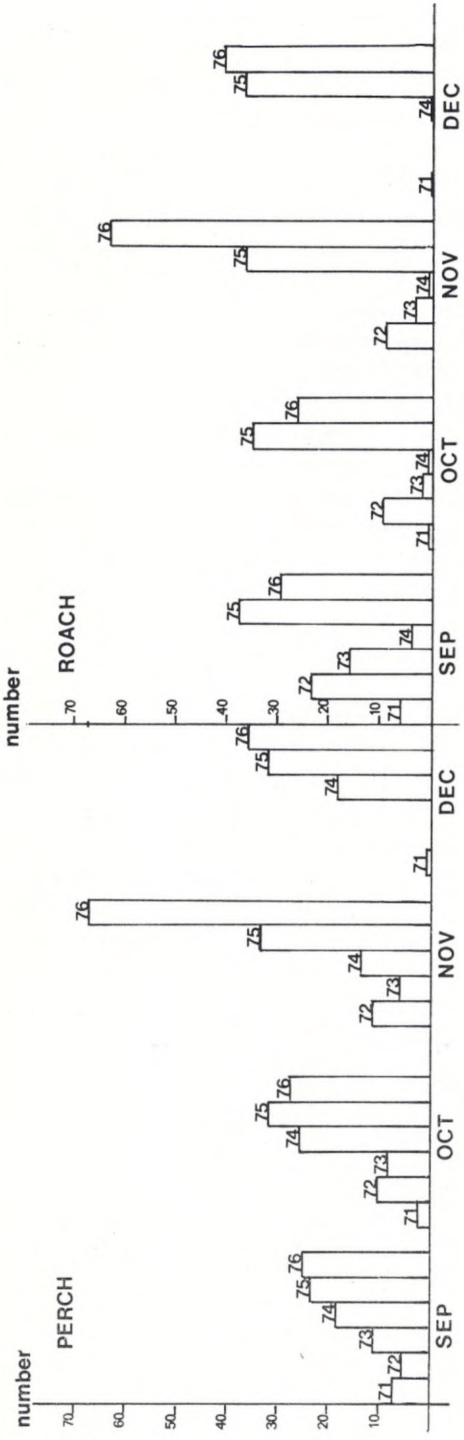


Fig. 3. Mean catches per detonation

In Fig. 3 the mean catch per detonation is presented for each of these months.

Fig. 3, together with Table 1, shows that of the years which are throughout coldest during the summer months, 1971 and 1974, poor catches were obtained in 1971. In 1974 the temperature was very similar to that in 1971 apart from May, when the temperature in 1974 was clearly higher. This temperature difference may be one explanation of the relatively large catches of perch in 1974. The years 1975 and 1976 have the highest temperatures and catches; 1972 and 1973 have an intermediate position as regards both abundance and temperature. Comparisons of catch levels of perch and roach show a remarkable similarity, except in 1974.

Length of growth season

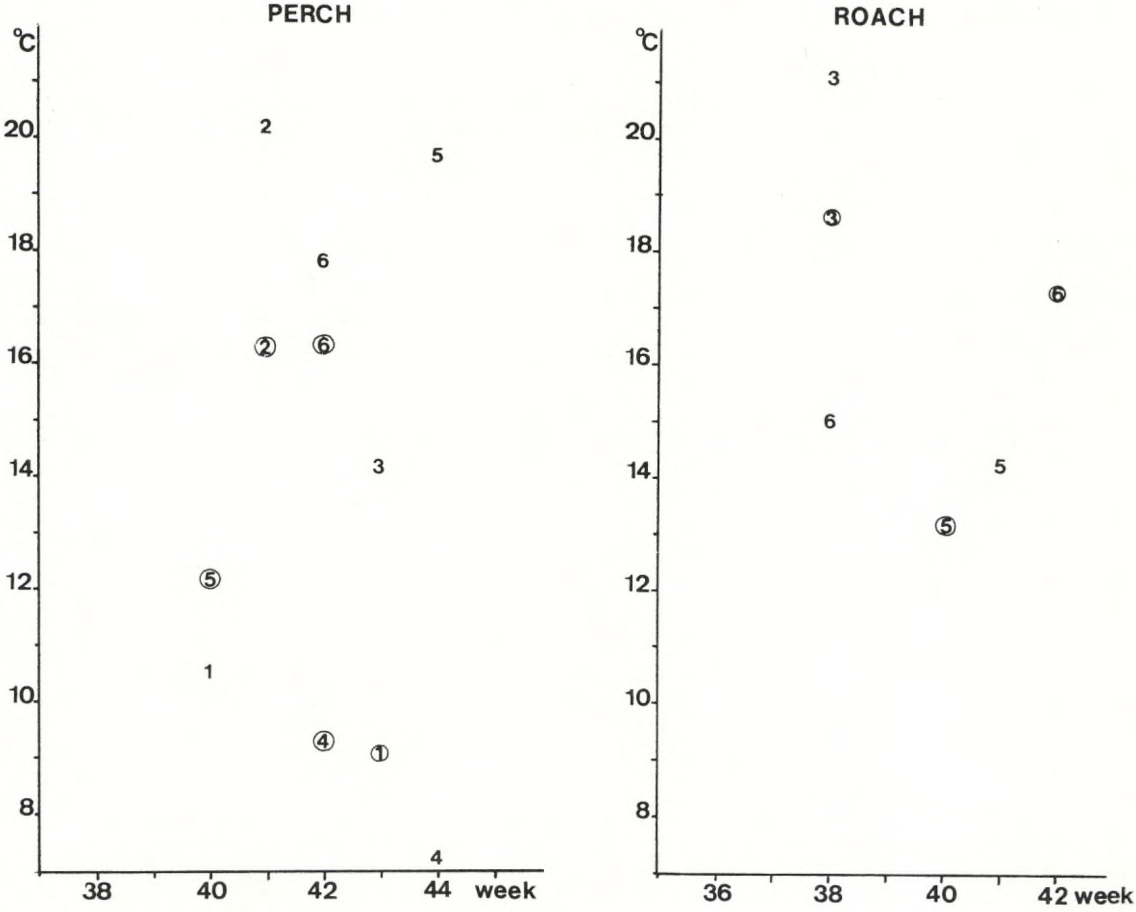
The growth of perch and roach fry was studied from July—August to the following spring. In Fig. 4 the week following the week with the last observation of a length increment has been plotted against the mean temperature of these two weeks. As can be seen, the growth season for perch ends in October (weeks 40—44) and that for roach in late September or early October (weeks 38—42).

There is no indication of any influence of the artificial heating on the termination of growth. For roach, however, the scarcity of observations from the cold autumns in 1971 and 1974 makes it impossible to exclude the possibility that a rise of temperature above a certain level could prolong the growth season.

In some years with heated discharges a small length increment started later than October. This "winter growth" is further described later. Rapid growth starts in the spring. The interval between observations in this season is often long, which makes it hard to establish when the growth season starts. In Fig. 5 the times for the first observation with a clear length increment and for the preceding one have been plotted against temperature on the latter occasion and the highest temperature measured in and between the weeks mentioned. The start of the growth season evidently varies considerably between years. For none of the species, however, was it observed to occur before the middle of April (week 15) and in temperatures below 9° C for perch and 10° C for roach.

Table 1. *Mean water temperature in Hamnefjärden for the year-classes 1971—76.*

Months	1971		1972		1973		1974		1975		1976	
	inner	outer	inner	outer	inner	outer	inner	outer	inner	outer	inner	outer
May	8.9	7.4	10.2	8.3	11.3	10.6	13.0	12.3	17.2	19.2	14.4	16.8
June	14.2	13.5	14.0	12.0	16.3	16.4	12.5	12.9	20.0	20.7	16.6	15.9
July	15.1	14.1	17.8	16.8	19.8	19.8	16.8	15.4	23.7	24.9	23.2	24.3
August	14.3	14.0	19.4	18.3	14.4	14.1	13.6	11.7	23.3	24.1	26.0	28.7
September	11.3	11.1	19.0	21.5	19.2	22.0	11.9	9.3	18.3	18.6	19.7	20.7
October	9.8	10.1	17.7	20.0	16.2	18.1	10.9	11.2	15.7	18.5	17.0	19.4
November	5.8	6.7	12.8	17.0	11.1	15.1	5.8	6.6	15.6	17.6	10.3	10.9
December	4.6	5.0	8.1	9.1	15.8	0.6	8.2	10.2	8.2	11.9	11.1	15.0
January	4.8	4.8	7.5	10.8	5.2	7.6	8.0	11.3	7.8	10.9	5.7	9.7
February	8.9	8.9	8.9	12.4	7.1	10.1	9.1	13.5	16.0	10.9	7.8	9.9
March	3.9	2.1	9.9	13.2	7.5	6.7	10.8	13.4	9.4	13.0	8.2	11.1
April	7.4	8.5	9.3	9.5	11.3	9.8	12.2	14.3	11.6	15.2	9.9	11.3
May	10.2	8.3	11.3	10.6	13.0	12.3	17.2	19.2	14.7	16.8	14.1	14.5
June	14.0	12.0	16.3	16.4	12.5	12.9	20.0	20.7	16.6	15.9	20.6	18.3
to late October	12.3	11.7	16.4	16.2	16.2	16.8	13.1	12.1	19.7	21.0	19.5	21.0



① inner Hamnefjärden 1 outer Hamnefjärden 1,2,3,4,5,6. Year-classes 1971—1976

Fig. 4. The end of the growth season. The weak following the weak with the last observation of a length increment is plotted against the mean temperature of these two weeks.

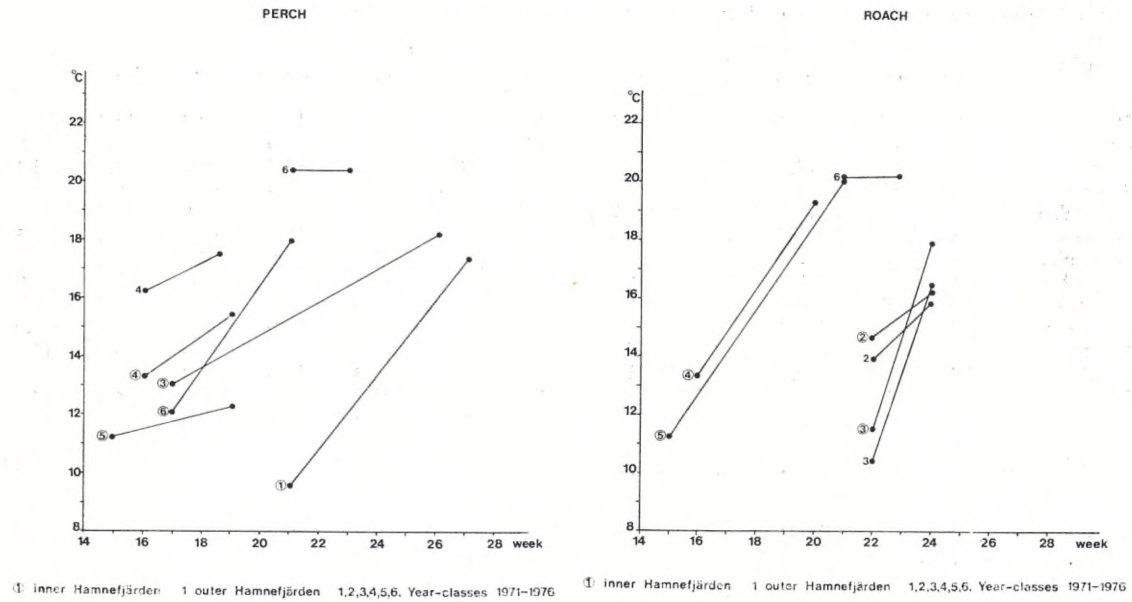


Fig. 5. The beginning of the second growth season. The times for the first observation with a clear length increment and for the preceding one are plotted against temperature on the latter occasion and the highest temperature measured in and between the weeks mentioned.

Influence of temperature on growth

The growth pattern until late October, when growth usually ceases, can be studied in Fig. 6. The length of the fry at this time is illustrated in the form of staple diagrammes in Fig. 7. Perch evidently has a clearly better growth than roach. Both perch and roach had the best length growth in the warmest years. The coldest years, 1971 and 1974, had the poorest growth.

The temperature dependency of growth during the period up to late October has been studied on the material from Hamnefjärden. Fry of perch and roach have not been obtained from the detonations until late July. The period between the last week in July and late October has been divided into three four-week periods roughly corresponding to the months August, September and October. Attempts have been made to correlate the growth to the temperature. Tests were thus made of both linear and exponential relationships. The correlation coefficients for the straight line are given in Table 2. The exponential functions give similar values.

Fig. 8 illustrates the length increase in the different years for the periods "to late October" and "August—October" in comparison with the corresponding mean temperatures. Fig. 8 and Table 2 indicate that during the longer periods—until late July, August—October and until late October—there is a positive correlation between the inter-year variations of temperature and growth up to the highest observed mean temperature, 20—25° C. Due to the low number of observations only the period "to late October" has values that are all statistically significant. The good fit of the material to a straight line does not, however, apply to the same extent to the period up to late July. The reason for this may be that growth has decreased during 1975 and 1976 on account of the temperature being too high for optimal growth during the end of the period. However, consideration must also be taken to the fact that the breeding period and consequently the hatching of fry in the years studied probably occurred at different times. Thus, the growth period until late July may have different lengths for the different year-classes.

If the material is divided up into short periods the good relationship between growth and temperature will disappear (Table 2). One reason for

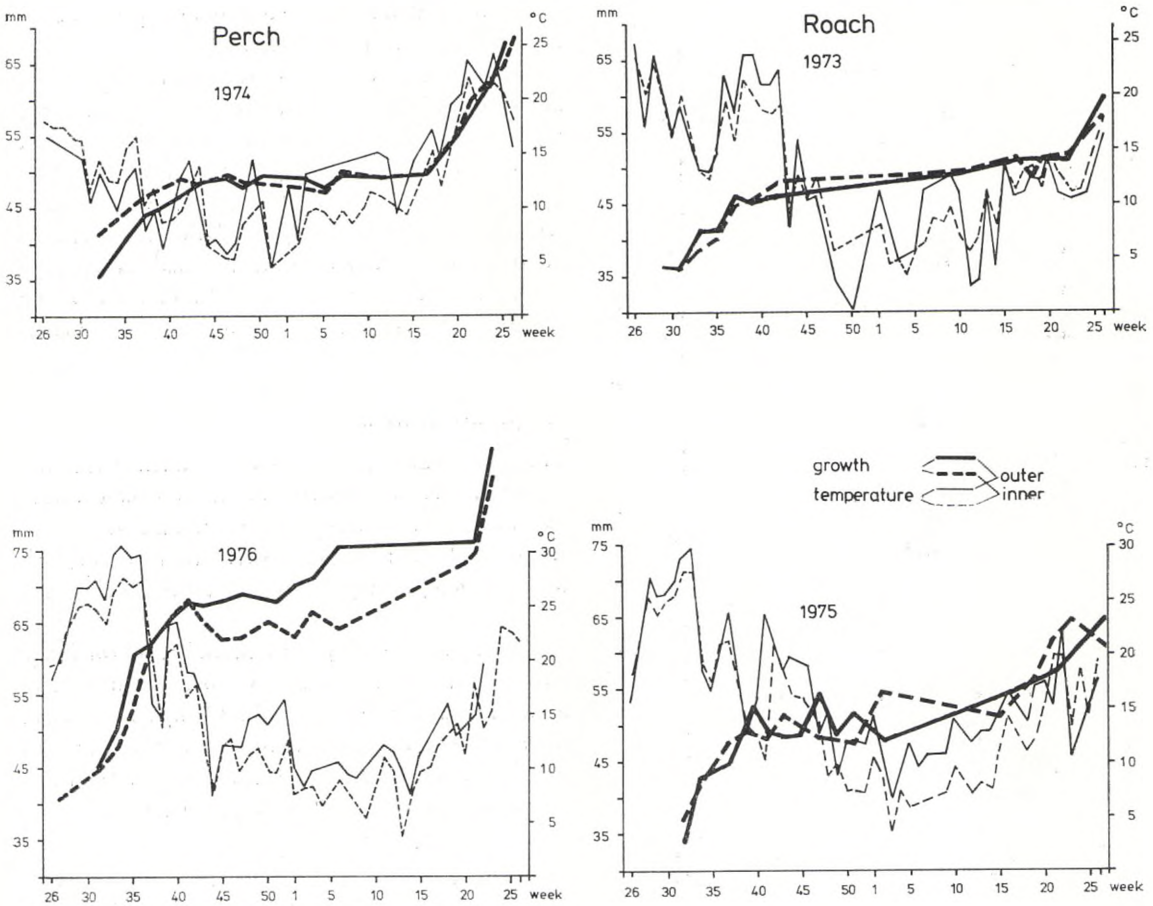


Fig. 6. Growth and temperature pattern for separate year-classes in outer and inner Hamnefjärden.

this is that the growth is estimated through comparisons between different individuals. This has the result that the shorter the time chosen the greater the importance of the individual variation. Thus, this would imply that growth should not be studied in this manner during periods that are too short; periods extending over about two months are preferable. However, the warmest periods, August 1975 and 1976, indicate that growth still occurred in the highest temperatures measured, 30—31° C. This can be seen in Fig. 6 and is also noticeable for perch in 1975 and roach in 1976.

The temperature dependency of growth is noticeable not only in comparisons between years but also between areas in the same year. Figs. 7 and 8 illustrate that the best growth of perch was usually found in the warmest part of Hamnefjärden, generally the outer part. This does not concern roach.

As was established above, the growth season ended no later than week 44 for perch and week 42 for roach, while the next season did not start earlier than week 15. From Fig. 7 it is evident, however, that a small length increment has taken place between these weeks. The differences between autumn and spring values shown in the figure are all significant at least at the 5 % level. The winter growths are entered in Table 3 together with the means of the weekly temperature observations from the corresponding periods. Year-

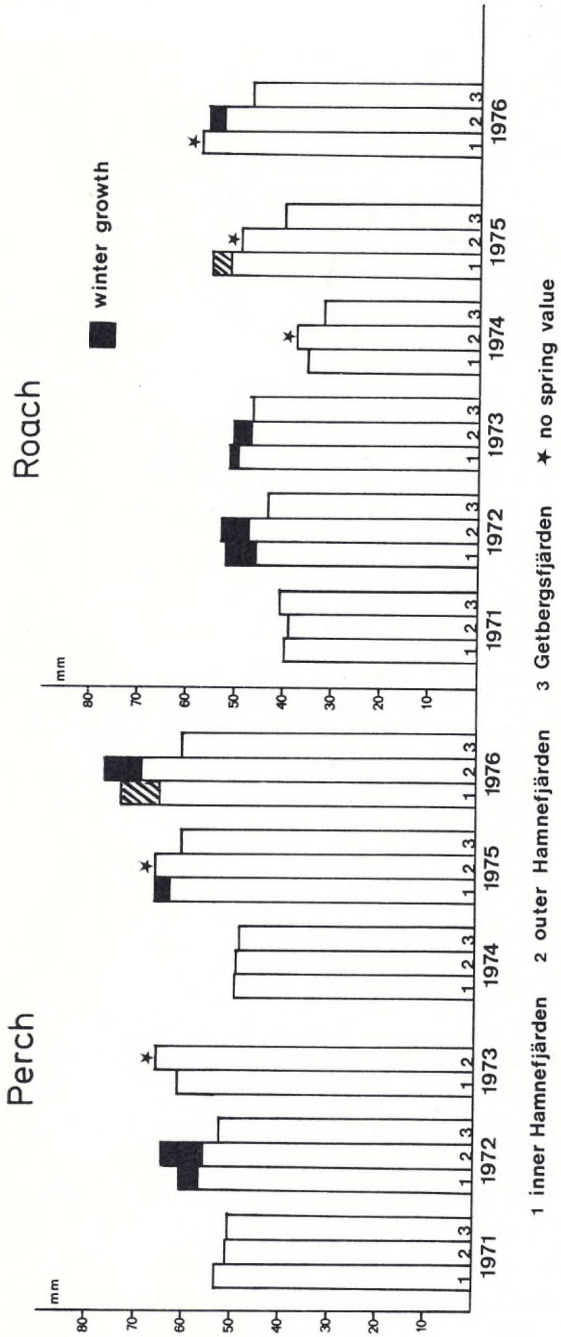


Fig. 7. Length after the first growth season. Winter growth denotes length increment during the period November—beginning of April (hatched staple the end of April).

classes for which adequate autumn or spring values are missing have been excluded.

Table 3 shows that the lowest mean temperature at which perch has grown is ca 9° C and the highest at which no growth was observed is ca 11° C. The corresponding values for roach are approximately 7° C and 9° C. However, in other respects there is no simple relationship between growth and mean temperature. This applies particularly to the year-classes 1973 and 1974, which experienced very varying temperature conditions (Fig. 6).

Length distribution

The mean values for length increment were discussed above. The distribution around these values has also been studied in an attempt to reveal whether skewed length distributions occur, indicating length dependent mortality during the first year.

Certain years with good material from the inner part of Hamnefjärden and Getbergsfjärden have been chosen for the analysis. Comparisons have been made of the same year-class in October and April. A purely mathematical concept of the form of the distribution can be obtained from the formula: $S = m_3/(m_2)^{3/2}$

$$m_2 = 1/N \sum_{i=1}^{n} f_i(x_i - \bar{x})^2 \quad m_3 = 1/N \sum_{i=1}^{n} f_i(x_i - \bar{x})^3$$

N = total number, f_i = number in each length group, x_i = length in mm, $\bar{x}$ = mean value.

S expresses the skewness of the distribution. A positive value shows that the emphasis is on the small fishes, a negative that it is on the big fishes. When values are between —0.5 and +0.5 it can be assumed that the distribution is symmetrical. It is very skewed at values greater than ±1. Values calculated for the selected years are presented in Table 4. Only in one case the value exceeds 0.5.

Condition

Calculations of the condition of the present material were made according to the formula $\frac{100 \times \text{weight}}{\text{length}^3}$ in order to study the variations in condition in the natural environment and that influenced by heated water. The calculations were

Table 2. *Correlations between growth and temperature. (The numbers of observations are presented between brackets.)*

	To late July	August—October	To late October	August	Sep-tember	October
Perch						
Inner	0.85 (5)	0.98 (4)	0.93 (6)**	0.01	0.07	0.02
Outer	0.73 (6)	0.86 (6)*	0.96 (6)**			
Roach						
Inner	0.78 (4)	0.94 (4)	0.92 (6)**	0.53	0.00	0.12
Outer	0.50 (4)	0.96 (5)**	0.98 (6)***			

*=level of significance 0.05, **=level of significance 0.01,
***=level of significance 0.001

Table 3. *Winter growth.*

Perch (weeks 45—14) Year-class	Growth (mm)	Mean tem-perature (°C)	Roach (weeks 43—14) Year-class	Growth (mm)	Mean tem-perature (°C)
1972 (o)	9	12.2	1972 (i)	6	9.5
1976 (o)	8	12.0	1972 (o)	5	12.7
1972 (i)	5	9.1	1976 (o)	3	12.0
1975 (i)	3	9.1	1973 (o)	3	7.8
1974 (o)	0	11.3	1973 (i)	2	7.1
1974 (i)	0	8.6	1974 (i)	0	8.7
1973 (i)	0	6.7	1971 (o)	0	6.0
1971 (o)	0	5.8	1971 (i)	0	5.1
1971 (i)	0	4.8			

(o)=outer Hamnefjärden, (i)=inner

Table 4. *Analysis of length distributions. (The numbers of observations are presented between brackets.)*

	Year-class	Inner Hamnefjärden October	April	Getbergsfjärden October	April
Perch					
	1971			0.40 (161)	0.16 (82)
	1974	0.26 (410)	—0.13 (138)		
	1975	0.20 (104)	0.24 (256)		
Roach					
	1971			0.46 (487)	0.42 (497)
	1972	—0.39 (88)	0.20 (27)	—0.12 (452)	0.10 (135)
	1974			0.28 (250)	0.60 (201)
	1975	0.05 (286)	0.00 (242)	0.05 (151)	—0.01 (103)

made on the total weight (g) and the total length (cm) for a certain sampling day and a certain area. As the individual distribution is unknown it is difficult to judge the level of significance in the material, and thus only rough estimations have been made on large amounts of material.

Fig. 9 illustrates the seasonal variation in condition in perch and roach. In this figure the two warmest years, 1975 and 1976, have been compared with the others, with the exception of 1974, where the condition pattern diverges (see discussion below). The values given in the diagramme

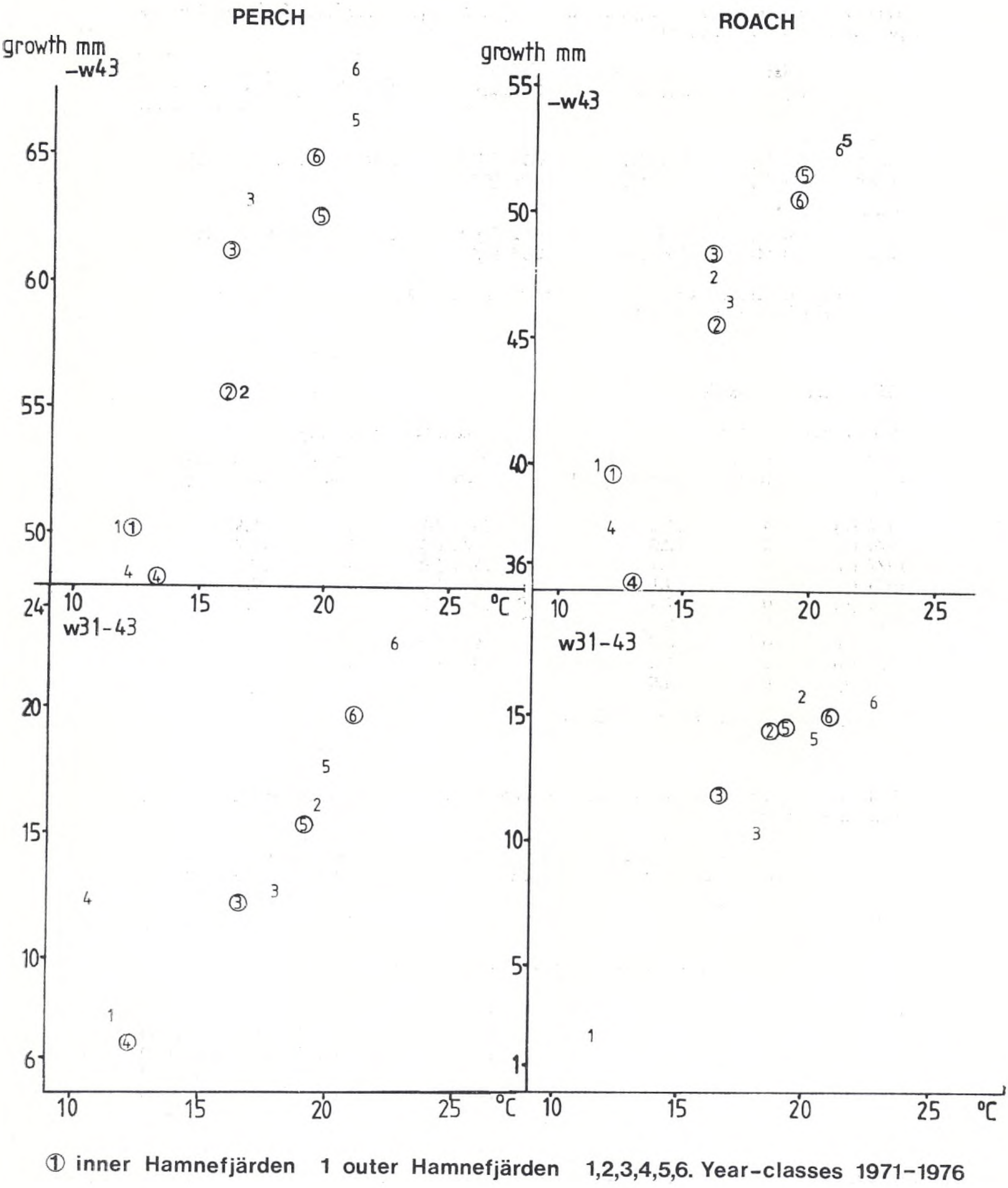


Fig. 8. The relationship between growth and temperature. Length increment is plotted against mean temperature for the period May—October and August—October.

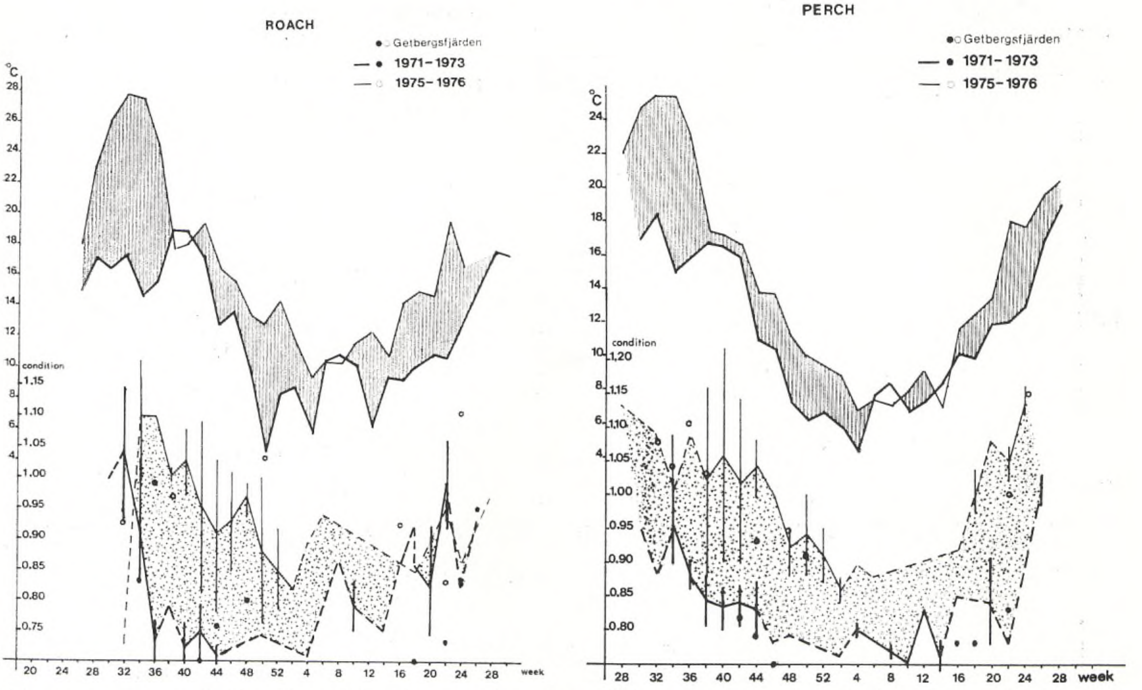


Fig. 9. Seasonal variation of condition. Mean values of condition for two-week periods are plotted against the corresponding ones for temperature The range of variation and the condition values for Getbergsfjärden are also included. Perch is represented by inner and roach by outer Hamnefjärden.

are mean values for two-week periods. The range of variation and the condition values for Getbergsfjärden are also included. Here, too, 1975 and 1976 were clearly warmer than 1971—73. The seasonal variations follow similar patterns for perch and roach. Good condition during the summer and autumn is followed during the late autumn by a deterioration. This is followed by relatively low values during the winter period. Condition then rapidly improves in connection with the fast rise in temperature in the spring. A difference in condition can be seen between the year-classes 1971—73 and 1975—76. This difference appears to mainly arise during the very warm period 1975—76, approximately ranging from late June to mid-September. This difference in condition could also be observed later in the year, but a decrease took place in the winter.

Table 5. *Correlations between condition and temperature. (The numbers of observations are presented between brackets.)*

Perch		Roach	
Inner	Outer	Inner	Outer
0.79 (6)	0.81 (6)	0.64 (5)	0.87 (5)

The mean value for condition in the period up to late October has been calculated and compared with the corresponding mean value for temperature for each year (Table 5 and Fig. 10). The fit to a straight line gives a highly positive correlation according to Table 5. However, due to the low numbers of observations none of the figures are statistically significant.

In order to observe the influence of the maximum temperature on condition, the condition values for mid-August, the warmest part of the year, were compared with the corresponding temperatures (Fig. 10). The relationship between condition and temperature for perch appears to be positive up to ca 26° C but at higher temperatures the correlation becomes negative. Roach show a positive correlation all the way up to the highest temperatures, ca 30° C.

Roach from 1974 has been omitted from Figs. 9

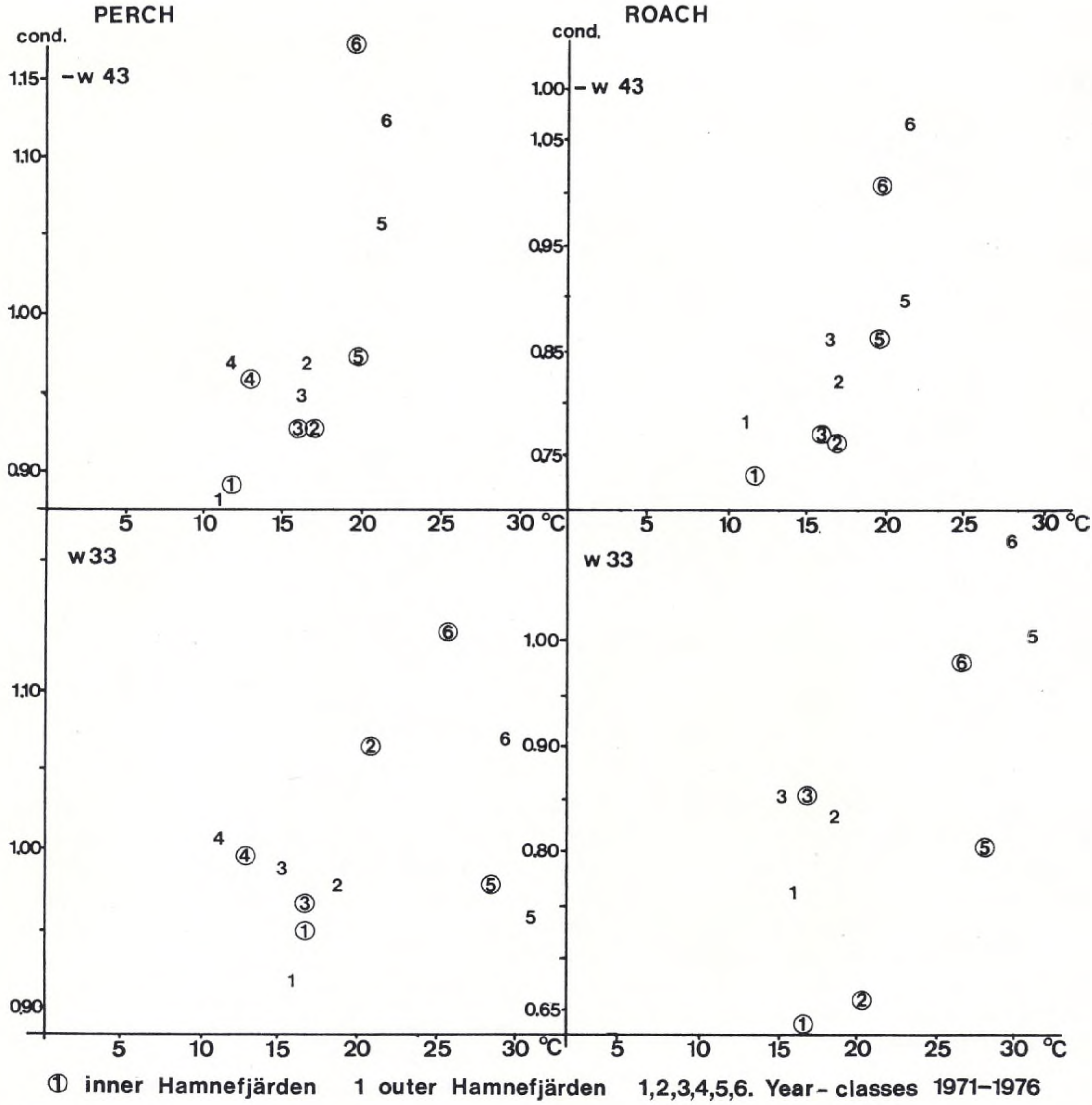


Fig. 10. The relationship between condition and temperature. Mean condition is plotted against mean temperature for the period May—October and for the middle of August, the warmest part of the year.

Table 6. *First year growth in different waters. (Total length, mm.)*

Perch		Roach	
49—67 (76)	Hamnefjärden 1971—76	35—52 (57)	Hamnefjärden 1971—76
48—64	Getbergsfjärden 1971—75	32—44	Getbergsfjärden 1971—75
64	Agnedal (1968)	40—45	Alm (1922)
56—83	Le Cren (1958)	45—50	Balon (1955)
55	Segerstråle (1933)	40	Frank (1959)
88	Wilkonska and Zurumska (1977) heated lake	40—45	Kempe (1962)
		43	Wilkonska (1970) 700 lakes
		80	Wilkonska and Zurumska (1977) heated lake

Length intervals refer to values for several year-classes or lakes. Values within brackets refer to the length following winter growth.

and 10 on account of insufficient material. As regards perch the condition was rather good in 1974 in spite of low temperatures. For that reason this year has been omitted from Fig. 9. The cause of the divergence is discussed below.

V. DISCUSSION

In spite of the heating of Hamnefjärden there is a check in the growth of both perch and roach fry in the autumn. A slow growth has been observed to start again, however, during late autumn and winter. According to BRETT (1979), a decreasing daylength has an inhibiting effect on growth of some freshwater fish, and KAYA and HASLER (1972) states that a certain minimum daylength is necessary for commencement of growth of winter fish. PESSAH and POWLES (1974) noticed that elevating the temperature could initiate a "false start" of the spring growth cycle of *Lepomis gibbosus* (RAFINESQUE), but the photoperiod was too short—12 hours—for the growth to continue. The winter growth in Hamnefjärden could thus be caused by one or more such "false starts". In the spring there is a marked increase of the growth rate. This increase has not been observed before mid-April even in heated water, which indicates that the daylength is too short earlier in the year.

Growth still appears to occur at the highest temperatures observed, 30—31° C. It can be noted that the lethal temperature is only some degrees higher; according to our own, unpublished, experiments in brackish water it is 33—35° C for perch and 34—37° C for roach. In heated waters in Poland it was found that optimal growth was attained between 26 and 28° C (WILKONSKA and ZURUMSKA 1977).

There is a positive correlation between the inter-year variations of growth rate and temperature. The correlation can be described by an exponential function or a straight line and applies between ca 10 and 20—25° C. For perch the temperature dependency is also indicated when comparisons within years are made between sites with different temperature conditions. In Polish lakes receiving heated discharge a clearly better growth of perch and roach fry has been found than in uninfluenced lakes (ZAWISZA and BACKIEL 1972). Apart from the winter growth, the extra heat in Hamnefjärden does not result in growth that is markedly better than that in other waters. Table 6 gives the mean values from other investigations together with those reported here.

The highest values in the above references are from inland lakes, which often are warmed faster in the spring and also reach higher temperatures than coastal waters. This may explain why some of the above values are higher than those from Hamnefjärden.

High temperatures may stimulate growth by accelerating metabolism and by increasing the production of food. In Hamnefjärden the fry of perch and roach live primarily on zooplankton during the summer and the early autumn (KARÅS 1979). During the autumn there is a change towards bottom fauna such as chironomid larvae for perch and algae for roach. The biomass development of zooplankton in the Baltic is favoured by high summer temperatures (HESSLE and VALLIN 1934 and HERNROTH and ACKEFORS 1979). In Polish investigations in lakes receiving heated water it has been found that there is a marked increase of biomass of zooplankton (HILLBRECHT-ILKOWSKA *et al.* 1976). In the inner part of Hamnefjärden the density of chironomid larvae shows a positive correlation with temperature (WILLNER 1979). This also applies to periphyton in the outer part of Hamnefjärden (ANDERSSON and KARÅS 1979). LE CREN (1958) considers it probable that the direct physiological influence of temperature on growth is more important than the indirect via the food. He bases this assumption on the fact that all age groups react similarly to temperature variations despite their different nutrient choices. It has also been demonstrated experimentally that there is a poorer development of perch at low temperatures despite optimal availability of food (KUDRINSKAJA 1970). The good correlations between length increment and temperature that have been demonstrated in the present report also speak in favour of a direct effect.

The density of fry during the autumn in Hamnefjärden appears to be positively correlated to the temperature during the summer and early part of the autumn. The importance of growth rate for survival has been discussed by many authors. One effect of the growth rate on survival has been proposed to be that individuals that have not reached a sufficient size by the winter should then die (KEMPE 1962 and SVÄRDSON 1976). This theory is supported by observations of a mean length increment during the winter. However, comparisons between length distributions in autumn and spring do not indicate any size-dependent mortality in the present material.

In addition to the above-mentioned factors, the condition can also be expected to be of importance for survival. Good condition naturally counteracts starvation and presumably increases the capacity for flight and hunting. In the present investigation the condition has been demonstrated to vary between seasons in similar ways for perch and roach. Good condition during the summer and autumn is followed by a decrease with relatively low values during the winter period. In connection with the rapid temperature increase in the spring the condition increases quickly. For adult perch this has also been demonstrated by LE CREN (1951), and for both fry and adults by LIND *et al.* (1973). The poor condition during the winter may lead to mortality, but it is probable that the low energy utilization resulting from the low temperature counteracts mortality. However, when energy utilization increases in the spring, in connection with the rise in temperature, increased activity is needed for nutrient uptake and consequently the situation may be critical for fish with a condition that is too low. The condition seems to be especially low after a cold summer which provides a poor starting point before the reduction in condition during the autumn.

Many authors have demonstrated that a correlation exists between the size of the year-class and temperature in the spring during the first fry stages. This has been done for roach by KEMPE (1962). However, the same author has also demonstrated a relationship between the size of the year-class and the temperature during August and September. In the present area of investigation a correlation of this kind was demonstrated in July—August for perch by NEUMAN (1976). The above-mentioned hypothesis that the condition may be decisive for the dimensioning of the year-classes supports the opinion that a correlation to this later period exists, since it is primarily during the height of the summer that the highest condition values appear to be obtained. A contributory reason for the year-class dimensioning occurring to a particularly large extent in the fry, could be that they reveal the largest alterations in condition and the lowest winter condition. This has been demonstrated for perch by LIND *et al.* (1973).

An interesting observation can be made in the present material with regard to the condition for perch of year-class 1974. Generally in this investigation more or less the same density values have been obtained for perch and roach. However, in 1974 perch had a fairly large year-class whereas it was very weak for roach. Despite the low summer temperature the condition of perch was good which might have partly been caused by reduced competition for food by the roach. This in turn may explain the high density of perch—good condition results in greater survival.

A rough temperature dependency has been demonstrated in the variations of the condition between years in Hamnefjärden. This also applies to the reference area where only a few estimates of the condition have been made. The warmest years lie at the same level as those from Hamnefjärden. This could be explained by the decline of the condition at least of perch observed at the highest temperatures. Within years the picture is more complicated. During the period when condition decreases in the late summer and autumn there is no corresponding fall in temperature. However, during this period there is rapid growth. This may imply that the fish's stored nutrients are used as a buffer for the growth in length. It is also possible that as long as the fish has a certain minimum condition, growth is rapid at high temperatures even when there is little food. This would explain the larger and more rapid changes in condition within and between years compared with those in growth.

VI. ACKNOWLEDGMENTS

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Impact of *Mysis relicta* Lovén Introduction on the Plankton of Two Mountain Lakes, Sweden

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ABSTRACT

Mysis relicta was introduced to two Swedish mountain lakes, Lake Mesvattnet and Lake Småvattnet in 1971. Dense *Mysis* populations were established in the two lakes about 1974—75. The mean summer phytoplankton biomass increased considerably in both lakes during the course of development of the *Mysis* populations. This increase was especially attributed to algae belonging to the genera Cyanophyta, Chrysophyceae and Dinophyceae. In Lake Mesvattnet the composition of zooplankton changed rather drastically after the increase in density of the *Mysis* population. Both the cladocerans *Eubosmina longispina* and *Holopedium gibberum* became almost extinct, while the rotifers have increased considerably. In Lake Småvattnet increased numbers of rotifers and a tendency to decreasing numbers of *Eubosmina* and *Holopedium* were recorded. However, in this lake the dominating cladoceran was *Daphnia longispina* which on the whole has remained unaltered. The copepod *Cyclops scutifer* seemed to be unaltered in both lakes, although *Mysis* in a set of experiments was shown to be capable of feeding on them. The changed plankton situation in Lake Mesvattnet after the introduction of *Mysis* is likely an effect of heavy *Mysis* predation on cladocerans. The cause of the changed plankton situation in Lake Småvattnet is to some degree more obscure.

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I. INTRODUCTION

Recently trophic interactions have been observed to play an important role in determining the structure of freshwater communities (*e.g.* HRBACEK *et al.* 1961, ZARET and PAINE 1973, ANDERSSON *et al.* 1978, STENSON *et al.* 1978, HENRIKSSON *et al.* 1980).

In particular much attention has been paid to the influence of vertebrate predation on the size-distribution and composition of the zooplankton population (*e.g.* HRBACEK 1962, BROOKS and DODSON 1965, GALBRAITH 1967, WELLS 1970, STENSON 1972, NILSSON 1972, DE BERNARDI and GUISSANI 1975). Predation on the zooplankton by invertebrate predators can also be significant (*e.g.* HALL 1964, MCQUEEN 1969, CONFER 1971, DODSON 1972, FEDORENKO 1975, KAJAK och RYBAK 1979). According to some authors this type of predation can be of equal or even greater importance to the zooplankton community structure than that of vertebrate predation (GLIWICZ *et al.* 1978, LANE 1979, LYNCH 1979).

Mysis relicta has been introduced to many lakes as a forage-food item for fish (for a review see GOSHO 1975). Changes in the composition of the zooplankton have been noted in some lakes with introduced *Mysis* populations (ZYBLUTH 1970, FÜRST *et al.* 1978, GOLDMAN *et al.* 1979). However, the actual cause of the observed changes is unclear due to other interfering changes such as the introduction of kokanee, fertilization by a phosphorous plant and also because of inadequate knowledge on the zooplankton population (NORTHCOTE 1972, RICHARDS *et al.* 1975, FÜRST *et al.* 1978). In this paper we present some results concerning the plankton community from a study undertaken to evaluate the effects of *Mysis relicta* introduction on the different levels of a freshwater ecosystem. The results strongly indicate that *Mysis* can have far reaching consequences for the structure and dynamics of the pelagic community of a lake.

II. MATERIAL AND METHODS

The study was designed as a whole-lake experiment. In 1971 *Mysis relicta* was introduced into two test lakes, Lake Mesvattnet and Lake Småvattnet, situated in the north-west mountain region of Sweden (64° 47′ N, 14° 10′ E). Both lakes are small, oligotrophic and uninfluenced by impoundments or outlets which could affect the results. For a closer description of the lakes the reader is referred to OLSÉN (1980).

Sampling of phyto- and zooplankton was performed with a pump (impeller type) and a tube at ten randomly selected sites. The tube was lowered at an approximately constant speed, from the surface down to twenty metres depth. After stirring, 1 litre was removed for the phytoplankton sample and the rest, approximately 7—8 litres, was filtered through a net (mesh size 30 µ). The procedure was repeated at each site. Hence the zooplankton sample contained about 75 litres while the phytoplankton sample (200 ml) was subsampled from the removed 10 litres.

The depth distribution of the zooplankton population was investigated by sampling with a RODHE-sampler (5 l) and on some occasions with a CLARKE-BUMPUS sampler. The samples were filtered through a net (mesh size 75 µ). All plankton samples were fixed with JJK and counted in an inverted phase-contrast microscope. Phytoplankton and zooplankton were analysed according to the UTERMÖHL technique (UTERMÖHL 1958) after sedimentation in 50—100 ml and 50 ml settling chambers respectively. The routine method used in analysing phytoplankton is described by WILLÉN (1976) and HOBRO and WILLÉN (1977). However, one modification with regard to the calculation of the mean volume of species with a complex shape, not easily approximated to geometric figures, was applied. For these species a model was constructed and the volume was calculated according to the formula $V = L \cdot B^2 \cdot C$ where V = volume, L = length, B = width and C = a species constant which can be easily determined from the model. This species constant was then used when the mean volume was estimated.

The sampling period normally extended from the break-up of ice in early June to the beginning of September with approximately 10 days between sampling occasions. During most years additional sampling was undertaken once in October. The lakes were surveyed from 1972 to 1976 but sporadic sampling continued until 1979.

The feeding of *Mysis relicta* was examined partly through gut content analysis and partly through feeding experiments designed for the verification of alterations in the plankton. Preliminary experiments with 30 litre plastic bags were carried out in Lake Småvattnet in 1975. In these experiments, the bags were filled with lake water and the zooplankton abundance was increased by the addition of net hauls taken from different parts of the lake, *i.e.* two different series of net hauls from the littoral zone and one series of hauls from the pelagial. The zooplankton from each zone was then stirred and an equal volume of this water containing zooplankton was transferred to each of the bags used in the experiment. Mysids of two different length classes, 7—11 mm and 18—22 mm were added to some of the bags. The other bags served as controls. All bags were suspended in the lake for the night. In the morning the water in the bags was filtered and the animals counted.

In 1979 several experiments, with more strictly controlled conditions, were run in Lake Mesvattnet in cooperation with DAVID C. LASENBY, Trent University, Peterborough, Canada. A detailed description of the methods used in these experiments is given in Lasenby and Fürst (1981, p. 75—76 in this issue).

III. RESULTS

The *Mysis* population in Lake Mesvattnet was very sparse during the first two years following the introduction in 1971, and during this period the lake could be regarded as uninfluenced by the *Mysis* introduction. From 1974 onwards, however, the *Mysis* population quickly became denser, and in 1976 and 1977 the carrying capacity was reached. The development of the population in Lake Småvattnet is less well-known, since sampling of the *Mysis* population in this lake did not start until 1975 and by then the population was fully established, indicating a faster rate of development of this population in comparison to the

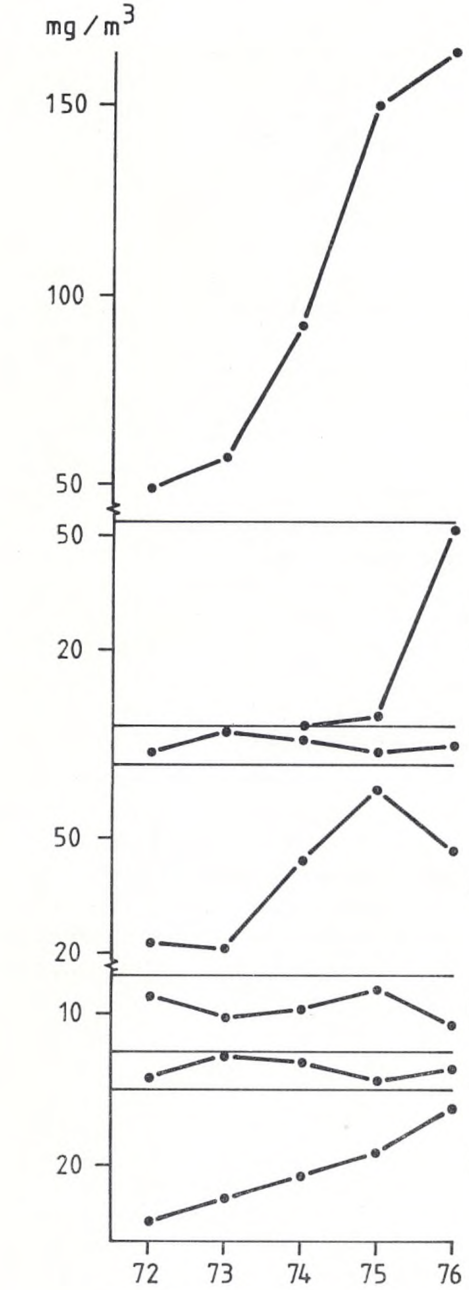

Fig. 1. Mean phytoplankton biomass in Lake Mesvattnet 1972—76 (1 = total biomass, 2 — Cyanophyceae, 3 = Chlorophyceae, 4 = Chrysophyceae, 5 = Bacillariophyceae, 6 = Cryptophyceae, 7 = Dinophyceae).

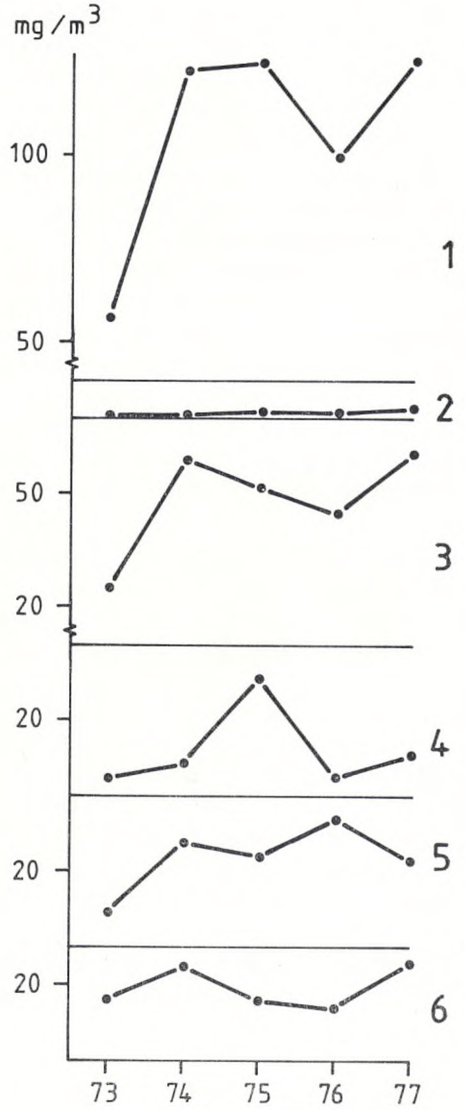

Fig. 2. Mean phytoplankton biomass in Lake Småvattnet 1973—77 (1 = total biomass, 2 — Chlorophyceae, 3 = Chrysophyceae, 4 = Bacillariophyceae, 5 = Cryptophyceae, 6 = Dinophyceae).

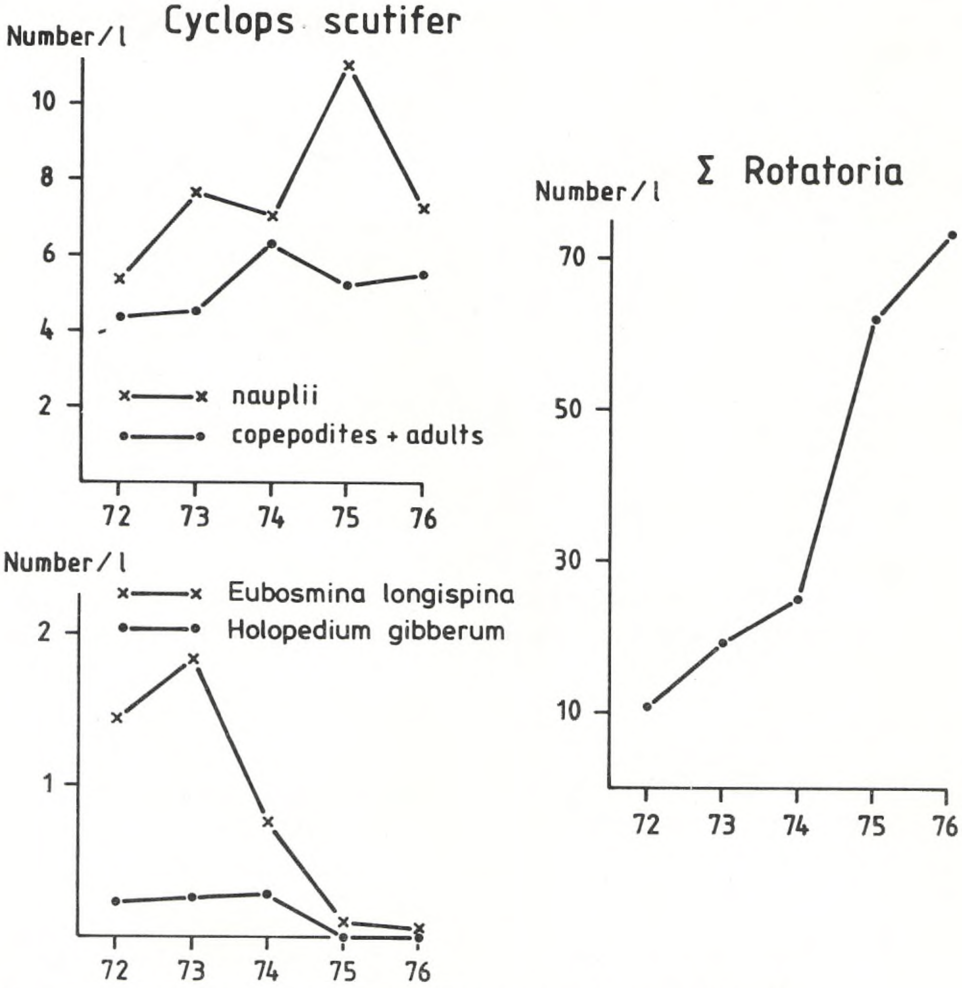

Fig. 3. Mean number of dominating zooplankton species in Lake Mesvattnet 1972—76.

population in the larger Lake Mesvattnet (Olsén 1980).

During the course of the development of the *Mysis* population, the summer mean phytoplankton biomass in Lake Mesvattnet has increased considerably (Fig. 1). This increase is especially attributed to algae belonging to the groups Cyanophyta, Chrysophyceae and Dinophyceae. Ordinarily blue-green algae (Cyanophyta) are sparse in oligotrophic lakes (*e.g.* Nauwerck 1963, Olsén 1980) and this was also the case in Lake Mesvattnet before the late summer of 1974, when *Rhabdoderma lineare* first appeared. Since then this algae has been present in enormous numbers, but because of its small size the influence on the phytoplankton biomass is still moderate. Among the Chrysophyceae, mostly small flagellated forms belonging to the genera *Ochromonas* and *Chromulina* have become more numerous. The dinoflagellates which have become more abundant are *Peridinium inconspicum* and *Gymnodinium uberrimum.* This trend also persisted in 1977—78 according to occasional samples taken during these summers. In Lake Småvattnet there was a general increase between 1973 and 1974, but since these summers mean biomass values have been rather constant (Fig. 2).

The composition of zooplankton in Lake Mes-

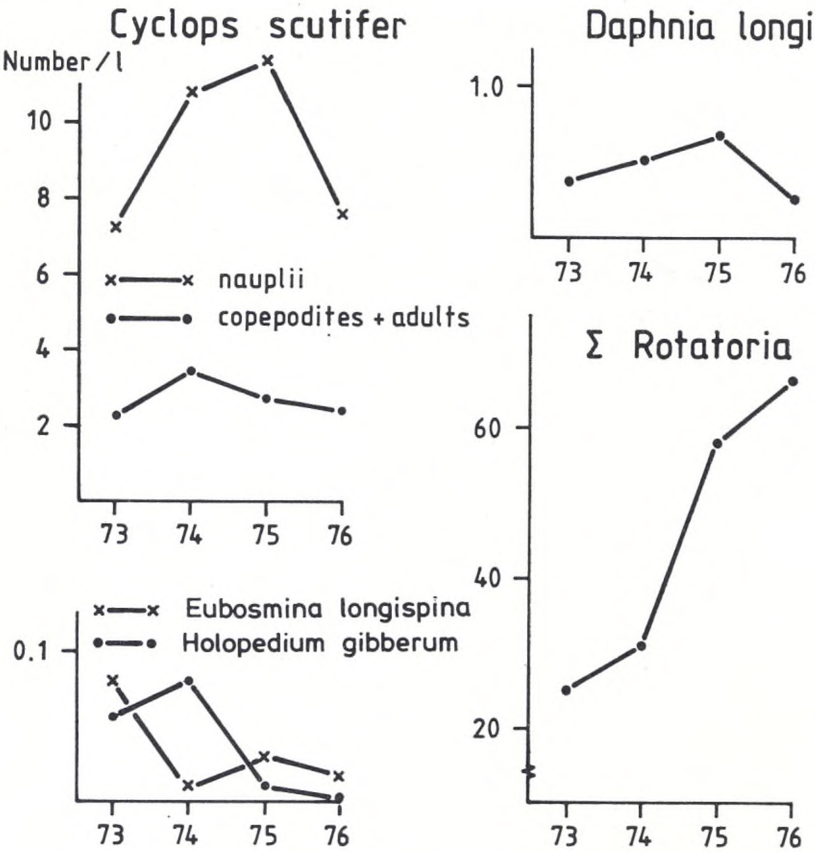

Fig. 4. Mean numbers of dominating zooplankton species in Lake Småvattnet 1973—76.

vattnet changed rather drastically following the increase in density of the *Mysis* population. Both the cladocerans *Eubosmina longispina* (LEYDIG) and *Holopedium gibberum* ZADDACH have become almost extinct (Fig. 3). These species, especially *Eubosmina*, were important food objects for char in the summer when *Mysis* was sparse (OLSÉN 1980). *Daphnia* has been sparse both before the introduction of *Mysis* as well as after. The copepod *Cyclops scutifer* SARS has remained unaffected, while the rotifers have increased considerably during the same time period (Fig. 3). In Lake Småvattnet the *Eubosmina* population and *Holopedium* populations were small during all years of investigation. Because of this it has been difficult to verify whether changes in population densities have occurred. But it is in any case possible to see that the sum of the numbers of *Eubosmina* and *Holopedium* have had a tendency to decrease during the years of investigation while the numbers of rotifers have increased. However, in this lake the dominating cladoceran was *Daphnia longispina* s. str. which on the whole has remained unaltered. Nor were any drastic changes in the *Cyclops scutifer* population noted in Lake Småvattnet (Fig. 4). The reduced numbers of zooplankton in the carboys containing mysids (Table 1) indicated that *Mysis* could feed on some zooplankton species. The other set of experiments showed that the mysids were capable of feeding upon the alive and swift-swimming copepod *Cyclops scutifer* (Table 2).

The ability of *Mysis* to feed on large zooplankters was also confirmed by the stomach content analysis. Remnants of *Cyclops*, *Arctodiaptomus*, *Eubosmina*, *Holopedium* and *Daphnia* were observed in stomachs of *Mysis*. In mysids from Lake Småvattnet *Daphnia* was especially abun-

Table 1. *Individual numbers of different zooplankton species after predation experiments with Mysis. One pelagial zooplankton mixture was used in experiment a. In experiment b and c resp. two different littoral zooplankton mixtures were used.*

Large *Mysis*=18—22 mm
Small *Mysis*= 7—11 mm

Number of *Mysis* in each plastic bag	*Cyclops scutifer*	*Arctodiaptomus laticeps*	*Heterocope saliens*	*Daphnia longispina*	*Sida crystallina*	*Polyphemus pediculus*
Exp. a)						
No *Mysis* (ref.)	498			37		
No *Mysis* (ref.)	448			17		
20 large *Mysis*	87			16		
20 large *Mysis*	74			10		
Exp. b)						
No *Mysis* (ref.)	0	19	122	89	39	4
No *Mysis* (ref.)	7	22	159	79	48	5
58 small *Mysis*	5	4	131	13	26	1
55 small *Mysis*	5	10	115	76	63	9
Exp. c)						
No *Mysis* (ref.)	751	13		194		6
No *Mysis* (ref.)	792	8		253		8
60 small *Mysis*	294	13		59		2
60 small *Mysis*	411	22		120		1

Table 2. *Predation experiments in Lake Mesvattnet 1979 to study the effects of Mysis predation on Cyclops scutifer.*

In experiment a 30 litre carboys were used
In experiment b 10 litre carboys were used

Number of *Mysis*	Length (mm)	Number of *Cyclops*			Number consumed per *Mysis* per hour
		Initial	Final	Diff.	
a)					
20	12	89	43	46	0.46
20	12	107	98	9	0.09
20	8	108	57	51	0.51
20	8	100	2	98	0.98
0		102	102	0	0
0		119	118	1	0
b)					
15	8	40	8	32	0.43
15	8	40	2	38	0.51
15	8	40	0	40	0.53
0		35	34	1	0
0		35	33	2	0
0		35	35	0	0

dant. Besides these larger zooplankters, large numbers of rotifers, *e.g. Kellicottia longispina* (KELLICOTT), *Keratella hiemalis* CARLIN and *Keratella cochlearis* (GOSSE), were found. The stomachs also contained several phytoplankton species, benthic algae and detritus. These observations are valid only for mysids caught in the later part of the summer, when zooplankton are relatively abundant and the mysids migrate vertically. At the beginning of summer, when the mysids are restricted to the bottom zone (Olsén 1980), the stomachs contained detritus, cysts and benthic algae, especially benthic diatoms.

IV. DISCUSSION

According to stomach content analysis, *Mysis* in Lake Mesvattnet and Lake Småvattnet feeds on detritus and benthic algae during the greater part of the year, and when they are migrating vertically, phytoplankton and zooplankton are also included in the diet. This feeding behaviour has also been found in several other lakes (Tattersall and Tattersall 1951, Holmquist 1959, Lasenby 1971, Lasenby and Langford 1973). According to Grossnickle (1979) *Mysis* can be primarily herbivorous during the nocturnal vertical migrations, but in our lakes this is probably not the case. According to Bowers and Grossnickle (1978) *Mysis* feeds mostly on large phytoplankters, but the phytoplankton species found in the stomachs of the mysids in the present study were mostly small ($< 30\ \mu$) and could possibly have originated from the zooplankton species eaten by the mysids. Moreover, the phytoplankters seemed unaffected by the passage through the chewing-stomach. Hence the extent and importance of *Mysis* feeding on phytoplankton in these lakes remain obscure.

The feeding experiments confirm that *Mysis* can actively catch and ingest several zooplankton species, even the swift copepods. However, they seem to have a preference for cladocerans such as *Daphnia* and *Eubosmina* rather than for copepods like *Cyclops* (Cooper and Goldman 1980, Lasenby and Fürst, 1981). The preferance for cladocerans is due to their comparatively low mobility, which means that they cannot avoid encounters with *Mysis* (Lasenby and Fürst, 1981).

According to the stomach content analysis and the feeding experiments, *Mysis* acts as a voracious predator on the zooplankton community and since there has been no change in the studied lakes except for the increased abundance of mysids, it seems likely that *Mysis* are responsible for the decline of the cladocerans *Eubosmina* and *Holopedium*.

Eubosmina is known to be able to survive in lakes with relatively high predation pressure from fish and is often the dominant cladoceran in lakes where the char are numerous and small-sized, indicating a high predation pressure (Langeland 1978). Lake Mesvattnet is such a lake with a small-sized char population which feeds heavily on *Eubosmina* (Olsén 1980). *Mysis* predation in this lake seems to have a powerful influence on the *Eubosmina* population, as *Eubosmina* can hardly be found in zooplankton samples after 1975.

Reduced numbers of *Holopedium* have also been recorded in Lake Mesvattnet since the expansion of *Mysis*, and it seems likely that this species may also have been influenced by *Mysis* predation. In another case the occurrence of *Holopedium* seems to have been markedly affected by fish predation (Stenson 1973).

Compared to Lake Mesvattnet the number of *Eubosmina* in Lake Småvattnet was small before the expansion of *Mysis*. Probably the *Eubosmina* population was hampered by competition from *Daphnia longispina* according to the "size efficiency hypothesis" (Brooks and Dodson 1965). During the years of investigation there has been a tendency to decreasing numbers of *Eubosmina* and *Holopedium* in Lake Småvattnet. It is likely that *Mysis* predation has also caused that change.

The numbers of *Daphnia longispina* in Lake Småvattnet have remained relatively unaltered although they constituted the staple-food of the char in the summer (Olsén 1980), and were also definitely preyed upon by *Mysis*. The discrepancy of *Daphnia* having persisted in Lake Småvattnet while *Eubosmina* have become almost extinct in Lake Mesvattnet can possibly be explained by differences in the behaviour of *Daphnia* and *Eubosmina* in these lakes. *Daphnia* in Lake Småvattnet are mostly found in close proximity to the surface, while *Eubosmin*a in Lake Mesvattnet stay preferably near the metalimnion (Fig. 5). This probably makes *Eubosmina* more vulnerable to *Mysis* predation than *Daphnia* in these lakes, since *Mysis*, when migrating vertically in the summer nights aggregate at the thermocline where *Eubosmina* most frequently occurs, while few *Mysis* ascend all the way to the surface (Olsén 1980).

The feeding experiments show that *Mysis* can consume relatively large numbers of *Cyclops scutifer*. Despite this fact *C. scutifer* have not shown any

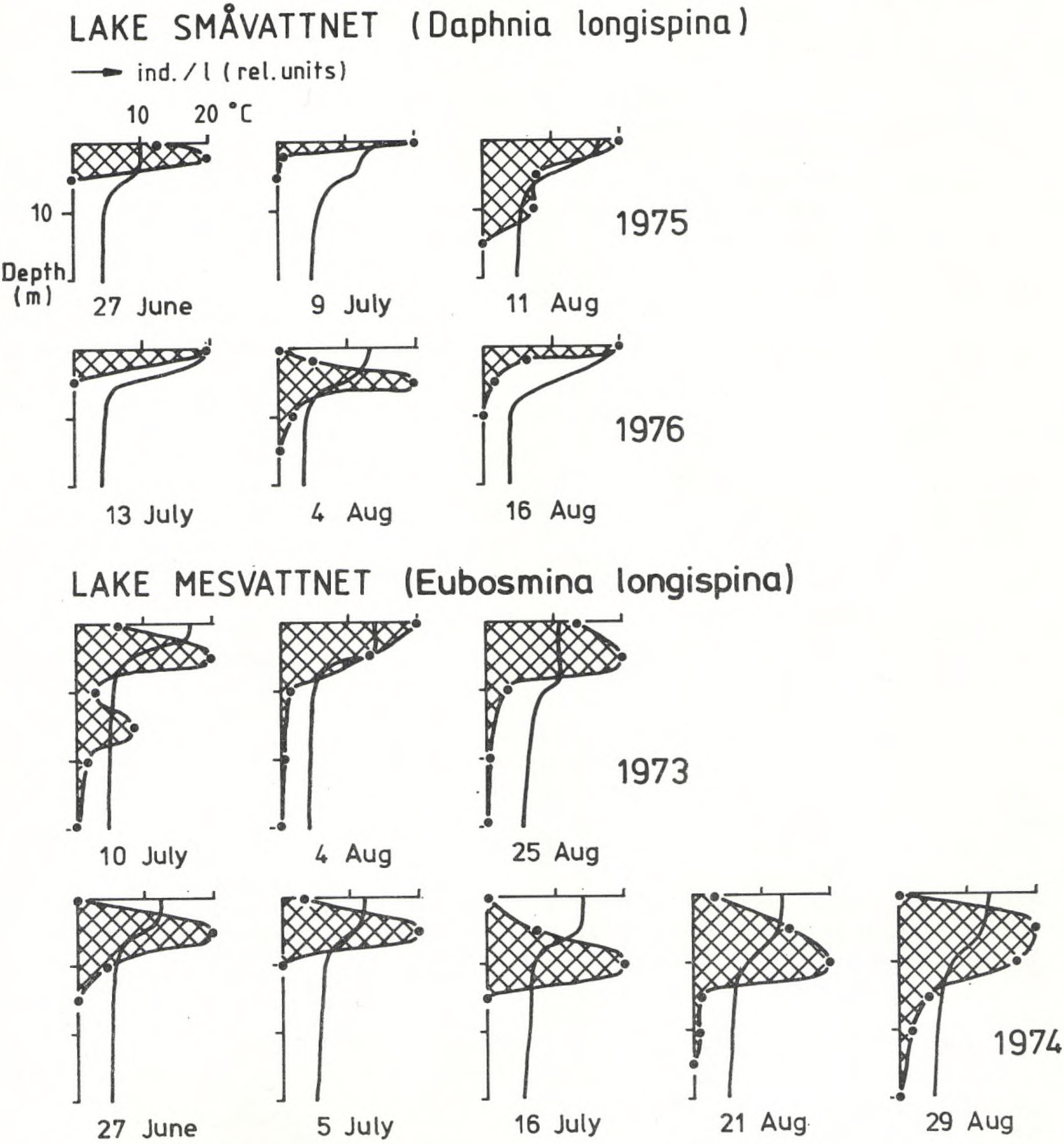

Fig. 5. Depth distribution of the dominant cladocerans in the study lakes in relation to temperature profiles.

definite signs of declining. Lasenby and Fürst (in press) have observed that *Mysis* has considerably greater difficulty in catching the swift copepods compared to the slow cladocerans, which could explain the relatively low predation pressure on *Cyclops*. Moreover, other *Cyclops* species like *Cyclops vernalis* seem to be only slightly affected when exposed to invertebrate predation (Lynch 1979). Possibly *Cyclops* was favoured also by the increased biomass of phytoplankton resulting from a decline in grazing zooplankters. In some lakes the numbers of crustaceans can be affected by the occurrence of large predatory members of the zooplankton community (*e.g.* De Bernardi and Guissani 1975, Lane 1979, Gliwicz *et al.* 1978, Mc Queen 1969). Conceivable species of this kind in these lakes are *Bythotrephes longimanus* Leydig and *Heterocope saliens* Lillj. However, zooplankton samples and fish stomach examinations do not show any signs of increase in these species.

The increased abundance of rotifers in the studied lakes probably, especially in Lake Mesvattnet, results from diminished competition from larger filtrators in accordance with the »size-efficiency» hypothesis (Brooks and Dodson 1965). A similar relationship has been reported from several other lakes (*e.g.* Hillbricht-Ilkowska and Weglénska 1973, Andersson *et al.* 1978, Lynch 1979). However, the fact that the increase was approximately the same in both the lakes in this investigation is somewhat peculiar, since in Lake Småvattnet the numbers of the dominating cladoceran remained at about the same level. Possibly other factors besides competition are involved.

The phytoplankton biomass in oligotrophic lakes generallly oscillates very little from year to year under natural conditions (Ramberg 1979, Olsén and Willén 1980, Nauwerck 1963), and the observed increase in phytoplankton biomass in Lake Mesvattnet can, at least to some extent, be attributed to the decline of the cladoceran populations. Several authors have observed a relationship between abundance of larger filtrators and phytoplankton biomass (*e.g.* Hurlbert *et al.* 1972, Schindler and Comita 1972, Porter 1973, De Bernardi and Guissani 1978, Andersson *et al.* 1978, Stenson *et al.* 1978). The increase in phytoplankton biomass in Lake Mesvattnet consisted principally of species within a size range of 2—15 μ, which are adequate food for most zooplankton (Gliwicz 1969, Burns 1968, Pourriot 1977).

Some larger phytoplankton species also increased, *e.g. Gymnodinium uberrinum.* This can also possibly be attributed to reduced grazing, since large species often have a slower turnover and according to some authors larger species like *Gymnodinium viride* are also utilized by cladocerans (Johansson and Olofsson 1976). Some zooplankton species apparently have a positive selectivity for the largest available food objects (Nadin-Hurley and Duncan 1976, Wilson 1973).

V. ACKNOWLEDGMENTS

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Feeding of *Mysis relicta* Lovén on Macrozooplankton

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ABSTRACT

In Kootenay Lake, B.C., Canada, *Mysis* feed on calanoids and cyclopoids. In Lake Mesvattnet in northern Sweden *Mysis* feed on cyclopoids. In aquaria experiments, we observed *Mysis* actively pursue and attack macrozooplankton. We suggest that the predatory feeding of *Mysis* is wide-spread and if cladoceran abundance is low, *Mysis* will prey on copepods.

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I. INTRODUCTION

In recent years the crustacean *Mysis relicta* has been introduced into many lakes in North America and Scandinavia to serve as a supplementary food source for fish (NORTHCOTE 1972, FÜRST 1972 a and b). *Mysis* feeding habits vary diurnally and seasonally (LASENBY and LANGFORD 1973) and from lake to lake. BOWERS and GROSSMICKLE (1978) describe the herbivorous feeding of *Mysis* in Lake Michigan whereas LASENBY and LANGFORD (1973) demonstrate that in oligotrophic Char Lake *Mysis* is primarily an omnivore while in eutrophic Stony Lake where cladocerans are abundant, *Mysis* is primarily carnivorous, feeding on *Daphnia*, *Bosmina* and *Kellicottia* during its vertical migration at night. In this study we examine the predatory feeding of *Mysis* in lakes where cladocerans are not abundant relative to other macrozooplankton.

II. MATERIAL AND METHODS

Two lakes in which cladoceran abundance was low, Kootenay Lake in southeastern British Columbia (49° 30′ N, 17° 00′ W) and Lake Mesvattnet in northern Sweden (64° 47′ N, 14° 10′ E), were chosen to study *Mysis* feeding. *Mysis* was introduced into Kootenay Lake in 1949 and the success of the mysid population as well as the decrease in *Daphnia* abundance after the introduction is described by ZYBLUT (1970). In 1976—77, the cladocerans *Bosmina* and *Daphnia* were still low in abundance (LASENBY, unpubl.), the dominant zooplankters being *Diaptomus ashlandi* and *Cyclops bicuspidatus thomasi*. Examination of the gut contents of Kootenay Lake mysids captured during the summer months revealed that the immature and adult mysids were feeding on calanoid and cyclopoid copepods.

To confirm that adult mysids were preying on active copepods, they were offered copepods in both pure prey cultures and natural zooplankton assemblages. Mysids were starved for 24 hours before all experiments.

For each pure prey experiment, a mixture of 140 late copepodid and adult *Diaptomus ashlandi* or *Cyclops bicuspidatus thomasi* were put into each of six 18 l plastic feeding chambers filled with filtered lake water (70 μ mesh net). Five adult female mysids were introduced into five of the chambers, the sixth being a control. The experiments were then run with the chambers suspended in the water column at the surface (approx. 18° C) and at 50 m (approx. 9° C), for either 12 hours daylight or 12 hours at night, after which the contents of each were filtered and the number of copepods counted. The temperature range encompassed that experienced by the mysids during their vertical migration into the epilimnion at night. The difference between the initial and final number of copepods was considered to be the number eaten by the mysids. The control was run to determine copepod mortality from factors other than mysid predation.

To examine mysid feeding in natural plankton assemblages, six feeding chambers were filled with water from 30 m using a VAN DORN water bottle. After 5 adult female mysids were introduced into 3 of the chambers, all six were suspended in 30 m of water for 5 hours. The chamber contents were then filtered and the macrozooplankton was counted. The difference between the mean number of copepods in the chambers with and without mysids was considered to be the number consumed by the mysids. The experiment was run on 3 consecutive days in July, 1977.

Mysis was introduced into Lake Mesvattnet in northern Sweden in 1971 and a dense population was rapidly established (OLSÉN 1980). KINSTEN and OLSÉN (1981) have reported a change in abundance of plankton during the period 1972—76. The situation seemed not to have changed considerably in August 1979. Extensive sampling at this time demonstrated that the plankton was dominated by *Cyclops scutifer*, cladocerans (*Eubosmina longispina*, *Holopedium gibberum*, *Daphnia longispina*) being present but still in low numbers (KINSTEN, pers. comm.).

To determine if immature, as well as adult mysids would prey on copepods, several experiments were run in cooperation with B. KINSTEN at Lake Mesvattnet in August 1979. In the first experiment immature *Mysis* (approx. 8 mm) and adult *Mysis* (approx. 12 mm) were used. Six 30 l carboys were filled with water from a depth of 7 m (depth of maximum zooplankton concentration) with a pump. The water in each carboy was filtered (no. 70 μ mesh net) and returned to the carboy. The filtered copepods (*Cyclops scutifer*) were counted and returned to the carboy. Of the 6 carboys, two contained 20 adult *Mysis* two 20 immature mysids and the remaining two were controls. The carboys were placed at the lake surface at 15° C in daylight. (In Lake Mesvattnet, mysids were found in high densities in the littoral zone even in bright sunlight.) After five hours the contents of the carboys were filtered and the copepods counted. The difference between the initial and final number of copepods, corrected for controls, was considered to be the number consumed by the *Mysis*. The experiment was repeated using only immature mysids, adult and copepodid *Cyclops scutifer*, and 10 l feeding chambers.

Examination of mysid gut contents from Lake Mälaren, (59° 24′ N, 17° 30′ W) in southern Sweden, which contains abundant cladoceran and copepode populations, revealed that the mysids were feeding almost exclusively on *Bosmina*, in August 1979. To determine if *Mysis* would feed on *Cyclops* sp. or *Bosmina* when given equal numbers of each, a feeding experiment was run using mysids from Lake Mälaren. Four 10 l plastic feeding chambers, each containing 40 *Bosmina* and 40 copepodid and adult *Cyclops* sp. (the approximate lake density), and filtered lake water (70 μ mesh net) were used. Ten adult mysids were added to two chambers, the remaining two being controls. After 5 hours at 10° C in the dark, the number of *Bosmina* and *Cyclops* was counted. As well, aquaria observations of adult *Mysis* feeding on zooplankton from Lake Mälaren were also made.

Experiments in cooperation with O. BERGFORS, Institute of Limnology, Uppsala were also carried out in Lake Mesvattnet to determine if *Mysis* was actively feeding on live *Eurycercus lamellatus*. Four cores 50 mm in diameter and 500 mm long were pushed down into the sediment in the littoral zone of the lake.

Mysis at approx. 12 mm length and *Eurycercus* were added and a counting of surviving animals was made after 24 hours.

III. RESULTS

Results of the pure prey experiments and natural plankton assemblage experiments in Kootenay Lake (Tables 1 and 2) indicate that adult mysids are capable of preying on both cyclopoids and calanoids under a variety of conditions. Under the experimental conditions of pure prey, the mysids consumed between 1.23 and 1.67 *Cyclops* per hour and between 1.36 and 1.76 *Diaptomus* per hour (Table 1). In the mixed zooplankton assemblage experiment the mysids consumed adult

Table 1. *Feeding rate of adult Mysis relicta and copepodid and adult Cyclops and Diaptomus from Kootenay Lake, in pure prey experiments in 18 l chambers at a concentration of 8 prey l^{-1}. Three replicates were run for each experiment.*

Prey type	No. consumed mysid^{-1} hr^{-1} (± S.D.)	Time	Depth	Temp. °C
Cyclops	1.67 ± 0.36	night	50 m	9
Cyclops	1.23 ± 0.81	day	surface	13
Cyclops	1.52 ± 0.40	day	surface	15
Diaptomus	1.52 ± 0.69	night	surface	16
Diaptomus	1.76 ± 0.37	day	surface	17.5
Diaptomus	1.67 ± 0.58	night	50 m	9
Diaptomus	1.36 ± 0.26	night	50 m	9

Cyclops (0.27 to 0.49 per hour), *Cyclops* copepodids (3.00 to 6.73 per hour), adult *Diaptomus* (0.04 to 0.45 per hour) and *Diaptomus* copepodids (0.04 to 1.16 per hour). The higher predation rates on the *Cyclops* copepodids was possibly a result of their higher density in the chambers (Fig. 1). At low densities of prey items there was no significant difference between the experimental and control chambers (Table 2).

In Lake Mesvattnet, results indicate that both immature and adult mysids feed on *Cyclops* (Tables 3 and 4). Immature mysids consumed between 0.43 and 0.98 *Cyclops* per hour and adults consumed between 0.09 and 0.46 *Cyclops* per hour.

When provided with both *Bosmina* and *Cyclops* sp. in equal densities from Lake Mälaren, adult mysids fed exclusively on Bosmina over the five hours time period of our experiment (Table 4).

The results of the core experiments in Lake Mesvattnet indicated a predation of *Mysis* on *Eurycercus* (Table 5).

Our aquarium observations indicated that mysids actively hunt their prey and would probably be described best as a "cruising, search and attack predator" rather than an "ambush predator" (GERRITSEN and STRICKLER 1977). When a mysid moved forward and a prey organism was encountered in the area between the antennae the mysid would lunge towards the prey, entrapping it with its legs. If the prey escaped in front of the mysid, the mysid moved quickly forward, actively pursuing it. However, if the prey escaped laterally, the mysid swam in one or two tight circles in the direction of escape, often getting a second chance at capturing the prey.

Although no direct observations were made of *Mysis* consuming copepods, a preliminary description of cladoceran consumption can be given. Once a mysid captures a cladoceran, it rotates the prey until the feeding appendages can penetrate the carapace walls. The mysid then proceeds to ingest the contents of the carapace including gut, ovaries and post-abdominal claw, often leaving only the empty carapace. This method of feeding would make it difficult to interpret the herbivorous

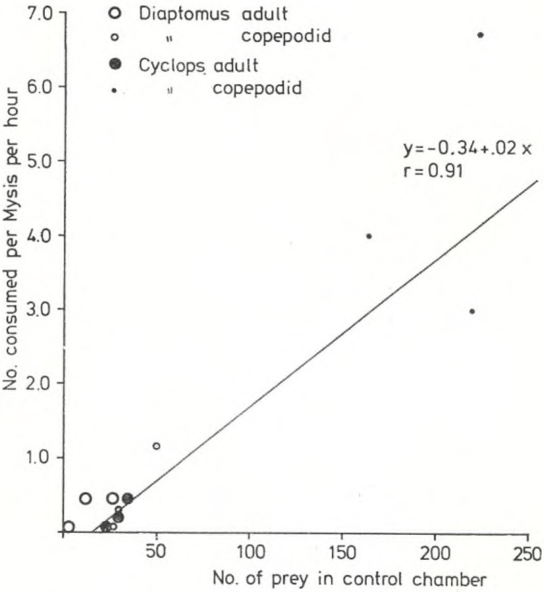

Fig. 1. Number of prey consumed per *Mysis* per hour at different prey densities in 18 *l* feeding chambers in Kootenay Lake (August 1977).

Table 2. *Feeding of adult Mysis relicta on adult and copepodid Diaptomus and Cyclops in natural plankton assemblages. Values in table represent mean (±S.D.) number of Diaptomus and Cyclops remaining in the 18 l chamber after 5 hours in Kootenay Lake (August 1977).*

Expt. No.	*Diaptomus ashlandi*				*Cyclops bicuspidatus*			
	Adult		Copepodid		Adult		Copepodid	
	mysids	no mysids	mysids	no mysids	mysids	no mysids	mysids	no mysids
1	4.3 ±2.9 (*)	11.3±4.7	23.7±9.5 (n.s.)	31.0± 1.7	25.3± 2.9 (*)	37.3± 8.0	97.3±14.0 (*)	164.0±22.9
2	19.3 ±8.0 (n.s.)	29.3±4.9	29.3±6.1 (*)	57.7±11.0	20.0±11.8 (*)	30.0± 5.2	149.3±23.5 (*)	225.7±27.2
3	6.67±4.5 (n.s.)	7.3±2.5	25.3±9.7 (n.s.)	25.7± 5.0	47.3±20.8 (n.s.)	55.0±22.6	144.3±20.67 (*)	220.0±68.2

* —significant difference between control chambers and chambers with mysids at 10 % level (t-test)

n.s. = not significant

Table 3. *Feeding rate of adult and immature Mysis relicta on adult and late copepodid Cyclops scutifer in Mesvattnet in "natural" plankton assemblages.*

No. *Mysis*	Length mm	No. *Cyclops* Initial	Final	Diff.	No. consumed $Mysis^{-1}$ $hour^{-1}$
20	12	89	43	46	0.46
20	12	107	98	9	0.09
20	8	108	57	51	0.51
20	8	100	2	98	0.98
*15	8	40	8	32	0.43
*15	8	40	2	38	0.51
*15	8	40	0	40	0.53
0	—	102	102	0	0
0	—	119	118	1	0
* 0	—	35	34	1	0
* 0	—	35	33	2	0
* 0	—	35	35	0	0

* 10 *l* containers

Table 4. *Feeding of adult Mysis relicta on Bosmina and Cyclops in 10 l chambers containing "natural" plankton assemblages (< 70 μ).*

No. *Mysis*	*Bosmina* Initial	Final	Diff.	*Cyclops* Initial	Final	Diff.
10	40	2	38	40	39	1
10	40	1	39	40	39	1
0	40	40	0	40	38	2
0	40	40	0	40	40	0

Table 5. *Predation experiment with Mysis and Eurycercus added to cores.*

Expt. No.	No. of added animals *Mysis*	*Eurycercus*	No. of surviving *Eurycercus*
1	5	20	20
2	10	20	11
3	10	10	7
4	5	10	7

feeding habits of *Mysis* from gut content analysis as material originally filtered by the prey cannot be distinguished from material filtered by the mysid.

IV. DISCUSSION

In both Kootenay Lake and Lake Mesvattnet *Mysis* fed on copepods. Since no dead copepods were observed in the control chambers at the end of the experiments, it is assumed that *Mysis* was feeding on live copepods. In Stony Lake in the summer, despite the presence of copepods (*Limnocalanus macrurus, Cyclops bicuspidatus thomasi*) *Mysis* fed almost exclusively on cladocerans (LASENBY 1970), although recently it has been shown that *Mysis* will prey on *Limnocalanus* in Stony Lake (LASENBY 1979). In this study, when offered *Bosmina* and *Cyclops* in equal numbers, *Mysis* from Lake Mälaren fed only on *Bosmina.*

In Kootenay Lake, both *Daphnia* and *Bosmina* abundance decreased after *Mysis* introduction (ZYBLUT 1970). A similar trend showing decreasing cladoceran abundance has been demonstrated for Lake Tahoe (RICHARDS *et al.* 1975, MORGAN *et al.* 1978, GOLDMAN *et al.* 1979) and Lake Mesvattnet (KINSTEN and OLSÉN 1981). FÜRST *et al.* (1978) have examined over 1,500 stomach contents of char captured in Lake Blåsjön in northern Sweden in July and October since *Mysis* was introduced in 1964 and document the gradual disappearance of the benthic cladoceran *Eurycercus* and the reduction of other cladocerans in the char stomachs. Although the observed decline in *Eurycercus* may simply reflect a preference of char for some other food (*e.g. Mysis*), we captured no *Eurycercus* in recent trawl hauls (July 1979) from Lake Blåsjön, indicating that they had decreased in number in the lake. The observation that *Eurycercus* is readily eaten by *Mysis* plus the step by step expansion of *Mysis* in Lake Blåsjön followed at each stage by the disappearance of *Eurycercus* from the char stomachs (FÜRST *et al.* 1978, 1981) does provide evidence that *Mysis* played a role in its decline. Under similar circumstances, *Eurycercus* is also reduced in number after *Mysis*' introduction into Lake Torrön (FÜRST *et al.* 1981).

From these observations, one might predict that when introduced into an oligotrophic lake *Mysis* would first prey on cladocerans such as *Eurycercus, Daphnia* and *Bosmina.* When the density of these species becomes low, they would then prey on copepods as they are now doing in Kootenay Lake and Lake Mesvattnet. It is unlikely that such a change would occur in more productive eutrophic lakes, where cladoceran abundance would be higher or in lakes where mysid distribution is restricted because of lake morphometry (*e.g.* Stony Lake, LASENBY 1971), or heavy fish predation. Also, such a trend would be considerably complicated by seasonal variation in the mysid diet, plus fluctuations in cladoceran and copepod numbers.

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Population Ecology of Salmonid Populations on the Verge of Extinction in Acid Environments

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ABSTRACT

The process of acidification is evident also in the Swedish high mountains. In the Fulufjäll area pH-levels have reached the range of variation which is critical to salmonid fish, and as a consequence some populations of char and grayling have become extinct and subsequent restocking experiments have proved unsuccessful.

pH-tolerances can be described by deliberately coarse limitations as follows:
char tolerated the pH register 5.5—5.0 but disappeared when pH dropped below 5.0. Burbot is preliminarily placed in the same class. Grayling disappeared when the pH dropped from 5.5 to 5.0. Trout did not disappear when the pH dropped just below 5.0. The tolerance to lower pH has not been studied.

Critical limits could be defined approximately from these observations, but there is rather a risky pH register than a risky pH-level and within such a register, pH or water qualities covarying with pH become increasingly important when pH decreases. Other factors influencing the reproduction and survival within this critical register are, e.g., intraspecies competition and a disease (char), fishing pressure (grayling), and competition from other species. Interspecies competition becomes particularly evident when establishing new populations.

Certain characteristics of populations living on the verge of extinction are particularly interesting. Growth is fairly good and recruitment still functioning in brown trout populations living at a pH just below 5, but the FULTON coefficient and the flesh colour have deteriorated. Intermittent reproduction in a char population living in the pH range 5.5—5.0 is rendered evident by liming in certain years.

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I. INTRODUCTION

The sedimentary Jothnian rock in the Fulufjäll high mountain region is very poor in lime, and it is probable that the alkalinity was low even in earlier days. In the 1960s increasing problems with the fish populations were encountered in combination with suspected acidification (ANDERSSON, GUSTAFSON and LINDSTRÖM 1971), a suspicion that was confirmed by analysis of snow and water chemistry (DICKSON 1973, 1975). In this district with a pH just above or below the level that salmonid species populations can endure, char and grayling populations have become extinct and some restocking experiments have been unsuccessful. The paper will discuss some traits of the population ecology of salmonid populations in acid environments.

The study stems partly from a coherent management programme that the owner of the fisheries

Table 1. *Number and mean weight of char from Lake Stora Rösjön, caught in gill net, with different mesh sizes, knot-to-knot measure. Inconsistent values of mean weight for mesh size indicate heterogeneity (F-char and normal char).*

Year	Date	Gill nets 50.0 mm	Catch of char	Gill nets 37.5 mm	Catch of char	Gill nets 33.3 mm	Catch of char	Gill nets 30.0 mm	Catch of char	Gill nets 27.3 mm	Catch of char	Gill nets 25.0 mm	Catch of char	Gill nets 21.4 mm	Catch of char
1957	3/9			9	26					10	11				
1958—60		26	9	32	64 $\bar{w}=0.428$	64	179 $\bar{w}=0.331$	64	281 $\bar{w}=0.223$			26	186 $\bar{w}=0.166$	32	307 $\bar{w}=0.099$
1968—70	8—17/9	4	2 $\bar{w}=0.630$	4	13 $\bar{w}=0.576$	8	23 $\bar{w}=0.364$	4	7 $\bar{w}=0.132$	2	5 $\bar{w}=0.328$	6	38 $\bar{w}=0.240$	8	60 $\bar{w}=0.081$
1963—70															
1971	22/4—16/9														
1972	29—31/8			2	5 $\bar{w}=0.274$	2	7 $\bar{w}=0.330$			4	27 $\bar{w}=0.052$				
1971—74 1976	Sept.	176													
1972, 73 74, 77	17/5—12/11														
1974, 76 79, 80	24/6—11/8														
1978, 79	10—13/6			2	5 $\bar{w}=0.710$			1	8 $\bar{w}=0.271$			1	6 $\bar{w}=0.368$	2	10 $\bar{w}=0.090$
1978, 80	28/8—5/9	6	18 $\bar{w}=0.889$	6	11 $\bar{w}=0.725$	6	28 $\bar{w}=0.512$	6	23 $\bar{w}=0.477$			6	58 $\bar{w}=0.206$	6	99 $\bar{w}=0.136$

on the Fulufjäll has carried through since the 1940s. In the beginning the programme aimed at increased mean size and a better sport fishery, in recent times at decreasing the damage caused by the acidification of the precipitation. The latter phase of the programme is a cooperative research with the National Swedish Environmental Protection Board and will be published in full later on.

The present paper is based on material from the years 1968 (1958) to 1980 and the material comprises char otoliths or trout scale samples and data connected there with, mainly obtained by gill netting, approximately 700 efforts (Table 1, 4 and 5).

II. INTERMITTENT REPRODUCTION: THE CHAR POPULATIONS OF LAKES STORA AND LILLA RÖSJÖN

Lakes Stora and Lilla Rösjön have long been inhabited by a fairly dense population of small-sized F-char (NYMAN *et al.* 1981) and a population of normal char. Gill-net catches are reported in Table 1. F-char are seldom caught in gill nets coarser than the 16.7 mm mesh size category. In the 16.7 gill nets the mean weight of the F-char is about 0.03—0.04 kg (details in Fig. 3). In gill nets of the 21.4 and 25.0 mm mesh sizes, the number of char caught by unit effort drops dras-

Gill nets 16.7 mm	Catch of char	Gill nets 12.5 mm	Catch of char	Gill nets 10.0 mm	Catch of char	Gear	Catch of char only number	Weight sum	Notes
						Two gill nets, 42.9 mm	0	10.60	
19	1,496 $\bar{w}=0.032$							269.33	Fishing for density estimate
9	794 $\bar{w}=0.033$							60.19	Fishing for density estimate
						Seine	29,600	486	Char transported to other lakes
2	542 $\bar{w}=0.034$			1	85 $\bar{w}=0.012$	Angling, seine	80		The last year of the 1963 year class
2	233 $\bar{w}=0.036$			1	122 $\bar{w}=0.014$			15.11	
1	103 $\bar{w}=0.051$			1	0			—	Erratic samples from spawning of normal char (left)
						Angling, gill nets	136	—	Fishing for various purposes
4	423								Check of the F-char population
1	31 $\bar{w}=0.046$	1	10 $\bar{w}=0.023$			Gill nets	34	17.94	
6	197 $\bar{w}=0.076$	2	212 —	1	53 —			89.67[1]	Fishing for density estimate

[1] Mesh sizes 12.5 and 10.10 excluded.

tically and the mean weight increases more than would have been expected with a homogeneous population. In extreme cases the normal char can attain 4—5 kg. The lakes are shallow (max. 3.5—4 metres) and very uniform, but the F-char is heterogeneously distributed within them. The F-char appears in incoming and outgoing brooks too, and in the 1960s it moved in midsummertime down the outlet of Lake Stora Rösjön to a pool between the two Lakes Rösjöarna (ANDERSSON *et al.* 1971).

For an ordinary sports fisherman, the sorting of the catch into two groups should not cause much hesitation, as almost every F-char in the catch is adult whereas normal char is juvenile up to and over the maximum size of F-char (~25 cm). Adult F-char as distinguished from normal char is recognized by dark colour, parr marks and a body less fusiform than normal char of the same size. Old F-char have a blunt nose and large eyes. Juvenile normal char between approximately 15 and 30 cm long have a silvery glow from their flanks in shades of red on their fusiform body (ANDERSSON *et al.* 1971). These characteristics are used when char is preliminarily sorted for protein analysis (NYMAN 1972). A gonad analysis has given the necessary basis for separating juveniles and adults (FLUMÉ 1978).

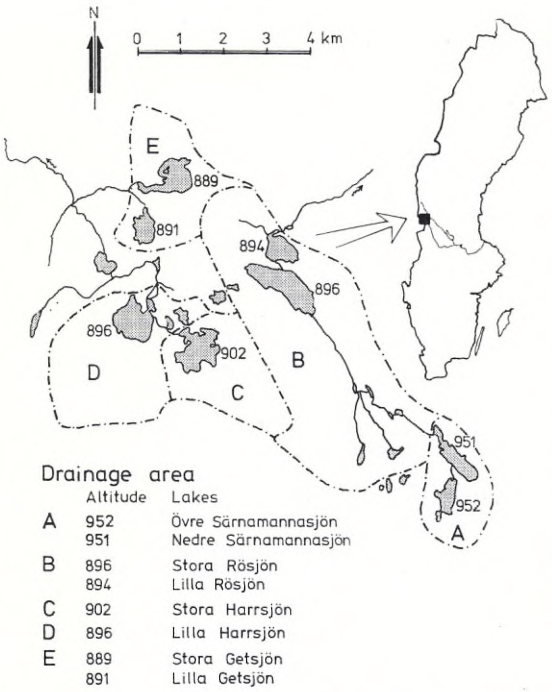

Fig. 1. Map of the Fulufjäll lakes and their drainage areas.

Only when the char are young, two summers and less, have no workable field characters been detected that could be used for a preliminary sorting into normal char and F-char. All the two-summer-old char are fusiform, have a yellowish-red or rosy colour, faint parr marks and a trace of silvery glow. There are indications that the growth of normal char is better than that of F-char during their second summer (LINDSTRÖM and ANDERSSON 1980). The catch in gill nets with a mesh size of 12.5 and 10.0 mm (Table 1) has been preliminarily sorted with the aid of this and other features.

There are several reports on the fishery in the Lakes Rösjöarna from different parts of this century, and the fishery has long been the object of management. In earlier days horse manure was used as fertilizer in the lakes. The acid state of the lake water was recognized (Table 2). In 1962 15 tons of lime and 5 tons of thomas-phosphate was distributed in Lake Stora Rösjön. These ingredients were described in general terms as artificial fertilizer, and they were so designated in our first report, when the effective agent was far from having been pinned down. Measured as total P, the amount of phosphorus equals approximately the levels reached as an accessory effect of liming the Fulufjäll lakes in 1977 (Dickson in Fiskeristyrelsen and Statens Naturvårdsverk 1979).

The treatement in 1962 was succeeded by the important 1963 year class, in the population both of F-char and normal char (ANDERSSON *et al.* 1971). The year class could be followed in the gill-net catches in the period 1967—71 (Fig. 2). Seining in the years 1964—69 in the exit from Lake Stora Rösjön at midsummer time gave important catches of F-char smaller than those caught in gill nets, mesh size 16.7 mm knot to knot, in the lake, but still those aged (in 1967) belonged to the 1963 year class. Such F-char remained in the pool between Lakes Stora and Lilla Rösjön during the summer. This is an indication of fractions with different growth within the F-char population.

In the years 1970—72 the seining was unsuccessfull and finally is was abandoned. The percentage of the 1963 year class decreased markedly in some catches during 1971, and this indicated the disappearance of the 1963 year class (Table 3).

F-char caught in the pool in 1971 and later were longer than before as were also F-char caught elsewhere in gill nets in 1974—76 (Fig. 3). Such changes might be the effect of growth changes and age structure. Beginning with age structure, the fairly important 1970 year class appeared in catches with a very fine-meshed gill net in 1971 and 1972 (mesh size 10.0 mm, Table 3). In 1974 they were within the catching range of the mesh size 16.7 mm illustrated in Fig. 3.

The maximum length in 1976 in Fig. 3 probably reflects one or two weak year classes (1972, 1974), but even the 1973 year class contributed to later catches, although 1973 shows the lowest pH recorded (Table 2, approx. pH 5). There is no longer a dominance of one single year class. In the catches from the latest years a new important year class is observed, the 1976 year class, and this may possibly develop into a new dominating year class (Table 3). The variation in the strength of year classes illustrated by this table does not follow the variation of pH in detail (pH observa-

Table 2. *Measurements of pH and report on liming of the Fulufjäll lakes. The pH is measured (1) with Radiometer with combined electrodes in the vicinity of the lakes, in some cases after a few hours in darkness, full bottles, (2) with Merck equipment at the border of the waters, marked*, or (3) in a laboratory after transport in darkness, full bottles, analysed by the National Swedish Board of Environmental Protection, marked**.*

The pH dropped a few tenths, if the electrode was dipped in running water directly or if the water was kept in an open bucket some time before being analysed with the Radiometer (such values are discarded).

Year	Date	Övre Särna-mannasjön		Nedre Särna-mannasjön		Stora Rösjön			Stora Harrsjön		Lilla Harrsjön			Stora Getsjön	Lilla Getsjön	Notes on liming
		Lake	Outlet	Lake	Outlet	Main inlet	Lake	Outlet	Lake	Outlet	Main inlet	Lake	Outlet			
1964					5.2*			5.6*		5.5*			5.5*	5.8*	5.8*	
1969	16—18/9				5.0*	4.7		5.3								
1970	10/3			5.0**			5.2**									
	29/4						5.6**									
	16—17/6				4.7	4.9		5.3		5.2						
	8—9/9					5.3		5.4		5.3						
								5.5								
1971	30/6				4.8*			5.3*								
	9/9	4.8	5.1		4.9			5.4								
1972	5/7	4.9*			4.9*			5.2*								Liming of Lakes Nedre Särnamannasjön and Stora Harrsjön with little effect
1973	11/4	4.4**		4.5**			4.8**									
	27/7	5.2*			5.2*	4.9**	4.8**	5.3*								
	18—20/9		4.9**		4.9**	5.1		5.2								
						5.6**		4.9**								
1974	21/8		4.9*		4.9*			5.5*		5.0*			5.0*			Liming of Lake Stora Rösjön in 1973—76, Lake Nedre Särnamannasjön in 1975—76 and Lake Stora Harrsjön in 1976
1975	1/4			4.8**				5.1**	5.1**			5.0**				
	2/7		4.2**		5.1**			4.5**								
	10—25/9	4.9		6.1	5.4			5.4**		5.0**						
1976	30/3	4.6**		5.3**		5.1**		5.0**	4.7**			4.8**		5.3**		
	9/6							5.3	5.8	5.9	5.4	5.0	5.1			
	28—30/6				5.4			5.8		5.9	5.5		5.2			
	3—5/8	5.1		6.3			6.1	6.2	5.5	5.5	5.4	5.1				
1977	30/8—2/9		4.9		5.2			5.4		5.1		5.0		5.6		Liming of Lakes Nedre Särnamannasjön and Stora Rösjön
1978	30/8							5.7*	5.0*	5.0*		4.8*				
1979	11/6							5.5		4.9					5.2	
	27—31/8	4.8		5.9				5.4	5.0	4.9		4.8		5.1		
	11/9							5.3						5.2 5.3	4.9	Liming of Lakes Stora and Lilla Harrsjön

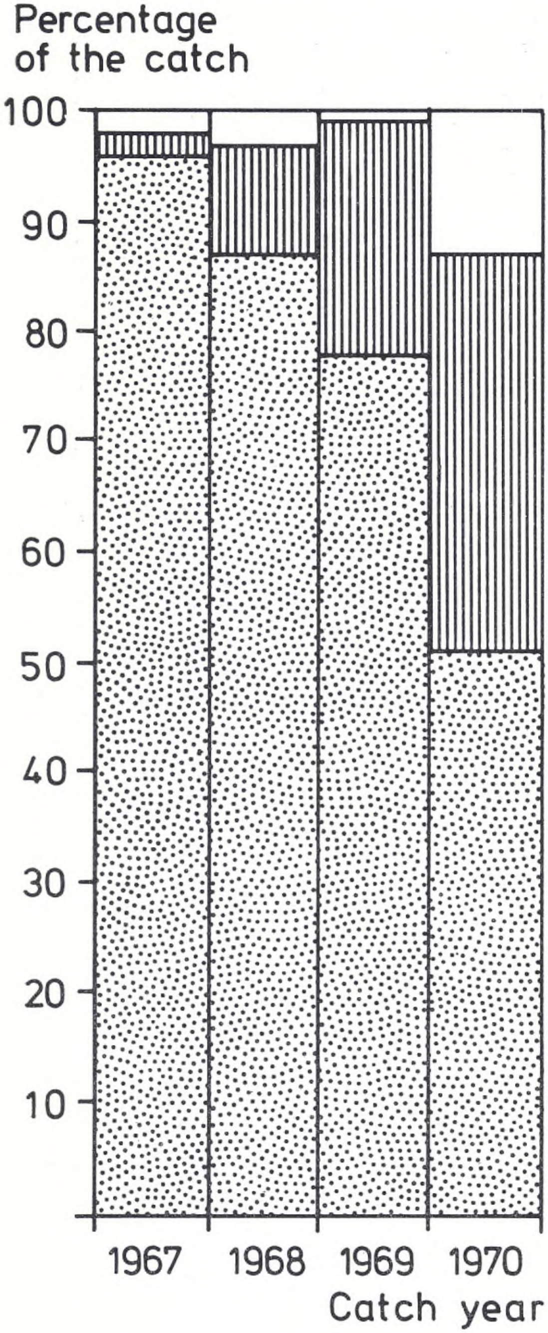

Fig. 2. The char catch in Lake Stora Rösjön, percentages for year class 1963 (stippled part of the columns), 1963 or adjacent year class (hatched) and other year classes (white). With old specimens the aging becomes more difficult.

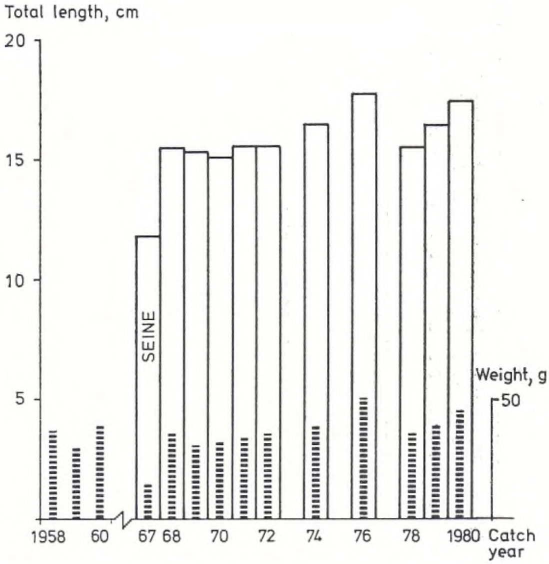

Fig. 3. Mean total length and mean weight of char caught in Lake Stora Rösjön in gill nets, mesh size 16.7 mm knot to knot. Increased growth of the F-char born in the 1970s and some weak (*e.g.* 1972) and some rich year classes (1976) have influenced the shape of the diagram. (Eleven normal char of 30—50 cm total length are excluded from the catches.) Mean total length and mean weight of F-char of year class 1963, caught with a seine in 1967, is also indicated.
Total length sample, variance:

1968	1.88	1974	1.83
1969	2.10	1976	2.32
1970	1.26	1978	3.11
1971	1.22	1979	1.59
1972	1.58	1980	14.1

tions from Fulufjället and Trysil, Dickson 1975, and Table 2), but the char populations have responded clearly to the important liming in 1962 and the short maximum in pH 1976.

Growth of the 1963 year class is illustrated in Fig. 4. The growth in year classes 1963—69 is reported by Flumé (1978). The better growth of year class 1966 and later year classes of F-char is illustrated in Fig. 4. The changes in length in Fig. 3 in fish caught with gill net, mesh size 16.7 mm knot to knot, are thus the compound effects of age structure and growth changes, the better growth dominating the end result from catch year 1976 onwards. The mean size of the char caught in gill nets with mesh size 16.7 mm responds very

Table 3. *Distribution of char year classes in catches from Lake Stora Rösjön according to aging of otoliths. The gill-net characteristics are knot-to-knot (bar) measurements. A stretched mesh is twice those values.*

Year	Date	Gill nets, mesh size (knot to knot) or other gear information	Total catch (if known)	The distribution of the catch of N- and F-char	Year Class															Notes
					1964 and older	–65	–66	–67	–68	–69	–70	–71	–72	–73	–74	–75	–76	–77	–78	
1971	22/4– 1/7	Angling seine	76	13N+2?	3			2?	4	6										
				61F	59			1												
1971	2–3/9	50.0–27.3		N	2		3	3	7	2										Erratic samples from spawning of normal char
				F	1					3	1									
1971 72	16/9 30/8	10.0	207	7N							6N?	1N?								
				133F	3	2				5	114	9								
1972– 74	29/8– 22/9	50.0–27.3		N			5	2	7	21	25	10								One normal and four F-char older than these.Erratic samples from spawning of normal char
				F																
1972 73 74	17/5–12/11 26/4–29/8 25/4–4/7	Various types of gear	26	20N				3	2	3	6	5								One normal char of year class 1965
				6F			2		2	2										
1974	24/6	16.7	41	1N							1									
				40F			1	2	1	1	8	1								
1976 78	1/9 11–13/6	Coarse meshed gill nets	56	31N									5	3	1	9	11			
				25F								2	2	4	1					
1976 77	5/8, 1/9, 30/8	16.7	310	14N										3	1	7	3			
				296F							4	7	2	7	1	2	2			
1978 79	29–31/8 10–11/6 28–30/8	50.0–21.4	193	96N							1		6	20	9	19	35	5		
				97F									1	2	1	6	27			
1978 79	29–31/8 10–11/6 28–30/8	16.7	161	32N									1	1	2	1	7	18		
				129F										1		8	53	1	1F?	
1978 79	29–31/8 10–11/6	12.5	212	N										1			4	3		
				F												2	28	3+9F?	2F?	
1979	30/8	10.0	53	53F															52	

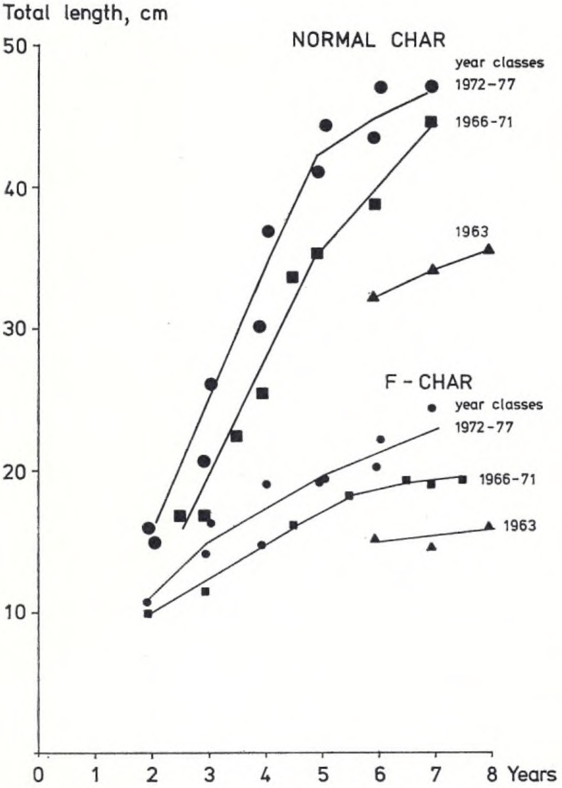

Fig. 4. Growth of normal and F-char from Lake Stora Rösjön. The best growth is shown by year classes 1972—77 caught in 1976—79 (black dots).

noticeably to changes in the F-char population. In the years 1976—79 about ten F-char over 25 cm total length are caught, a fact which is explained by the better growth, and F-char can now also be expected in catches from mesh size 21.4 mm and coarser. For a detailed analysis of the relation mesh size—fish size see Johnson (1976).

The normal char of the 1966—71 year classes attained in the 1970s a greater total length than did the year class 1963 and the normal char of year classes born in the 1970s grew better still (Fig. 4). The otoliths grow in thickness to an extent that soon makes them difficult to read without grinding (LINDSTRÖM and ANDERSSON 1980). To the five two-summer-old normal char reported there can be added another 19, giving a total length of 15.9 cm for 24 two-summer-old normal char with a mean otolith with width of 1.4 mm.

The F-char is not fully ripe in catches at the beginning of August and the spawning is mainly ended in late August and the beginning of September. In catches from middle and late September eggs from normal char are obtained for the hatchery. Age at first spawning is lower for F-char (three summers) than for normal char (five summers), and otoliths and growth of F-char changes markedly (LINDSTRÖM and ANDERSSON 1980). The material does not admit of an analysis of small changes in age at maturity that may exist in combination with the better growth of both F-char and normal char after 1971.

Strong year classes 1963 and 1976 and better growth in the 1970s concerns normal char as well as F-char. It would be interesting to know whether the ratio between the densities of the two populations has changed. Owing to the heterogeneous distribution of F-char, standing crop and recruitment estimates are difficult to obtain. Maximum catch of F-char in gill nets with mesh size 16.7 mm occurred in 1970—71 with 200—300 per unit effort (Table 1), and in later catches with corresponding nets the number dropped drastically. It may be that in 1971, just before the disappearance of the 1963 year class, even the slow growing fraction of this year class had reached a size that made them catchable with this mesh size. Catch per unit effort in gill nets of coarser mesh sizes does not fluctuate much (Table 1, the lines "Fishing for density estimates") with one exception. The number of char per unit effort increased in 1978 in mesh size 21.4 mm owing to catches of F-char in this gill net. Some knowledge of total yield is necessary for an analyse of the ratio between the densities of the two populations. When the seining stopped, the total yield of F-char dropped and did not later reach the level of the 1960s. Catch of normal char (char above 0.1 kg) has been good in the last few years and in the summer season 1980 amounted to 96 kg. A winter season will normally give much of the total yield and 1980—81 the reported catch of normal char was 102 kg, giving a reported total of 198 kg. The existing data thus indicate that the ratio of normal char to F-char has increased. This is probably also indicated by Table 6, where an estimate of the proportion of young normal char in certain catches is attempted. The only strictly comparable samples are those marked 'Fishing for density estimates'.

Table 4. *Catch of different species and distribution on total length groups of trout in the gill-net catches from Lakes Stora and Lilla Harrsjön.*

Lake	Year	Date	Grayling, totals	Trout, totals	Trout, length distribution (of sample in some cases) 0–10	10–15	15–20	20–25	25–30	30–35	≥35	Char, totals	Gear Mesh size (mm knot to knot) and number of gill nets	Notes
STORA HARRSJÖN	1964	23/6	2	18		1	2	4	5	5	1		33.3–1, 25.0–1, 16.7–1, 11.1–1=4	
	1966	17/6		6								28	50.0–1, 37.5–1, 33.3–2, 30.0–2, 25.0–1, 21.4–1, 16.7–1=9	
	1969–72	15/6–3/7		?								16	Various types of gill nets	Trout not noted. Angling
	1972	1/9		13			2	2	2			3	27.3–3, 25.0–1, 21.4–1, 16.7–1=6	
	1976	9/6, 4/8 31/8		75		1	10	16	23	23	2	12	50.0–1, 37.5–1, 33.3–1, 30.0-1, 27.3–22, 21.4–1, 16.7–1=28	
	1977 1979	16/6 11/6		63			33	19	8		1	2	50.0–1, 33.3–2, 27.3–5, 21.4–2, 16.7–2, 12.5–4, 10.0–2=18	
	1978	30/8		16			2	3	6	5			27.3–3, 12.5–1, 10.0–2=6	
LILLA HARRSJÖN	1968	12/6	4	2				2					27.3–2	Grayling spawning site
	1975	4/6		4				1	2		1		27.3–10	— „ —
	1976	2/6, 10/6 3/8, 3/9	2	129		3	31	15	15	10	5		50.0–1, 37.5–2, 33.3–2, 30.0–1, 27.3–32, 21.4–3, 16.7–3=44	(A few nets on grayling spawning site in June.) Burbot-1
	1977 1979	16/6 11/6		41		1	18	10	8	3	1		50.0–1, 37.5–1, 33.3–1, 30.0–3, 27.3–5, 25.0–1, 21.4–1, 16.7–1=14	
	1977 1978	1/9 30/8		50		1	13	21	13	1	1		27.3–7	

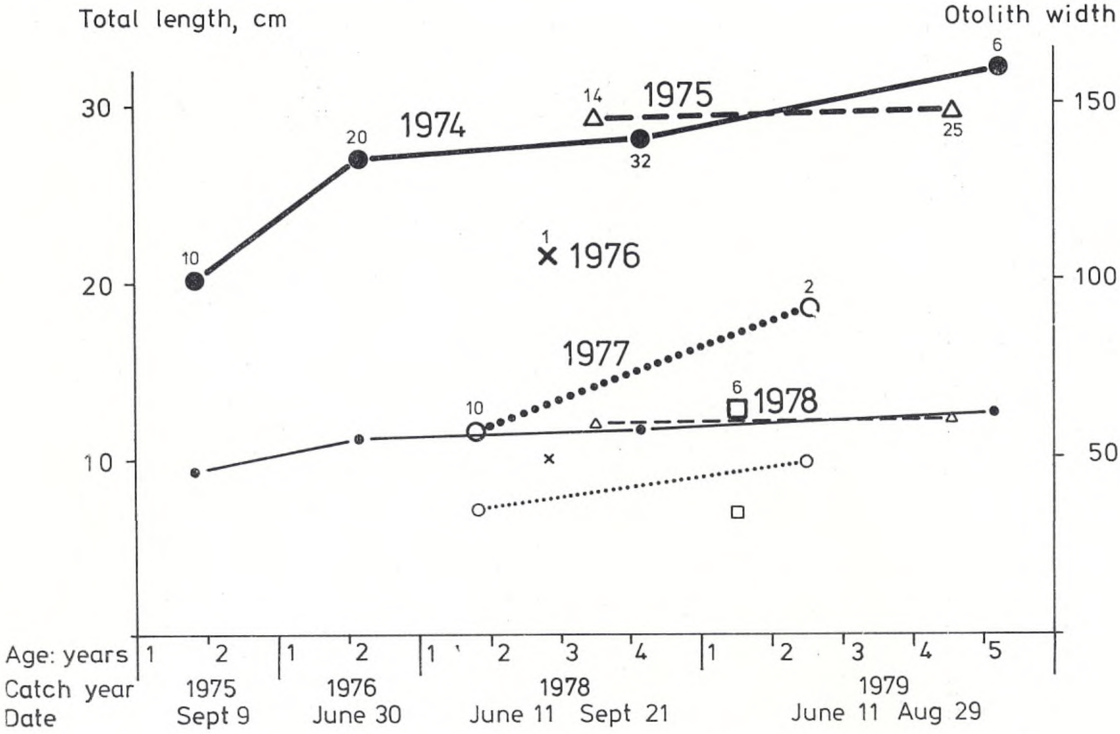

Fig. 5. Growth of char in Lake Nedre Särnamannasjön: ● △ × ○ □
Year classes and sample sizes are indicated in the figure.
Otolith width of char in Lake Nedre Särnamannasjön: • △ × ○ □
The otolith width is given in ocular micrometer units (30 units = 1 mm).

There are some irregularities in the length-for-age data when the char is 4 summers old and more (not shown in the diagram). There is not much growth in this period and the char starts spawning after its fourth summer.

III. TWO TROUT LAKES WHERE GRAYLING IS NOW EXTINCT, LAKES STORA AND LILLA HARRSJÖN

Lakes Stora and Lilla Harrsjön are two trout lakes where single char and burbot respectively are nowadays obtained in the catch, while grayling has recently become extinct (Table 4). Char and grayling will be discussed below. The stray burbot obtained have been small. In looking for effects of acidification on the population of trout, the growth and condition of the trout have been studied. The growth is fairly good, the trout reaching 30 cm total length in both lakes before they are six years old (Wickström 1978). The trout from Lake Stora Harrsjön was once known for its remarkably good condition and even small specimens had red flesh (Lidman 1951). For a catch on June 23, 1964, the Fulton coefficient was 13 of fish between 20 and 30 cm total length, Lake Stora Harrsjön. Both spring and late summer values are lower in the 1970s for both lakes, varying between 8 and 11. The flesh varies from faint pink to white.

When the salt content is low, pH-values between 5.5 and 5.0 can be risky for trout populations (Leivestad *et al.* 1976). The pH in the two lakes reached down to the lower level in the 1970s, although the pH was temporarily raised through liming, locally in 1972 and over most of Lake Stora Harrsjön in 1976 (Table 1), but there are still trout populations in both lakes. The spawning places are not completely known, but the trout is still reproducing and surviving in the stream running from Lake Lilla Harrsjön.

Grayling tolerated the water quality in 1964, at any rate in Lake Lilla Harrsjön and its outlet. At that time a pH of 5.4 is reported from April 29 (PUKE 1971) and 5.5 in the summer from both lakes (Table 2). When the last two grayling were caught in the Harrsjö lake system (in 1976) the pH remained around 5 in Lake Lilla Harrsjön and the grayling spawning stream running from this lake.

The existence of an important grayling population living sympatrically with trout in these lakes is documented in several ways—their names in English are the Grayling Lakes. There are Memoranda from the National Board of Forestry from 1940—47 speaking of the grayling populations in these two lakes and grayling eggs taken for fish culture, two papers (LIDMAN 1951, KJELLIN 1958) about the sport fishing, and several personal communications about grayling eggs obtained from lakes (Table 2). When the last two grayling were waters. A fisherman's journal reports grayling from Lake Lilla Harrsjön between 1947 and 1963 (Evert Halvarsson). In Lake Lilla Harrsjön there was still an acceptable grayling fishing at the end of the sixties. In the survey fishing with gill nets of different mesh sizes (Table 4) between 1964 and 1979, the last two grayling were caught in 1964 in Lake Stora Harrsjön and in 1976 in Lake Lilla Harrsjön. Char from Lake Stora Rösjön were planted in Lake Stora Harrsjön in 1964 and they may have competed with grayling there.

IV. THREE CASES OF UNSUCCESSFUL ATTEMPTS TO ESTABLISH NEW POPULATIONS

The management of the Fulufjäll lakes has included attempts to establish new populations of their original species in other lakes on the high mountain.

Char introduced in Lake Stora Harrsjön

In the years when grayling was receding in the two Lakes Harrsjöarna, F-char and young normal char were caught with seine in Lake Stora Rösjön and transported to Lake Stora Harrsjön, 3,400 in 1964 and 350 in 1971 (ANDERSSON *et al.* 1971). Char were caught up to and including 1979 in Lake Stora Harrsjön but not in Lake Lilla Harrsjön, situated a short distance downstream (Table 4).

Most of 13 studied char caught in Lake Stora Harrsjön between 1964 and 1971 belonged to the 1962 year class and had in 1969—71 either achieved a length well over 40 cm or were between 22 and 29 cm long. The F-char in Lake Rösjön did not grow over 20 cm at that time, and the 22—29 cm group was probably F-char, benefiting from the new environment. The char caught in Lake Stora Harrsjön in 1972—79, *i.e.* after the second introduction, belonged to 1963—70 year classes, and four were between 28 and 33 cm and the other 16 well over 40 cm in total length. No small char are obtained in the fine-meshed nets (Table 4), and there are no other indications of reproduction. Residual eggs are often noted on the char female caught in the spring.

Introduction of char into Lakes Lilla and Stora Getsjön

In 1963 800 char from Lake Stora Rösjön were planted in Lake Lilla Getsjön. Char were obtained in the catch up to 1967 and they were also obtained in Lake Stora Getsjön (G. ZACHRISSON, pers. comm.). The outlets from the two lakes join a short distance downstream. Lake Lilla Getsjön is very shallow and the amount of liquid water is substantially reduced in the winter. It is probably greatly influenced by the character of the precipitation. The pH measured in the lake was 5.6 in April 1964 (PUKE 1971) and the pH in the outlet was 5.8 in 1964 and 4.9 in autumn 1979 (Table 2). Lake Stora Getsjön is one of the deepest lakes on the Fulufjäll high mountain, but this only means that there is a pit with a maximum depth of over 7 metres. There is a bog in the precipitation area and the lake water is slightly brownish in colour. The pH is higher than in most other lakes before liming on the Fulufjället (Table 2). The pH was 5.6 in April 1964 (PUKE 1971) and 5.8 in the outlet in 1964, and in autumn 1979 it was 5.2—5.3. A survey fishing in 1977 in Lakes Lilla and Stora Getsjön with 15 gill nets of various mesh sizes gave in Lake Stora Getsjön 76 trout and 9 burbot. The fishing by local fishermen can be exemplified by a report from 1978 when Lake Stora Getsjön was fished with 66

Table 5. *Catch of char in gill nets in 1967–80. Lakes Övre och Nedre Särnamannasjöarna. The second lake was limed in 1972—77 and restocked in 1975—76.*

Year	Date	Lake	Catch of char Number	 Weight	Gill nets Number	Mesh size, mm
1968	11/9	Övre Särnamannasjön	24	2.25	11	27.3, 25.0, 21.4 and 16.7
1969	18/9	”	4	0.20	3	25.0, 21.4 and 16.7
1971	10/9	”	1	0.06	10	27.3, 16.7 and 14.3
1972	30/8	”	0		5	27.3, 25.0, 21.4, 16.7 and 12.5
1980	2/9	”	0		12	30.0, 27.3, 21.4, 16.7 and 12.5
1967	21/6	Nedre Särnamannasjön	0		3	30.0, 21.4 and 16.7
1968	11/9	”	3	0.39	19	27.3, 25.0, 21.4 and 16.7
1971	10/9	”	0		5	27.3 and 16.7
1975	10/9	”	40	—	3	21.4 and 16.7
1976	30/6	”	20	3.68	3	27.3, 21.4 and 16.7
1978	11/6	”	37	7.11	5	27.3
1978	21/9	”	21	2.47	4	27.3 and 10.0
1979	10/6	”	18	3.37	5	27.3, 25.0, 21.4, 16.7 and 12.5
1979	29/8	”	27	6.24	4	27.3, 12.5 and 10.0

gill nets, mesh size 3 cm knot to knot. No char was obtained in this fishing either, but 263 trout were caught (the burbot being uncounted). No reproduction seems to have followed the char introduction.

Introductions of trout into the Lakes Rösjöarna and adjoining brooks

Some 20—30 half-grown trout from Lake Lilla Getsjön were planted in Lake Lilla Rösjön in 1951 and 10,000 trout fry were planted in the brook running to Lake Stora Rösjön in 1944 (National Board of Forestry, memorandum 1952). The planting did not result in a trout population. There has been a fishing camp between Lakes Stora and Lilla Rösjön since 1956 and trout has never been reported in the catches, in spite of intensive fishing. The rock of the Fulufjäll is very poor in lime, but the pH decrease through air pollution had not started at that time, so far as is known.

V. A SUCCESSFUL RECLAIMING OF A CHAR LAKE, LAKE NEDRE SÄRNAMANNASJÖN

The uppermost lakes studied, Lakes Övre and Nedre Särnamannasjön, were inhabited by small char and single char of better size up to the 1960s (National Board of Forestry, memorandum 1940, Lidman 1951; gill-net fishing, Table 5; several personal communications). Occasional plantings of char fry and small-scale fertilizing were included in the management of these lakes in those days.

According to Table 5 the catch was, however, poor. A fish disease was observed at the end of the 1960s (Lundborg in MS). The pH in natural state in lakes with such small catchment areas can be guessed to have equalled that of rain in a natural situation, but it dropped below 5 at the beginning of the 1970s — older observations are lacking with the exception of a pH=5.4 from April 29, 1964 (Puke 1971) and a pH of 5.2 in Table 2. Fig. 5 shows the absence of year classes from the beginning of the 1970s. The bottom fauna is not known from that period but the zooplankton has been described (Hanson 1974). In September 1975 the zooplankton in Lake Övre Särnamannasjön was very poor and some *Diaptomus* were of an aberrant shape and colour (bright red, probably dying).

In Lake Nedre Särnamannasjön a new development occurred in the mid-1970s as a liming and char introduction programme started, Table 2, Fig. 5, and the introduction of 1+ old char in July 1975 was successful. Fry of normal char from Lake Stora Rösjön were raised at the Färnäs hatchery and in July of their second summer had reached about 15 cm in total length. In September 1975 a sample taken with gill nets and an otolith study has made it possible to assign the fish to

Table 6. *Juvenile normal char ♀♀ ≤ 25 cm, percentage of total catch in Lake Stora Rösjön. The seasonal variation is great, and the effect on the samples related to spawning time is obvious.*

	Early summer netting		Seine and angling	Caught just before the F-char spawning	Erratic samples from spawning of normal char	Fishing for density estimates			
Year, date	1974 June 24 and 1979 June 10—11		1971 June 30, July 1	1976—80 July 30—Aug. 11	1971—72 Aug. 29—Sep. 22	1968—70 Sep. 8—17		1976—80 Aug. 28—Sep.5	
Mesh size, mm (Gill nets)	37.5—21.4	16.7	—	16.7	50.0—27.3	50.0—21.4	16.7	50.0—21.4	16.7
Number of normal char	11	3	13	4	45	63	2	115	45
Number of F-char	14	43	23	378	9	39	416	90	255
Juvenile normal char ♀♀ ≤ 25 cm, percentage of total catch	0	2.2	16.7	0.3	20.4	2.0	0.2	8.3	6.3

the year class 1974 — and not to char fry of the same stock introduced in 1973 (LINDSTRÖM and ANDERSSON 1980). With a total length of 20 cm and an otolith width of 1 1/2 mm, the growth up to the age of nearly two years was very good. At midsummer the following year, single specimens had started to become sexually mature and offspring of a spawning in autumn 1976 were obtained (Fig. 5). A similar introduction of 1+ char in July 1976 was also successful. Later on, the growth deteriorated, and 4, 4+ and 5 year-old fish no longer surpassed the growth curve of normal char in Lake Stora Rösjön (Fig. 4). The progeny born in Lake Nedre Särnamannasjön did not grow so well as the 1+ normal char from Lake Stora Rösjön in the 1970s (LINDSTRÖM and ANDERSSON 1980). It seems that any surplus food production that may have been accumulated in Lake Nedre Särnamannasjön during the early 1970s when the lake was fishless has now been used up, and there is no F-char for the normal char to feed on when attaining 30 cm total length. The number of char young per hectare introduced in 1975 and 1976 is in conformity with general practice. The feeding habits of char in Lake Nedre Särnamannasjön after the reclaiming are analysed and compared to those in Lake Stora Rösjön (HANSON 1976 and in MS).

VI. DISCUSSION

The distribution of roach, which is very sensitive to acidity, ends at an altitude of ∼750 metres in the River Härjeån in the neighbouring River Österdalälven (KURT DAHLQUIST, pers. comm., ANDERSSON *et al.* 1980). The River Härjeån passes through porphyries. The River Västerdalälven passes through sedimentary Jothnian rock in its upper part and diabases commence at the inflow of River Galån (MAGNUSSON *et al.* 1958, Länsstyrelsen i Kopparbergs län 1975). Roach has not advanced in the main river past the inflow of River Galån, but exists in Lakes Bornåsjön and Hönselhån in the River Galån (KURT DAHLQUIST pers. comm.). The roach populations in the Rivers Härjeån and Galån are probably depending on local occurrence of less acid rock and quarternary deposits.

At the starting point of River Västerdalälven on the Fulufjäll such elements are lacking. There the indigenous populations of char, trout, grayling and burbot have long lived under a risk of becoming extinct through a change in the water quality, due to the specific characters of this high mountain district. The alkalinity of the lakes in this district in a natural state has probably not exceeded 0.02 meqv/l (Dickson 1978), the rock is very poor in lime, and the soil is thin and barren (Lundquist 1951, Magnusson *et al.* 1958). The precipitation cannot change much in quality before reaching the lakes, particularly in the uppermost lakes with very small catchment areas. It was in the uppermost lakes that the water first became intolerably acidic for fish (Andersson *et al.* 1971. *Cf.* also Lakes Särnamannasjöarna, p. 92).

Many factors may be responsible for the reduction or extinction of a population in the sense that they affect the reproduction and survival governing the population size. Competition from transferred char and fishing pressure on the spawning stock may have contributed to the extinction of grayling from the Lakes Harrsjöarna. The pH approached 5 when the grayling population of Lake Lilla Harrsjön finally disappeared. The grayling is a little more sensitive to low pH than is char. The pH may well have dropped below 5 in the small tributaries several years earlier when they were filled with melting snow in the spring, but the known spawning site was in the outlet of Lake Lilla Harrsjön, where the water was drained from the central bulk of lake water in Lakes Stora and Lilla Harrsjön.

When a species is living in an environment that becomes more intolerable but the unfavourable values are not developing according to a simple time curve, better years are intercalated in a series of unfavourable years. The favourable years may result in a reproductive success, and the resulting year classes may even help towards the suppression of reproduction in the bad years (Alm 1952). Such intermittent reproduction, rendered evident by the artificial effect of liming, is reported from char in Lake Stora Rösjön in the sixties p. 84—88). The intermittent reproduction is in this case an indication that the population is on the verge of extinction.

The difference between reproductive success and failure is a question not only of winter and spring pH but also of intraspecies competition; furthermore the reaction of the food animal populations may be important. This development in Lake Stora Rösjön has taken place at a pH level 5.5—5.0. When the pH in the two Lakes Särnamannasjöarna dropped below 5, the char populations disappeared. A disease has played a hitherto little known role in the population control (p. 92).

In the Lakes Harrsjöarna the trout populations still exist at a pH that now and then drops below 5, in one lake in competition with adult char, in the other lake without this competition. The very small population of burbot existing in Lake Harrsjön at the same pH level can hardly be an important competitor to trout, and it is difficult to judge how sensitive burbot is to acidification. The burbot population is, however, somewhat denser in Lake Stora Getsjön, the least acidified of the lakes studied.

The fish species have been ranked according to their sensitivity to acidification (*e.g.* EIFAC 1968, Almer 1972, Leivestad *et al.*, 1976). The ranking of the Fulufjäll grayling as a little more sensitive than char, and the char as more sensitive than trout and burbot preliminarily placed on the same level as char, does not conflict with the ranking in the literature. The repetition of the fish species ranking in rather different types of lakes is an affirmation of the general ecological theory that physicochemical factors gain in importance over biological factors in the control of animal populations when extreme environments are approached. Nevertheless some factors have been referred to above as contributing to the population decrease in grayling and char.

When approaching the problem from another angle, i.e. when reclaiming a lake by introduction of a species, success is not only dependent on the pH rising over some critical level. Even in quite normal environment, the establishment of a new population is successful only if the spawners find a spawning place that allows the progeny to survive, and if such spawning places are maintained by tradition (*e.g.* Gönczi 1970, char). Establishing new char populations is not known to be difficult in normal lakes when trout is the only competing species. Establishment of char is rather described as a misfortune in good trout lakes. The Fulufjäll lakes are shallow, and trout may benefit from that condition (NILSSON 1955, GUSTAFSON *et al.* 1969). Char establishment in trout lakes and trout establishment in char lakes have not, however, been successful in the Fulufjäll lakes, although the pH was not a definite obstacle, judging from the pH in the donor lakes. The only successful introduction so far is char introduction in an empty and limed lake where the char population had just been extinguished. The observations indicate that the existence of another fish species in the lake has been the main obstacle to new introductions. The strategy for disposal of resources in acid lakes did not involve slow growth in trout. Growth of char did not respond to liming of the lakes or to changes in population density in a simple, consistent way.

VII. ACKNOWLEDGMENTS

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VIII. SUMMARY

pH-tolerances can be described by deliberately coarse limitations as follows:
char tolerated the pH register 5.5—5.0 but disappeared when pH dropped below 5.0. Burbot is preliminarily placed in the same class. Grayling disappeared when the pH dropped from 5.5 to 5.0. Trout did not disappear when the pH dropped just below 5.0. The tolerance to lower pH has not been studied.

Critical limits could be defined approximately from these observations, but there is rather a risky pH register than a risky pH-level and within such a register, pH or water qualities covarying with pH become increasingly important when pH decreases. Other factors influencing the reproduction and survival within this critical register are *e.g.*, intraspecies competition and a disease (char), fishing pressure (grayling), and competition from other species. Interspecies competition becomes particularly evident when establishing new populations.

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Addition of Artificial Fertilizers as a Means of Reducing Negative Effects of "Oligotrophication" in Lakes After Impoundment

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ABSTRACT

There have hitherto been few biological methods at hand for compensating the most adverse effects of impoundment. Four seasons of "partial fertilization" in the impounded Lake Anjan have indicated that nutrient enrichment (nitrogen and phosporus in a fixed ratio) is an effective way of locally restoring fish populations in such lakes.

Continuous nutrient enrichment of a small stream leading into a half-secluded bay of the lake promoted the development of an exceedingly rich zooplankton fauna in the bay which primarily favoured the char which largely became attracted to the area and rapidly improved in quality. Also the stream bottom fauna improved considerably for the benefit of brown trout, grayling — and char. The rich availability of prey animals (especially zooplankton) is reflected in a high degree of niche-overlapping in the food of the fish species mentioned.

The results of the present study suggest that it is possible to produce and retain positive "damming-up effects" (NILSSON 1973), which generally follow — though for a limited time — the damming of water, provided the enrichment is kept under proper control. An obvious case of seasonal feeding migration has simultaneously been studied in a system of small, organically polluted lakes connected with a larger obligotrophic lake via a narrow stream about 5 kilometers long.

Balanced nutrient enrichment of ideally shaped bays of oligotrophic lakes is here suggested for the twofold purposes of improving the condition and the stock size of salmonid fish and increasing the buffering capacity against acidification — now rapidly in progress even in northern Scandinavia. The method is partly in controversy with the general policy of indiscriminately purifying sewage water as much as possible.

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I. INTRODUCTION

It has long been known that nutrient enrichment of oligotrophic lakes often results in a drastic increase in fish populations in these lakes provided that eutrophication has not been allowed to proceed too far. The ideal state would be a "balanced eutrophication" where a variety of salmonids still dominate the fish fauna (*cf.* SVÄRDSON 1976). In the last decade a trend towards nutrient enrichment of inland waters has developed along parallel lines in Sweden, Norway and Canada, partly causing a controversy with the policy of purifying waste water as far as technically possible. Large-scale and small-scale fertilization projects have been started in these countries with very promising results.

Controlled nutrient enrichment of oligotrophic waters in order to improve fish production is an old idea that was revived in the 1970's. In Canada a growing interest for fertilizing regulated lakes and small coastal streams has resulted in a number of fertilization projects, most of which have turned out quite successfully. In western Canada it is well-known, for instance, that a surplus of nutrients from decaying carcasses of sockeye salmon shortly after spawning in practice means effective natural fertilization of numerous small streams for the benefit of young sockeye fry (*cf.* KROKHIN 1959, DONALDSON 1967). Experience of this kind has been used in large-scale application of commercial fertilizers to coastal oligotrophic lakes in British Columbia, where young sockeyes stay for about a year before running into the sea (Drs J. I. MANZER and J. STOCKNER, pers. comm.). The number of returning sockeyes has increased up to 5—7 times (MANZER 1976, LEBRASSEUR *et al.* 1978). Great resources have hitherto been allocated by the Fisheries Authorities of Canada for research into the consequences of nutrient enrichment of these waters.

NORTHCOTE (1972) has described the combined effects of nutrient enrichment and mysid introduction into the regulated Kootenay Lake, British Columbia, and STOCKNER and SHORTERED (1978) have performed fertilizing experiments in a coastal stream in British Columbia in order to increase the rearing potential for fish etc.

We also know from large-scale modelling in the Experimental Lakes Area (ELA) in Ontario in series of nearly identical lakes how oligotrophic shield lakes may react to the addition of nutrients (SCHINDLER and FEE 1974).

Similar basic research performed in small lakes in the Kuokkel area near Lake Torne Träsk in northern Sweden has provided further information of this kind—on long-term effects on phytoplankton and zooplankton development (PERSSON *et al.* 1975, Kuokkel Progress 1972—80). In this project, however, the final consumer—the fish—is lacking.

Among other fertilization projects performed with the aim of improving the condition of fish, mention can be made of PYEFINCH (1960) in Scotland, FAGERSTRÖM (1966) and FILIPSSON *et al.* (1968) in Sweden, the two former working with brown trout and the latter with char.

The present method of fertilizing parts of large impounded lakes in northern Sweden, so-called "partial fertilization", is intended to be an economic but still effective way of restoring parts of the original fish fauna of these waters.

Our fertilizing experiments were inspired by a series of very promising results from a Norwegian project in which nitrogen and phosphorus had successively been added to a lake in the Trondheim area (Lake Langvatn) for the study of interactions between phyto- and zooplankton and predation effects upon zooplankton by fish. Another object was to study the population dynamics between brown trout and char in the course of the experiments (LANGELAND *et al.*, 1977). The first results clearly indicated that the surplus of nutrients fairly rapidly passed from one trophic level to the next and finally reached the fish, *i.e.*, char in the first hand, which successively became adapted to a pelagic life and rapidly gained weight by feeding on the superabundance of zooplankton.

II. WATER REGULATION AND FERTILIZING AS A METHOD. THE LAKE ANJAN STUDY

In the first few years after impoundment the condition of most fish, especially char, improves quite significantly in a manner which is recognized as "the damming-up effect" upon fish (NILSSON 1973, LINDSTRÖM 1975). When land is flooded a surplus of nutrients, organic matter etc. may dissolve in the water. This stage of enrichment, which is generally noticeable throughout entire food chains and thus is ultimately canalized into fish, gradually fades off and within a few years of damming a process of "oligotrophication" has started.

Due to considerable water fluctuations—often 10—20 metres over the year—which are more or less characteristic of impounded lakes, the littoral is becoming increasingly eroded, loose deposits are gradually transported into the deep profundal

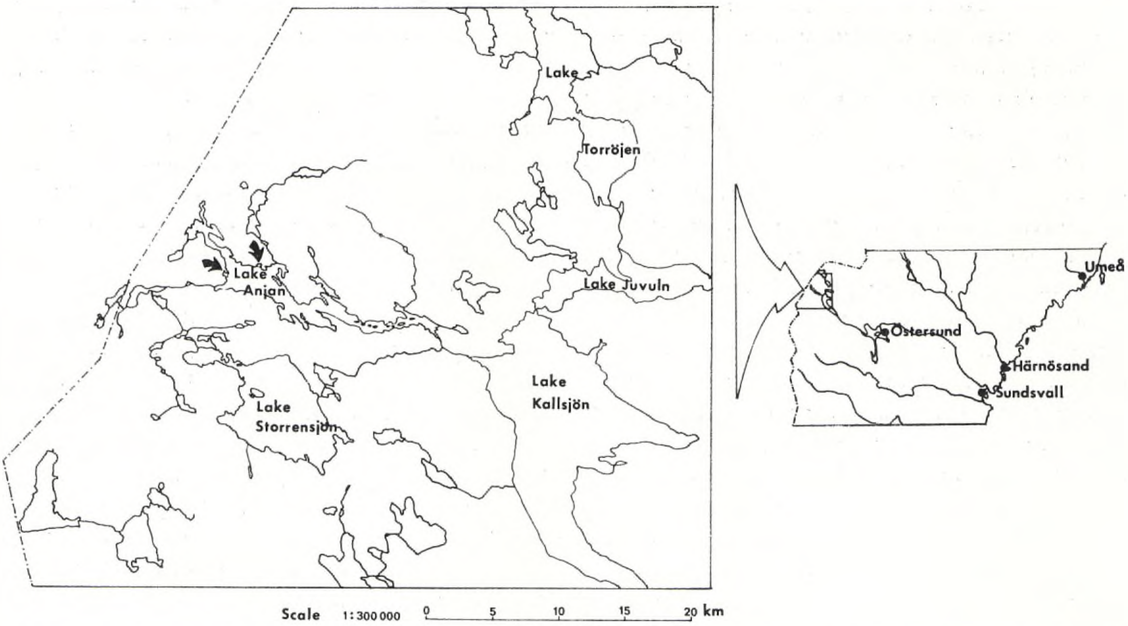

Fig. 1. Map of a section of the Province of Jämtland. The two experimental bays of Lake Anjan indicated with arrows. The fertilized bay is to the left.

where they are trapped. A considerable share of the nourishment of the pelagic zone may also be lost via the outlet during periods of extensive tapping. Extreme silting due to erosion may also negatively affect primary productivity in impounded lakes and thereby influence entire food-webs. The bottom fauna which is normally most abundant in the littoral of the lake rapidly declines when the loose material is carried downwards and the shallow littoral bottoms dry out in the winter, thus being exposed to freezing.

When a lake becomes impoverished in nourishment most fish are bound to feed on whatever bottom fauna objects are available. *i.e.*, in situations of damming in river outlets or in "pools" connected with these outlets (GRIMÅS 1965; AASS *et al.* 1972 see below), and on "surface fauna". "Drift", *i.e.*, mostly insect larvae transported via streams, is also a possible although temporal source of food. The wide range of zooplankton on which char and pelagic whitefish are normally dependent—when occurring sympatrically with other salmonid fish—are not sufficiently abundant any more to provide food for large populations of these fish.

In order to survive on a scarce diet most fish species are bound to switch to food objects of their second or third choice (see discussion below). The predation pressure exerted on the food objects still remaining will be severe and a stage of intensive interactive segregation for food commences (*cf.* MILBRINK and HOLMGREN 1981).

With the aim of testing whether the addition of fertilizers to a limited area of a large impounded lake could positively affect all levels of the food chain, including the fish, the Institute of Freshwater Research, Drottningholm, together with the County Administrative Board of Jämtland started a pilot study in Lake Anjan close to the Norwegian border (Fig. 1). The lake has been subjected to long-term regulation since 1940 (area about 26 km², amplitude of regulation 9.2 m). The main reason for choosing Lake Anjan was that the fish populations were in a very bad state due to impoundment. Other motives were that the fish fauna as well as the invertebrate fauna and other conditions of interest for a study of this kind were comparatively well-known.

Lake Anjan was formerly well-known for its large populations of brown trout and char. Both species are now scarce and the condition of the fish is below average for the region. Grayling (*Thymallus thymallus*) was accidently introduced into the lake in 1952 and rapidly spread in the littoral of the lake and into the inflows. Burbot (*Lota lota*) is a common profundal species and minnow (*Phoxinus phoxinus*) may be found in the littoral.

By working with small-scale application of commercial fertilizers and thereby making use of old practices of "baiting" etc., *i.e.* attracting fish to the fertilized areas and keeping them there by offering a superabundance of potential food organisms, a number of advantages could be obtained. Provided the fertilizers could be largely locally bound in the food chains a good economy and an adequate control would be secured. Furthermore, working with relatively small quantities of chemicals, the personnel and economic resources available would allow the method to be tested simultaneously in a number of different localities within one and the same lake or in different water systems. Another advantage would be that nutrient enrichment could be discontinued if, for instance, the balance between fish species developed in an unexpected direction or if other negative effects appeared. The presence of — and even "explosions" of, for instance, sticklebacks and roach may turn the balance between fish species in an undesired direction (MILBRINK and HOLMGREN 1981). The sequence of biological events following nutrient enrichment is generally fairly predictable. According to our original hypothesis "partial fertilization" would effectively favour planktivorous fish such as char both qualitatively and quantitatively—via a local increase in the production of zooplankton—for the benefit of a local fishery.

III. MATERIAL AND METHODS

Since June 1976 phosphates and nitrates have been more or less continuously dissolved into a stream entering Lake Anjan in a narrow bay (area about 1/2 km^2). A row of small islands delimits the bay from the open lake. It was our hope that the morphometry of the bay would to some extent prevent the nutrients from diffusing into the lake proper. For comparison, an untreated reference bay — with a similar stream — and with roughly the same characteristics had been selected. It is important that comparisons could be made directly with an unaffected reference area, in order to eliminate possible effects of climate shifts, water level fluctuations etc. The fertilizers used were commercially available ammonium nitrate and superphosphate added in a N:P-relationship of roughly 10:1. The fertilizers were filled into a culvert underlying the road about 50 metres from the bay (Fig. 2, point A) at 10—14 day intervals. The fertilizers slowly dissolved into the stream-water in a manner similar to an automatic food dispenser. Totally 1,800 kg of the above salts were used in 1976, 2,400 kg in 1977, 1,800 kg in 1978 and finally 1,800 kg in 1979, *i.e.* 440 kg N and 40 kg P in 1976, 610 kg N and 55 kg P in 1977, 460 kg N and 40 kg P in 1978, and 460 kg N and 40 kg P in 1979. It should be stressed that the effects of fertilization on different levels of the food chains registered in the present study have been attained by a relatively modest input of nutrients. If, supposedly phosphorus is the limiting constituent for primary productivity, this input is equivalent to a hypothetical case in which sewage from a small population of about 30 residents reaches the stream (each person contributes in this case about 3.5 g of total-P each day). The course of events in Lake Anjan — in the enriched bay as well as in the reference bay — has been followed at roughly 2-weekly intervals from June until mid-September each year. Samples have been regularly collected for analyses of chemical and physical variables, phyto- and zooplankton, littoral bottom fauna and fish. Complementary samples have also been taken of the sessile flora and fauna of the two streams entering the bays.

Chemical analyses were performed by the County Administrative Board of Jämtland and by the National Swedish Environment Protection Board, Solna, staff members of which also participated in planning the experiments. Most of the other analyses were made at the Institute of Freshwater Research, Drottningholm and at the above County Administrative Board. The methods used were standard limnological routines.

Water samples for chemical analysis were taken about 10 cm under the surface and stored in plastic bottles. pH, $\varkappa$, $KMnO_4$, A′ and colour

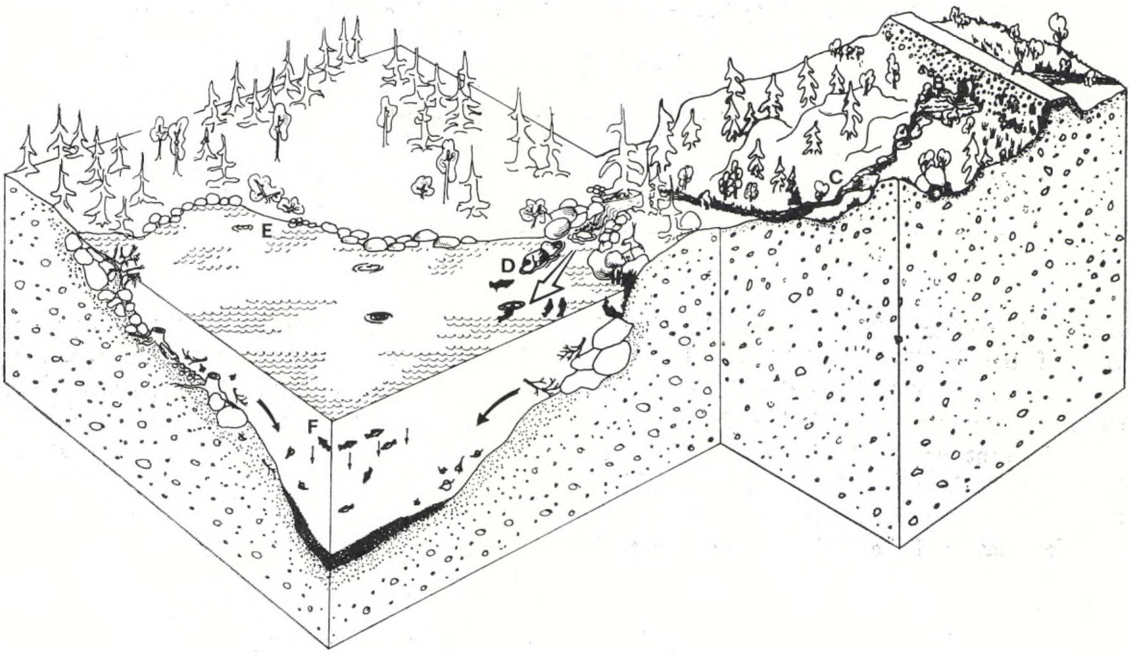

Fig. 2. Section of the fertilized bay. Nitrogen and phosphorus were added to the stream at point A, *i.e.* in a culvert under the road. Point B is a pool downstream. Point C is an natural migration obstacle for fish and point D the mouth of the stream where trout, in particular, have assembled. Point E symbolizes the shallow reaches of the bay where grayling now are common and point F the deeper parts of the bay inside a row of islands where char thrive.

were analysed on the same day or the day after the sampling. The bottles for nutrient analysis were frozen as soon as possible (about one hour after sampling) for later analysis.

Phytoplankton samples were taken directly in 100 ml glass bottles about 10 cm under the surface and preserved immediately with LUGOL's solution. To estimate the numbers of zooplankton 100 litres of surface water from different parts of the bays were filtered through a plankton net with 25 microns mesh width and the samples were immediately preserved in formaline.

The phytoplankton biomass and the composition of species were estimated by direct counting in an inverted microscope according to the method developed by UTERMÖHL (UTERMÖHL 1958, WILLÉN 1976).

The bottom fauna of the innermost parts of the two bays was considered to be of considerable interest in the evaluation of its role as potential fish food. The depths of sampling were accordingly 1—1.5 m.

Bottom samples were obtained on three occasions — in 1976, 1978 and 1979 — with the help of a perspex tube sampler with an aperture of about 40 cm^2. The bottom material was sieved through a 0.6 mm gauge net and preserved in formaline. Representative samples of the stream bottom fauna inside the carpets of sessile algae were obtained by simply removing the algae from the stony substrate — 1 dm^2 each time. After preservation in formaline each sample was thoroughly examined under a binocular microscope.

Drift nets with an aperture of about 600 cm^2 were used in both streams in August 1979, each time covering 17 hours (one night and half a day).

In the summer of 1976 most interest was devoted to changes in the primary steps of the food chains, but in the summers of 1977 and 1978 more time was devoted to the fish. In 1979, finally the entire work concentrated on the fish.

Full test-fishings with ordinary survey nets and pelagic survey nets (FILIPSSON, 1972) were simultanously carried out in the two selected bays,

Table 1. *Chemical and physical properties of the water in the central parts of Lake Anjan.*

August 14, 1972	Temp. 14.1°C	Secchi depth 590 cm	$KMnO_4$ 17 mg	$\varkappa$ 16 µS/cm	A′ 80 µekv/l	NH_4-N 20µg/l
	NO_3-N 30 µg/l	Tot.-N 190 µg/l	PO_4-P 2 µg/l	Tot.-P 3 µg/l		
June 22, 1975	Temp 8.8°C	Colour 10 mg Pt/l		$\varkappa$ 28 µS/cm	A′ 130 µekv/l	

first in September 1976—three months after the start of the fertilizing activities—and in June and September 1977. Since the chances of detecting increased growth during the first year of enrichment appeared highly unrealistic, the first two of these test-fishings were considered to be suitable references for later analyses.

Unfortunately, Lake Anjan turned out to be fairly hazardous to fish efficiently in the littoral and in the sub-littoral, since numerous branches, stumps and twigs remained accumulated in the inner parts of the bays following the flooding in connection with regulation. Locally, the bottom topography is fairly uneven, which makes efficient testfishings even more difficult to carry out.

Since 1978 parallel fishings have repeatedly been undertaken on comparable reaches of the two bays, a method which should enable fair estimates to be made of the abundance and the species composition of fish.

Separate fishings with a trawling device specially designed for catching fish fry was used in 1978 (1+ fish and older as a complement to the ordinary nettings).

Electro-fishing was performed in the lower reaches of both streams in July 1979. FULTON's formula for the estimation of the condition (K) of the fish (RICKER 1975) was used, $K = \frac{w \cdot 100}{l^3}$ where w is the weight in g and l is the length in mm.

Non-linear regressions of the yearly length increase of grayling were made through "back-calculations" based on the growth rates of the scales. An empirical "ruler" (GUSTAFSON 1949) based on the known increase in length of graylings has been of particular value for these estimations. The annual growth of the otoliths was used in age-determinations of the char.

The percentage composition of the food intake of various fish was obtained by calculating the occurrence of the various volumetrically predominant food items in the way described by NILSSON (1960).

IV. RESULTS

Water chemistry, phytoplankton, rooted vegetation and zooplankton

The physico-chemical qualities of the water in Lake Anjan are presented in Table 1. The values are typical for an impounded Scandinavian lake with very low nutrient concentration, moderate *secchi* depth reading and rather high organic contents ($KMnO_4$) compared with surrounding natural waters.

The conditions in the experimental parts of Lake Anjan are presented in Tables 2 and 3. The pH and A′ of the two streams are remarkably low while the corresponding values in the bays are more normal.

As expected, the nutrient contents of the bays were very low before fertilization. After addition of nutrients the concentrations of phosphorus and nitrogen increased drastically but values returned to normal in a day or two.

The phytoplankton biomass was always larger in the fertilized bay than in the reference area. The difference was rather small as compared to other fertilized waters where five-fold to twenty-fold increases have been observed. (SCHINDLER and FEE 1974, KUOKKEL Progress Reports 3—7 1974—80.) Considering the errors of the method the observed difference is barely significant. The real difference between the two bays was probably,

Table 2. *Water chemistry in the experimental parts of Lake Anjan.*

Fertilized bay (before addition of nutrients)							
July 12, 1977	pH	A′	$KMnO_4$	$\varkappa$	NO_3-N	NO_2-N	NH_4-N
	6.4	36 μekv/l	12 mg/l	21 μS/cm	90 μg/l		< 30 μg/l
	Tot.-N	PO_4-P	Tot.-P				
	130 μg/l	2 μg/l	2 μg/l				
Fertilized bay (the day after the addition of 150 kg of NH_4NO_3 and 50 kg of superphosphate)							
July 13, 1977	pH	A′	$KMnO_4$	$\varkappa$	NO_3-N	NO_2-N	NH_4-N
	6.2			119 μS/cm	6100 μg/l	5 μg/l	5100 μg/l
	Tot.-N	PO_4-P	Tot.-P				
	19 430 μg/l	116 μg/l	119 μg/l				
Fertilized bay							
July 29, 1977	pH	A′	$KMnO_4$	$\varkappa$	NO_3-N	NO_2-N	NH_4-N
	6.6	45 μekv/l	21 mg/l	21 μS/cm	80 μg/l		30 μg/l
	Tot.-N	PO_4-P	Tot.-P				
	180 μg/l	< 2 μg/l	2 μg/l				
Reference bay							
July 12, 1977	pH	A′	$KMnO_4$	$\varkappa$	NO_3-N	NO_2-N	NH_4-N
	6.6	30 μekv/l	11 mg/l	21 μS/cm	100 μg/l		< 30 μg/l
	Tot.-N	PO_4-P	Tot.-P				
	150 μg/l	< 2 μg/l	2 μg/l				
Reference bay							
July 29, 1977	pH	A′	$KMnO_4$	$\varkappa$	NO_3-N	NO_2-N	NH_4-N
	6.7	46 μekv/l	14 mg/l	21 μS/cm	90 μg/l		< 30 μg/l
	Tot.-N	PO_4-P	Tot.-P				
	130 μg/l	< 2 μg/l	2 μg/l				

however, much larger. As is shown below, the zooplankton were more abundant in the fertilized bay and they must have been grazing heavily on the algae. Knowing that, the difference is highly significant. Only biomass was recorded and not the production. An algal assemblange of small forms can be very productive even if the biomass is small and a large biomass does not always imply an intensive primary production.

Phytoplankton biomass and species composition varied roughly in the same manner over the seasons in both bays with two growth maxima every year (Fig. 3). The fertilization seemed, however, to have promoted the growth of small chrysophyceans of the genera *Chromulina*, *Ochromonas* and *Pseudokephyrion*, since they were more abundant in the enriched bay. Also some cryptophyceans like *Cryptomonas* and *Rhodomonas* were more common in the fertilized bay. The observed difference might also have been due to different grazing intensities in the two bays.

In 1977 and 1978 *Chlamydomonas* increased considerably in the fertilized bay. In 1978 filaments of *Spirogyra* and *Oedogonium* occurred occasionally in the plankton indicating increased growth of benthic algae. Sampling performed in the streams verified this (p. 107). No increase of bluegreen algae was observed. Individuals of the genera *Merismopedia*, *Chroococcus* and *Anabaena* appeared in samples from both bays but no significant difference between the two could be demonstrated.

The overall impact of the fertilization on phytoplankton seemed to have been a moderate growth of almost all species. The reason was probably the relatively small amounts of nutrients added to the large body of water. In other fertilization experiments often one or a few species invade the plankton and constitute the whole biomass for shorter or longer periods (Kuokkel Progress Reports 3—7, 1974—80, Schindler and Fee 1974). It is of course advantageous to the herbivores if the

Table 3. *Water chemistry in the experimental parts of Lake Anjan.*

	Date	pH	A′	$KMnO_4$	Colour	NO_3-N	NH_4-N	Tot.-N	PO_4-P	Tot.-P
Fertilized stream (before addition of nutrients)	June 23, 1976	4.9	0 µekv/l	31 mg/l	60 mg Pt/l	5 µg/l	50 µg/l	200 µg/l	4 µg/l	6 µg/l
Fertilized stream (about 15 minutes after the addition of 150 kg of NH_4NO_3 and 50 kg of superphosphate)		4.9	0 µekv/l	31 mg/l	60 mg Pt/l	20 µg/l	50 µg/l	450 µg/l	10 µg/l	40 µg/l
Fertilized bay (Inner part after addition of fertilizers- about 20 minutes after)		6.3	13 µekv/l	13 mg/l	10 mg Pt/l	25 µg/l	75 µgl/	160 µg/l	3 µg/l	19 µg/l
Reference stream	June 23, 1976	5.5	0 µekv/l	35 mgl/	70 mg Ptl/	5 µgl/	45 µg/l	180 µg/l	3 µg/l	6 µg/l
Reference bay	June 23, 1976	6.4	17 µekv/l	11 mg/l	10 mg Pt/l	< 5 µg/l	50 µgl/	200 µg/l	2 µg/l	4 µg/l

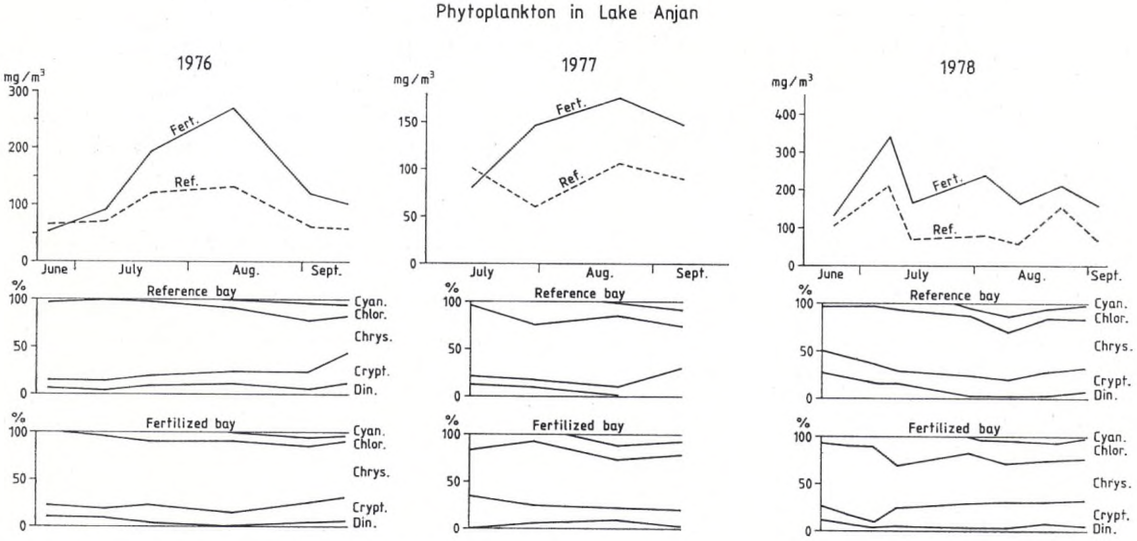

Fig. 3. Phytoplankton in Lake Anjan 1976—78.

Table 4. *Abundance of zooplankton in Lake Anjan in the summer of 1976. (Number of specimens/100 litres of water). f=fertilized bay, r=reference bay.*

Date	July 8.		July 21.		August 12.		September 2.		September 13.	
Locality	f	r	f	r	f	r	f	r	f	r
Asplanchna priodonta	2	0	0	7	3	0	0	0	1	0
Bosmina coregoni	25	5	119	23	2	1	72	46	18	3
Daphnia galeata	4	0	48	9	1	0	4	33	9	0
Polyphemus pediculus	0	0	32	6	4	3	6	0	0	0
Holopedium gibberum	3	1	46	14	1	1	5	4	2	7
Heterocope saliens	0	0	0	0	25	2	12	1	0	0
Arctodiaptomus laticeps	6	16	0	0	48	2	64	30	24	39
Cyclops scutifer	117	5	252	30	7	1	0	0	2	0
Total numbers	157	27	497	89	91	10	163	114	56	49

food supply increases only quantitatively; the same well-known algae occur and they are just more abundant. No new and perhaps less palatable species appear and the herbivores utilize the same diet as before.

A well-designed fertilization programme must not disturb the species composition of phytoplankton. When new species invade the plankton and the biomass increases rapidly, the fertilization is no longer a fish-promoting act but a pollution of the water.

Parallel with the increase of phytoplankton, increased rooted aquatic vegetation could be observed in the fertilized bay. The dominating species were *Callitriche verna* and *C. humulata* in roughly equal proportions. The same species also dominate the sparse vegetation in the inner parts of the reference bay in comparable reaches.

Zooplankton were significantly more abundant in the fertilized area than in the reference bay (Tables 4—6). This was especially the case with herbivores, while predators were influenced only to a small extent or not at all. *Bosmina coregoni* increased very much and the largest concentration was observed on September 4, 1978, when 53 animals per litre were counted in the inner parts of the fertilized bay (Table 6). In the other bay only 1—2 animals per litre were counted and no concentrations were observed in the inner parts. Also other cladocerans like *Daphnia galeata, Chydorus sphaericus* and *Holopedium gibberum* were more abundant in the enriched bay. Among copepods *Arctodiaptomus laticeps* and *Heterocope saliens* were more common in the fertilized area than in the reference bay. *Eudiaptomus graciloides* was observed only on a few occasions and no conclusions on its preference occupancy could be drawn. Only a few species of rotifers were observed and it is difficult to interpret the results. However, some of the smaller animals might have escaped through the meshes of the plankton net used. *Notholca squamula* was more abundant in the enriched bay while *Kelicottia* and *Asplanchna* were more common in the reference area.

As seen in Tables 4—6, the total number of animals is 5—10 times larger in the enriched area. The difference between the reference bay and the enriched one is quite significant if all observed animals are considered.

Bottom fauna and drift fauna

A comparatively limited bottom sampling programme has been carried out. The samples were all taken in the inner parts of the two bays, since further out there is hardly any soft bottom fauna at all due to erosion and also because possible changes in the bottom fauna would first be obvious close to the source of enrichment. It is likely, however, that the actual abundance of different bottom animals—as well as the zooplankton fauna in the inner parts of the fertilized bay-represent minimum values considering the predation pressure from the fish roaming here in relatively high densities during the last couple of years.

Of the real bottom fauna components, oligochaetes seem to have been favoured most by the nutrient enrichment (Table 7), followed by chironomid larvae. As far as we could find, the oligo-

Table 5. *Abundance of zooplankton in Lake Anjan in the summer of 1977. (Number of specimens/100 litres of water). f=fertilized bay, r=reference bay.*

Date	July 7.		July 29.		August 21.		September 2		
Locality	f	r	f	r	f	r	f	f	r
							Outer part	Inner part	
Bosmina coregoni	22	0	0	0	10	0	64	338	4
Daphnia galeata	4	3	30	10	10	0	16	0	4
Holopedium gibberum	1	2	0	0	0	0	8	0	2
Eurycercus lamellatus	0	0	0	10	20	0	0	0	0
Heterocope saliens	0	0	20	10	10	0	48	0	0
Arctodiaptomus laticeps	2	2	230	0	10	0	65	806	24
Cyclops scutifer	182	18	110	20	0	0	4	39	12
Total numbers	211	25	390	50	60	0	205	1183	46

Table 6. *Abundance of zooplankton in Lake Anjan in the summer of 1978. (Number of specimens/100 litres of water). f=fertilized bay, r=reference bay.*

Date	June 23.		July 3.		July 13		August 3.		August 12.	
Locality	f	r	f	r	f	r	f	r	f	r
Asplanchna priodonta	23	52	10	60	0	0	0	0	0	0
Notholca squamula	0	0	0	0	0	0	360	0	100	0
Bosmina coregoni	20	8	216	65	520	360	620	420	340	60
Daphnia galeata	0	0	0	0	0	0	20	0	80	0
Holopedium gibberum	0	0	0	0	0	0	0	0	20	0
Chydorus sphaericus	0	0	0	0	0	0	160	0	86	0
Heterocope saliens	0	0	0	0	80	0	180	0	120	40
Arctodiaptomus laticeps	232	80	170	108	63	20	40	20	126	10
Cyclops scutifer	12	56	150	60	18	80	42	85	60	60
Total numbers	287	196	546	293	681	460	1422	525	932	170

Table 6. *Continued.*

Date	August 23.		September 4.		September 4.
Locality	f	r	f	r	Innermost part of the fertilized bay
Kellicottia longispina	144	280	—	—	—
Bosmina coregoni	56	16	56	12	5300
Daphnia galeata	4	0	12	0	0
Chydorus sphaericus	64	0	0	0	200
Heterocope saliens	16	0	0	0	0
Arctodiaptomus laticeps	24	8	8	8	0
Cyclops scutifer	20	120	44	88	0
Total numbers	328	424	120	108	5500

chaetes were all *Eiseniella tetraedra* a very mobile species (perhaps a most useful quality in a long-term regulated environment) favoured by situations of organic enrichment (MILBRINK 1980). The chironomid larvae of the fertilized bay were *Sergentia* sp. and *Diamesa* sp. of the sub-family Chironomini and *Cricotopus* sp., of the sub-family Orthocladinae (the same species as the one dominating the fertilized stream; see below). In the reference bay the relatively few chironomid larvae were all predatory tanypodines. A simple field inspection of the bottom surface at shallow

Table 7. *Bottom fauna composition in the inner parts of the two bays. (Specimens/m². f=fertilized bay; r=reference bay; n is the number of samples.*

Date	12.8.-76		4.9.-78		5.9.-79	
	f	r	f	r	f	r
chir. larvae	160	80	1000	250	750	110
oligochaetes	80	120	3000	1375	2625	0
nematodes	80	280	310	550	60	0
Pisidium sp.	0	0	0	150	560	0
ostracodes	0	0	0	0	1750	0
Eurycercus lamellatus	200	0	1375	825	2000	125
various Diptera larvae	40	40	0	150	560	0
	560	520	5685	3200	8305	235
n	8	8	12	12	13	12

depths in the inner parts of the fertilized bay revealed a high activity level of various invertebrates, especially of *Eurycercus lamellatus* — in a proliferous vegetation of *Callitriche*. A similar inspection of the reference bay also revealed the existence of *Eurycercus* although in low abundance and a sparse *Callitriche*-vegetation.

The littoral bottom substrate of the innermost parts of both bays consisted of thick, soft layers of organic debris causing considerable difficulty when looking for small crustaceans in the voluminous sieving residues. In the bottom samples the numbers are obvious underestimates due to sieving losses.

Bottom samples taken in the fertilized stream also revealed the existence of chironomid larvae—*Cricotopus* sp.—in great abundance within the luxuriant carpet of *Stigeoclonium tenue*. Abundance values of about 1500 larvae/m² were repeatedly recorded (Table 8) Both the algal species as well as the orthocladinae larvae are species which normally dominate under organically enriched conditions (Kronborg 1975, and Dr. L. Eriksson, pers. comm.). The reference stream was largely dominated by the alga *Microspora palustris* var. *minor*, characteristic of oligotrophic streams in the north (Kronborg 1975). Of the chironomid larvae, only a few tanypodines were recorded in the algal and moss carpet of the stream.

The bottom fauna and the drift fauna of the fertilized stream corresponded very well with each other. The drifting chironomids, for instance, were all *Cricotopus* sp. Also the bottom fauna and the drift fauna of the reference stream corresponded well with each other, simulid larvae being the most frequent animals.

Table 8. *Stream bottom fauna (specimens/dm²) and drift (one full night and half a day, 17 hours).*

Date	Stream bottom fauna								Drift	
	3.8.-79		13.8.-79		19.8.-79		6—7.9.-79		18.8.-79	
	f	r	f	r	f	r	f	r	f	r
chir. larvae	60*	0	50*	1	16*	0	61*	0	16*	1
various Diptera larvae	1	22	8	19	5	0	9	1	32	9
other insect larvae	1	0	3	2	0	0	4	0	0	0
insect imagines	—	—	—	—	—	—	—	—	—	2
oligochaetes	—	—	—	—	—	—	3	—	—	—
terrestrial spiders	—	—	—	—	—	—	—	—	—	1

* *Cricotopus* sp. (Orthocladinae).

Table 9. *Test-fishing results, Lake Anjan 1976, 1978 and 1979. n=number of fish, w=weight in kg.*

Date	Fertilized bay									Reference bay								
	Char		Trout		Grayling		Burbot		Total weight	Char		Trout		Grayling		Burbot		Total weight
	n	w	n	w	n	w	n	w		n	w	n	w	n	w	n	w	
13.9—16.9. 1976 (pelagic survey nets/bay)	10	1.124	—	—	—	—	—	—	*1.124*	8	0.835	1	0.127	1	0.015	1	0.102	1.079
13.9.—16.9. 1976 (12 survey nets/bay)	8	0.757	7	0.717	5	1.086	1	0.136	2.692	5	0.599	3	0.367	10	2.379	1	0.177	*3.522*
29.6.—1.7. 1977 (pelagic survey nets/bay)	—	—	—	—	—	—	—	—	—	3	0.170	2	0.240	—	—	—	—	*0.410*
29.6.—1.7. 1977 (17 survey nets/bay)	2	0.172	3	1.746	16	3.196	2	1.693	*6.807*	6	0.570	4	1.169	12	1.989	—	—	3.728
25.9.—26.9. 1977 (pelagic survey nets/bay)	8	0.996	—	—	—	—	—	—	0.996	2	0.318	—	—	—	—	—	—	0.318
25.9.—26.9. 1977 (6 survey nets/bay)	—	—	4	0.328	3	0.650	2	0.694	1.672	2	0.235	4	0.879	8	1.618	2	0.640	*3.572*
22.6.—23.6. 1978 (6 /bay)	1	0.050	1	0.100	5	0.950	—	—	*1.100*	1	0.030	—	—	3	0.325	—	—	0.355
24.7. 1978 (4 survey nets/bay)	—	—	2	0.235	2	0.685	—	—	*0.920*	2	0.275	1	0.080	—	—	—	—	0.355
22.8.—23.8. 1978 (7 and 5 survey nets/bay, resp.)	9	1.020	1	0.350	8	1.630	—	—	*3.000*	1	0.100	5	0.270	1	0.110	4	0.520	1.000
8.9. 1978 (5 and 2 survey nets/bay respectively)	15	2.410	1	0.120	6	2.080	—	—	*4.610*	—	—	1	0.290	1	0.360	—	—	0.650
30.5.—31.5. 1979 (5 survey nets/bay)	2	0.390	5	0.690	2	0.120	1	0.270	*3.970*	—	—	1	0.210	4	0.730	—	—	0.940
17.8.—18.8. 1979 (5 survey nets/bay)	2	0.760	4	0.470	4	1.360	2	0.140	*2.730*	1	0.050	2	0.680	—	—	1	0.130	0.860
18.8.—19.8. 1979 (5 survey nets/bay)	2	0.200	4	0.340	6	1.610	—	—	*2.150*	1	0.130	—	—	1	0.020	—	—	0.150
19.8.—20.8. 1979 (5 survey nets/bay)	1	0.080	1	0.020	3	0.650	2	0.130	*0.880*	2	0.160	—	—	—	—	—	—	0.160
27.8.—28.8. 1979 (Inner) (5 survey nets/bay)	3	0.560	1	0.040	—	—	2	0.250	*0.850*	—	—	—	—	—	—	1	0.160	0.160
27.8.—28.8. 1979* (Outer) (5 survey nets and 4 survey nets resp.)	2	0.210	—	—	6	0.940	—	—	*1.150*	—	—	2	0.120	—	—	—	—	0.120
5.9. 1979 (Inner) (3 survey nets/bay)	8	1.445	1	0.450	2	0.750	—	—	*2.645*	—	—	—	—	—	—	4	0.800	0.800
5.9. 1979* (Outer) (6 and 5 survey nets/bay, resp.)	6 +(1 lost)	0.810	—	—	2	0.600	—	—	*1.410*	3	0.520	—	—	—	—	—	—	0.520
6.9. 1979 (Inner) (3 survey nets/bay)	5	0.635	1	0.010	2	0.525	—	—	*1.260*	—	—	—	—	—	—	—	—	—
6.9. 1979** (Outer) (5 survey nets fert. bay only)	5	0.635	1	0.100	4	0.710	—	—	*1.615*	—	—	—	—	—	—	—	—	—

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* Inner and outer parts of the bays fished separately and parallelly.

** Nets in the outer part of the reference bay did not fish properly.

The fish

The results of the first three test-fishings in 1976 and 1977 did not contradict the assumption that the fish populations of the two selected bays were reasonably alike at the start (Table 9). The total number of fish per fishing unit is unsuitable for use as a measure of fish population density since different parts of the bays were netted on each occasion. It is reasonable to believe, however, that 12 survey-nets in each bay for two nights in September 1976 and 17 nets for two nights in June 1977 provided fairly accurate estimates of the fish populations in these bays on each particular occasion. No species of fish was found to be more abundant in one bay relative the other at any time, grayling and char being the most frequent, followed by brown trout. The balance between fish species was nearly the same in both bays.

By July 1978 the first indications that effects of enrichment had finally reached the fish populations were shoals of yearlings occupying the shallowest reaches of the fertilized bay and chasing zooplankton. Most fish were undoubtedly minnows and, according to observations and diet analyses, they fed on *Eurycercus*, *Daphnia*, *Bythotrephes* and *Bosmina*. Other young fish which could be seen moving in the bottom-vegetation were 1+ grayling. Few—if any—of these fish were observed in the reference bay or in the fertilized bay prior to 1978.

In 1978 catches of fish in the fertilized bay had increased dramatically in relation to the reference bay. Catches per fishing effort tended to be 200—300 % higher, on average, in the former bay, a tendency which was even more accentuated in 1979 with average values around 400 % (range 215—1400 %). No single fishing event gave less than about a 200 % increase in the fertilized bay over the reference bay. In all, 12 test-fishings were performed in 1978 and 1979 (Table 9). Even if total catches in the fertilized bay — with an average input of 6 survey-nets per night were still relatively low in comparison with standards from natural lakes, they were now fairly close to average catches in Anjan and other subalpine lakes before impoundment.

In July 1978 trawling for fry was performed in both bays with a small trawling device hauled from land. An average haul of about 15—20 metres in the fertilized bay yielded 15—20 graylings of 1+ and 2+ years of age, whereas in the reference bay considerable efforts failed to yield the catch of even a single fish. From 1978 on there has been ample evidence of numerous fish being particularly active in the enriched bay.

Dry-fly fishing has proved to be an interesting and apparently effective way of estimating these activities. In an effort to standardize this method, the inner parts of the two bays were fished for one hour at a time. On one particular occasion in July 1979, one hour of fishing in the fertilized bay yielded 9 grayling and one char. There has been no success at all in the reference bay (no single bite) and very few indications of nibbling or otherwise moving fish.

Test-fishings also revealed a slightly changed feeding behaviour among the three dominant fish species. In 1976 and 1977 single specimens of brown trout and grayling could be caught or observed feeding in the inner parts of both bays—close to the inlets of the streams (Fig. 2, point D). Judging from the results of stomachs analysed (see below) these fish largely fed upon running water fauna, (drift fauna) and surface fauna. Char, on the other hand, seldom fed—nor were observed —at shallow depths in the inner parts of the bays. In 1978 young grayling were particularly common in the inner parts of the fertilized bay (see above) but in 1979 also the char had entered the shallow areas (Fig. 2). Stomach analyses revealed that the latter fish had switched from a *Daphnia-Bythotrephes*-diet into a *Eurycercus*-diet, a species which had become particularly common in the *Callitriche* vegetation, thereby competing not only with grayling but also with brown trout (see below). Relatively large grayling were also caught at the very mouth of the fertilized stream. Diet analyses indicated an almost total dominance of chironomid larvae and pupae (see below).

Electro-fishings performed in July 1979 confirmed what was indirectly known previously, *i.e.*, that young grayling, trout, minnow and burbot entered the fertilized stream up to the migration obstacle (Fig. 2, point C) to feed on the surplus

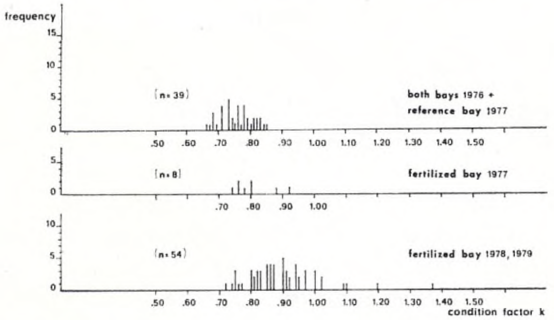

Fig. 4. The condition of char (Fulton's formula) from 1976 to 1979 (for further details, see text).

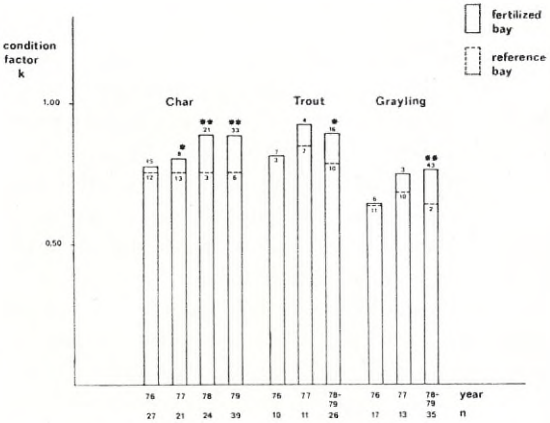

Fig. 5. Changes in the condition (according to Fulton) of char, brown trout and grayling in the course of the experiments. *n* is the underlying number of fish. Upper figure denotes *n* for the fertilized bay, lower figure the reference bay. Single star means a statistically significant increase in condition, double stars a highly significant increase.

of insect larvae present within the dense carpets of sessile algae.

Even if the first indications of a change within the fish populations were noticeable among grayling the most significant changes took place within the char populations. The average condition of char, when calculated in accordance with Fulton's formula (Ricker 1975), had increased from 0.76 in 1976 to 0.89 in 1978—as well as in 1979. This change was highly significant on a risk level of $p < 0.001$. Already in 1977 there was a fully discernable increase in the condition of char significant on a risk level of $0.10 > p > 0.05$. Fig. 4 illustrates this gradual rise in the condition of char in the fertilized bay.

Grayling responded next with an average rise in condition from 0.65 in 1976 to 0.76 in 1978/79 (pooled values). This change is highly significant on a risk level of $p < 0.005$ (Fig. 5).

All through this study brown trout has remained less abundant in the catches than char and grayling. This is probably the reason why quality changes from 1976 to 1979 have been particularly difficult to discern. Statistical tests (t-tests), however, have confirmed a significant rise also in the quality of trout from 0.81 in 1976 (in both bays, and in the reference in 1978 and 1979) to 0.89 in 1978/1979 in the fertilized bay (pooled values) on a risk level of $p < 0.20$. (Fig. 5.)

Char seem to have best taken advantage of the new situation. Different kinds of length-weight relationships are the traditional ways of illustrating the condition of fish and Fig. 6 illustrates such relationships of individual fish caught in the two bays from 1976 to 1979. In the figure the conditions of individual char caught each year are plotted. Small dots refer to fish caught in either bay in 1976. Most of these dots lie within the shaded area in the figure. Large dots referring to fish from the reference bay 1977—79 also mainly fall within the same shaded area. Open rings, finally, represent char caught in the fertilized bay during the same periods. It is easily recognized that most char in the fertilized bay have gained weight very efficiently. Few circle symbols are found within the shaded area (in fact less than 20 %).

An average char from Lake Anjan of about 250 mm in length weighs about 110—120 g. After fertilizing, char of the same length class may weigh up to 170 g. Fish of about 280 mm have increased from an average of about 150—160 g to about 200 g or even 220 g.

The average difference in weight between char from the two bays progressively increases from about 25 g at lengths around 240 mm to about 75 g at lengths exceeding 300 mm. The weight increase tends to accelerate for fish of about 250 mm and above, *i.e.*, for fish of 3 years of age and older.

Fig. 7 is a simple estimate of the yearly gain in weight of char of different year-classes. Only fish caught in late August and early September

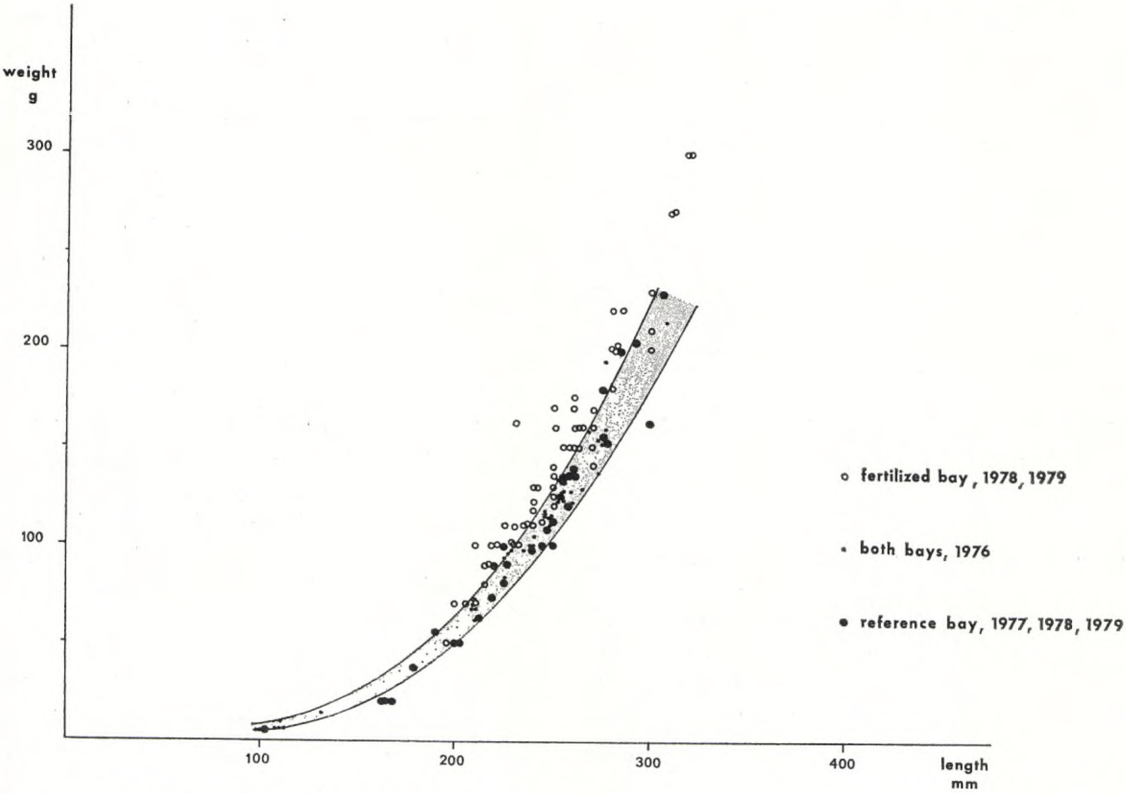

Fig. 6. Length-weight relationships of char caught in August—September each year (for further details see text).

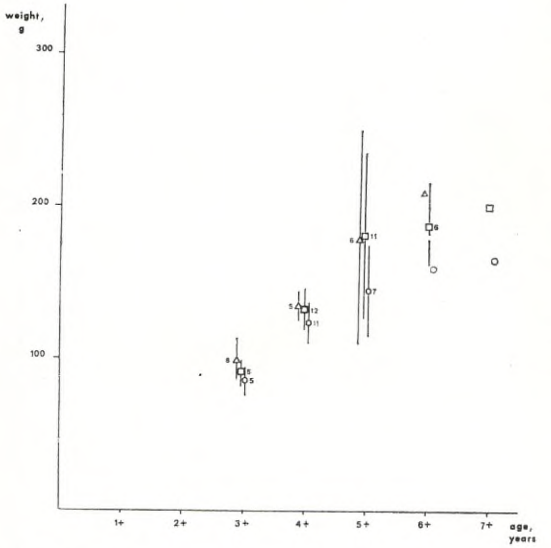

Fig. 7. The average weight (with standard deviation) of char of different age classes in the late summer each year. Open circles denote fish from both bays in 1976, triangles and squares denote fish from the fertilized bay in 1978 and 1979. *n*-values given beside symbols.

each year, have been considered here, which means that there are comparatively few fishes involved in these estimations, *i.e.*, 25 fish in 1976, 35 in 1978 and 20 fish in 1979 (The last two figures refer to the fertilized bay only). Even if there is little doubt that fish from the reference bay are growing more slowly, there would seem to be, however, a fairly limited difference in weight between fish of 3+ and 4+ in either bay, the mean difference being about 10 g and the range of values comparatively small, *i.e.* ±10—15 g. From the age of 5+, however, individual char seem to gain weight at an impressive rate in the fertilized bay, which is also reflected in an icreased range of values. Accordingly, an average char of that age-class weighs about 180 g in the fertilized bay (range about ±50—60 g), but only about 145 g in the reference bay. The weight increase for 5+ fish is highly significant on a 0.5 % risk level ($p < 0.005$). Figs. 8 and 9 illustrate back-calculated average lengths of each age-group of grayling

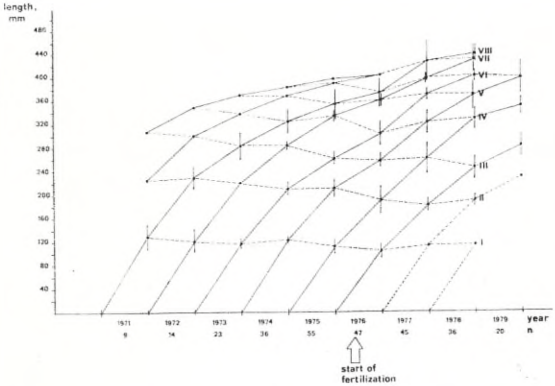

Fig. 8. The growth rate of different year-classes of grayling in the fertilized bay (for further details, see text).

in the two bays. The purpose of the diagrams is to illustrate the response of older grayling to the nutrient enrichment. Due to a fairly limited number of fish caught in the reference bay in the autumns of 1978 and 1979 and also of the youngest age-groups in the fertilized bay in 1977—79, parts of these diagrams may seem less reliable. From 1977 on, however, there is a fully discernable acceleration in the weight gain of fish older than about 4 years. Fish of 6, 7 or 8 years apparently enter a new growth period. Fig. 9 is an attempt to illustrate the parallel development of the 1970, 1972 and 1973 year-classes, respectively, of grayling in the bays studied. The mean values from the fertilized bay have been superimposed upon those from the reference bay. Nothing significant appeared to happen until 1977, when values from fish older than 4 years start to diverge.

Other more subjective indications of an improved quality of the fish in the fertilized bay were positive changes in the palatability of the char, changes in the colour of the meat from greyish to orange-red and other changes such as in the texture of the meat, all of which are suggestive of char subject to recent impoundment—the so-called "damming-up effect" (see above).

Nilsson (1960), Keast (1965) and others have convincingly demonstrated the obvious risk of generalizing about the feeding ecology of fish by relying upon a few random samples from a

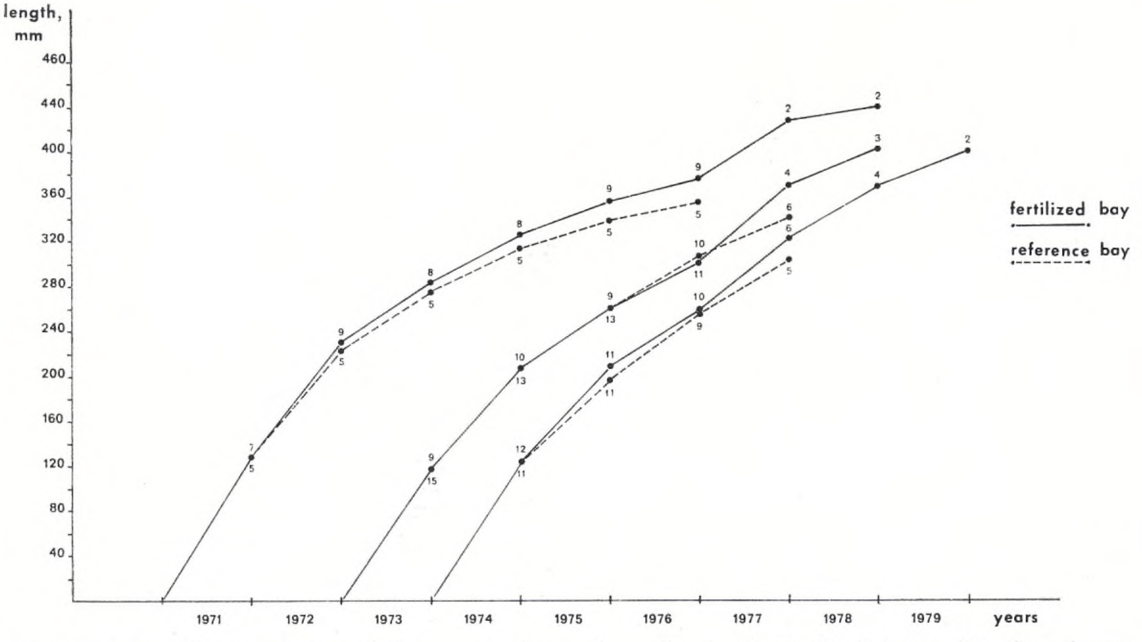

Fig. 9. The growth rate of three different year-classes of grayling in the fertilized bay and in the reference bay. Values of *n* given above and below each value in the figure, respectively.

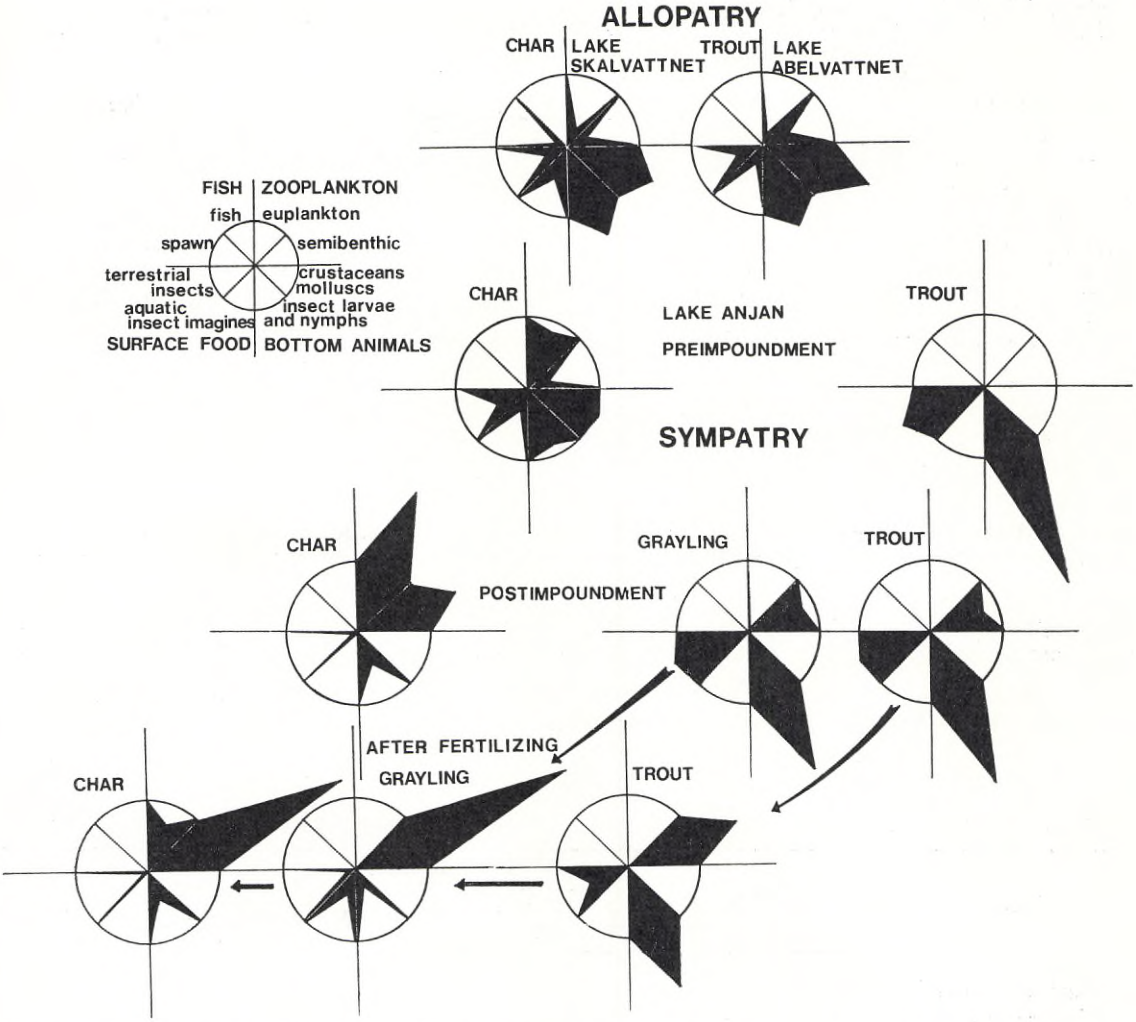

Fig. 10. The food of char and brown trout in allopatry and the food segregation between salmonid fish in Lake Anjan before and after impoundment and after nutrient enrichment. The analyses refer to fish caught in the late summer in 1960 (Lakes Skalvattnet and Abelvattnet), 1938 (Lake Anjan, preimpoundment), 1976 and 1979 (Lake Anjan, postimpoundment and after fertilizing, respectively). The radius of each circle represents an average of 25 % of the stomach volume (partly from Nilsson 1963). For further details, see text and Table 10.

single lake. The diet of most fish in sub-arctic lakes tends to change during the course of the summer and the autumn. According to Nilsson, the percentage overlap in feeding habits between trout and char in a number of impounded lakes steadily decreased from about 40 % in April—June, when food resources were superabundant, to about 20 % in September when the food segregation had reached a maximum due to limited food resources.

Due to the fact that it was impossible to catch enough fish for full analysis of the feeding habits of each species throughout the year we have used Nilsson's experience from a variety of sub-arctic lakes and concentrated only on fish caught in late August and in September, *i.e.* totally about 70 fish in 1976, 50 in 1978 and 90 in 1979. Table 10 illustrates that the diet of char and grayling in the fertilized bay changes considerably from year to year. Whereas *Eurycercus*

Table 10. *The food of char, grayling, trout and burbot in one fertilized bay and one reference bay of Lake Anjan in late August—late September 1976, 1978 and 1979. Volumetrical percentages of predominant food items.*

	Fertilized bay											
Preferred food items	Char			Grayling			Trout			Burbot		
	1976	1978	1979	1976	1978	1979	1976	1978	1979	1976	1978	1979
Eu- and semizooplankton												
Daphnia galeata	18.2	70.7	8.2	—	—	—	—	—	—	—	—	—
Bythotrephes longimanus	21.3	16.3	0.7	0.5	—	—	—	—	—	—	—	—
Holopedium gibberum	4.5	1.3	2.2	—	—	—	—	—	—	—	—	—
Bosmina coregoni	—	—	5.9	—	—	—	—	—	—	—	—	—
Eurycercus lamellatus	35.3	1.11	72.3	19.7	10.8	79.0	19.2	(47.0)	40.0	—	43.3	30.0
Miscellaneous Crustacea	7.8	—	—	—	—	—	—	—	—	—	—	—
Bottom fauna												
Trichoptera	11.3	—	0.1	23.0	—	6.5	42.2	(3.0)	37.1	(62.5)	25.0	70.0
Chironomidae	0.1	0.6	8.9	25.5	50.2	—	4.7	—	5.6	—	27.3	—
Miscellaneous water insects	—	—	0.8	3.9	—	10.3	8.9	—	3.3	(37.5)	—	—
Surface fauna												
(Terrestrial insects and imagines of water insects)	1.2	—	0.4	27.3	39.0	3.3	25.0	(50.0)	14.0	—	—	—
	—	—	—	—	—	—	—	—	—	—	—	—
Fish												
Plant residues	0.2	—	0.4	0.1	—	—	—	—	—	—	4.3	—
Miscellaneous food objects	0.1	—	0.1	—	—	0.9	—	—	0.3	—	0.1	—
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	(100.0)	100.0	(100.0)	100.0	100.0
Number of fish analysed	18	9	17	6	5	15	7	2	9	1	3	7

Table 10. *Continued.*

	Reference bay											
Preferred food items	Char			Grayling			Trout			Burbot		
	1976	1978	1979	1976	1978	1979	1976	1978	1979	1976	1978	1979
Eu- and semizooplankton												
Daphnia galeata	34.4	—	40.5	—	0.9	—	—	—	—	—	—	—
Bythotrephes longimanus	40.5	—	20.9	—	0.1	—	—	—	—	—	—	—
Holopedium gibberum	0.9	—	18.5	—	—	—	—	—	—	—	—	—
Bosmina coregoni	—	—	0.5	—	0.2	—	—	—	—	—	—	—
Eurycercus lamellatus	7.7	—	—	46.4	29.6	—	—	4.0	—	(44.5)	3.0	24.2
Miscellaneous Crustacea	0.6	—	—	—	7.9	—	3.9	—	—	—	—	5.0
Bottom fauna												
Trichoptera	—	—	—	10.1	11.7	—	82.7	96.0	80.8	(2.8)	75.0	65.0
Chironomidae	—	—	1.0	0.7	17.0	—	—	—	—	—	—	—
Miscellaneous water insects	0.2	—	—	3.8	—	(5.0)	—	—	1.2	—	—	5.8
Surface fauna (Terrestrial insects and imagines of water insects)	15.7	—	18.5	29.2	32.6	(95.0)	13.4	—	18.0	—	—	—
Fish	—	—	—	—	—	—	—	—	—	(50.0)	22.5	—
Plant residues	—	—	—	9.4	—	—	—	—	—	(2.7)	—	—
Miscellaneous food objects	—	—	—	0.4	—	—	—	—	—	—	—	—
	100.0	—	100.0	100.0	100.0	(100.0)	100.0	100.0	100.0	(100.0)	100.0	100.0
Number of fish analysed	13	0	7	10	9	1	4	4	5	2	4	8

Table 11. *Average degree of stomach fill of char and grayling in the two bays (in %).*

	Fertilized bay		Reference bay	
	1978	1979	1978	1979
Char	$80_{(n=11)}$	$80_{(n=25)}$	—	$40_{(n=7)}$
Grayling	$80_{(n=7)}$	$100_{(n=15)}$	$50_{(n=7)}$	—

dominated the food bolus of char in 1976 (35 %) with *Bythotrephes* as a second choice (21 %), *Daphnia galeata* took over in 1978 (70 %) together with *Bythotrephes* (17 %). *Eurycercus* was again a first choice in 1979 (68 %) with no obvious second choice. In 1976 grayling displayed a most diverse food intake with *Eurycercus*, trichopteran larvae, chironomid larvae and terrestrial insects in about equal proportions. In 1978 chironomid larvae were the most preferred food items (50 %) with terrestrial insects as a second choice (39 %). In 1979, however, *Eurycercus* was the totally dominating food item (56 %) also of grayling.

Trout, on the other hand, does not seem to have changed its diet much during the period, trichopteran larvae is the first choice (about 40 %) followed by terrestrial insects and *Eurycercus* (both roughly 20—25 %). Unfortunately, too few trout were caught in the late summer of 1978 to allow a detailed diet analysis. Burbot is a minor constituent in both bays of the lake. In the fertilized bay burbot had chosen only insect larvae in 1976 and insect larvae (70 %) plus *Eurycercus* (30 %) in 1979.

The increasing importance of *Eurycercus* in the diet of all fish species roaming in the fertilized bay and the very obvious increase in food intake during the period will be further discussed below.

The number of fish caught in the reference bay each year during the period late August to late September was comparatively low due to the fact that fish populations are normally very weak in the lake. The 1976 analyses, however, are based on the stomach contents of 32 fish and it is also possible to discern a diet pattern for the dominating species during the succeeding years.

In 1976 char had largely preferred *Bythotrephes* (40 %) and *Daphnia galeata* (34 %), grayling had *Eurycercus* as the first choice (46 %) and terrestrial insects as the second (29 %), trout, finally, had fed mainly on trichopteran larvae (83 %) and to some extent on terrestrial insects. These results verify that resource partitioning is very intense. The 1978 food analyses of grayling and trout show about the same tendency, the former species choosing *Eurycercus* and terrestrial insects and the latter largely trichopteran larvae. The diet of burbot depends to a large extent on the size class of the fish. Large burbot switch from a preponderant trichopteran larvae diet into a diet of fish.

It is worth noticing that the exceedingly rich abundance of chironomid larvae in the fertilized stream—as well as in the drift—in 1978 and in 1979 is reflected in great quantities of these larvae in the stomachs of grayling in 1978 and of several char caught in the inner part of the bay in 1979 (especially during the peak of the summer). The likewise great abundance of *Daphnia galeata* and *Bythotrephes* in the stomachs of char from the same bay in 1978 is reflected in a simultaneously great availability of these species in the bay.

Cladocerans made up a substantial part of the diet of char in the fertilized bay in 1976 with little or no obvious interference from other fish species. In 1979, however, *Eurycercus* became by far the most preferred food item for most fish (Table 10). The percentage overlap between char and grayling is now about 72 %, between char and brown trout about 40 % (total overlap about 46 % chironomid larvae included), between grayling and brown trout also about 40 % and between burbot and the other fish species roughly about 30 % (mainly due to *Eurycercus*). Since grayling and brown trout also have trichopterans, other water insects and surface fauna in common the total diet overlap is here close to 53 %.

Results from the diet analyses of fish from the reference bay show characteristically little overlap — with few exceptions — between species (often about 20 % or less) and a good correspondence with similar results from both bays in 1976.

An indirect method of estimating the extent to which nutrients are canalized into fish meat is by examining the degree of stomach fill. Table 11 shows the average degree of stomach fill of char and grayling caught from late August to late September in 1978 and in 1979. With regard to the fertilized bay, a first impression was that the 4-degree scale commonly used for estimating the degree of stomach fill was inadequate, since most stomachs turned out to be so full that the walls of the anterior part of the intestinal canal were often distended due to an excess of food items. Even if the number of fish caught each autumn remained on a relatively modest level, the average differences in food intake between fish caught in the fertilized bay in comparison with fish caught in the reference are fully noticeable.

V. DISCUSSION

There are few biological methods at hand for the compensation of damages on fish caused by water regulation. The fisheries authorities of Sweden have actively worked for the introduction of new fish-food organisms into impounded lakes, such as *Mysis relicta* LOVÉN, *Pallasea quadrispinosa* SARS and *Gammaracanthus lacustris* SARS—as a compensation for a nearly completely ruined littoral bottom fauna, which normally form the food-base of the main fish competitors. New fish predators that are better adapted to a pelagic life in impounded lakes, such as lake trout, have likewise been introduced with some success. Compensatory measures of this kind have naturally offered unique possibilities of studying "interactive segregation" with reference to available resources between different fish species such as char, brown trout, whitefish, etc. but also between the new fish-food organisms mentioned above on one hand and the already established cladoceran fauna dominated by *Eurycercus lamellatus, Bosmina coregoni* etc., on the other (NORTHCOTE 1972, FÜRST 1972, FÜRST *et al.* 1978, LASENBY 1979).

The MAUCHA diagram of Fig. 10 is an illustrative way of demonstrating the food spectrum of char and brown trout—and hence the food niches occupied by these species—in allopatry and in sympatry under different environmental conditions (partly from NILSSON 1963). In allopatry both char and trout utilize the bottom fauna to roughly the same extent, which was shown by NILSSON from Lakes Skalvattnet and Abelvattnet. The diet of the char of Lake Anjan prior to impoundment in August 1938 (NILSSON 1960) was almost identical with the former, while brown trout had specialized on "insect larvae and nymphs". After impoundment—as given from the data from 1976 presented in this paper—char had switched into a diet of euplankton and semibenthic cladocerans, while trout still mainly fed on "insect larvae and nymphs plus terrestrial" insects. The level of food segregation had reached a relative maximum. It is interesting to note the role of the grayling under the successive phases of impoundment and nutrient enrichment. Before fertilizing the diet of grayling very much reminded of that of brown trout while after fertilizing the diet had become more close to that of the char—with a remarkably high percentage of semibenthic cladocerans (*Eurycercus*). Since the food intake of brown trout after fertilizing has become clearly modified by an increasing share of semibenthic cladocerans, the three fish species now partly occupy the same planktonic food niche and the level of food segregation has reached a relative minimum due to a superabundance of zooplankton.

Results of test-fishings repeated night after night in Lake Anjan (Table 9) did not suggest that netting was an effective means of removing fish populations from the fertilized bay, as had been intended in order to get an estimation of the size of the fish populations. On the contrary, the number of fish caught in each locality remained fairly constant. One hypothesis could be that each fish occupies a feeding territory which is defended, and every time a particular fish is caught a new recruit takes its place (cf. NILSSON 1960). Another hypothesis is that fish migrate in and out every day, *i.e.*, after feeding in shallow water they may return to deeper bottoms. There are indications that both explanations may hold true to some extent.

Different kinds of migration behaviour characterize salmonid fish in general. Both short-distance and long-distance migration for spawning are well-known phenomena. Less so is seasonal feeding migration, which has been described for Arctic char in various places in northern Sweden (CURRY-LINDAHL 1957), in Norway (AASS 1970) and in Canada (JOHNSON 1975). Char, like brown trout, brook trout, etc., are clearly capable of orienting against a gradient of organic compounds (*cf.* HÖGLUND and ÅSTRAND, 1973), which makes these fish inclined to congregate wherever a surplus of suitable food items are available. CURRY-LINDAHL describes a case of summer feeding migration performed by populations of char in the Lake Torne Träsk area in northern Sweden. The fish climb small streams in the birch-tree region to feed on terrestrial insects, which are sometimes particularly abundant here. Later in the summer they return to their home-lakes, where they spend the rest of the year.

A very special case of probable feeding migration may be given by the present authors from the Storlien area not far from Lake Anjan. Downstream of the vacation resort of Storlien, a series of small lakes—Åsvallstjärnarna—have long served as recipients of sewage. The lakes drain via a narrow stream, about 5 km long, into Lake Visjön, which is a fairly small lake (2.8 km^2) with a particularly fine population of large char (condition factor according to FULTON 0.9—1.3). In the summer these lakes hold very dense populations of char, brown trout and brook trout in very good condition, the average coefficient for char—again according to FULTON's formula—being well above 1.0.

In winter there is an almost total depletion of oxygen in these lakes. Test-fishings have revealed that the fish leave the lakes in late September and return one—two weeks after the breaking up of the ice in late May. No large fish have ever been caught after September each year. In all probability the fish migrate downstream to Lake Visjön. Through interactive segregation of available resources the three species of fish very effectively avoid competition by strict food segregation. On September 5, 1978, for instance, test fishing with survey-nets revealed that food at that time might even have been in short, *i.e.* that char largely fed on *Eurycercus* and, to some extent, on terrestrial insects, that stomachs of brown trout were full of trichopterans and small ephemeropterans, and that brook trout, finally, had concentrated on large trichopterans of the genus *Phryganea.*

It is well-known from Swedish recipients—both in lakes and in running-water habitats—that fish tend to congregate close to outfalls from sewage treament plants. It is far from uncommon that fish populations—most often "coarse fish"—which have thrived in the vicinity of sewage plants with merely mechanical purification or poorly working biological treatment, have drastically declined after an improvement in effectiveness, (B. ALMER, from the productive Lake Ivösjön, South Sweden, pers. comm.). One particular example from the River Muonio Älv—a tributary to the River Torne Älv in northern Sweden—may serve as an illustration. Electrofishing revealed that populations of yearlings of salmon and trout were particularly dense downstream of the outfall from the sewage plant of Muonio. The same phenomenon has been observed in the River Ängesån (KARLSTRÖM 1977). Another example from the Province of Jämtland at Duved—not far from Storlien and Lake Anjan —may likewise illustrate the very close connection between outflows from a sewage treatment plant and fish populations—here whitefish, perch and pike—all thriving in the same recipient.

According to available experience of nutrient enrichment in Norway and in Canada in various recepients, (see above) those fish species more or less bound to a zooplankton diet should respond first to an increased nutrient standard, *e.g.* char and some whitefish. Later, bottom feeding fish, such as brown trout should be favoured as well. The final results from Lake Anjan would seem to confirm these findings. It is interesting to note that the rise in condition of char in the fertilized bay from 0.76 to 0.89 (*cf.* Fig. 4) corresponds very well to the similar rise in condition of char from Lake Langvatn, *i.e.* from 0.72 to 0.90 over a three-year period (LANGELAND *et al.* 1977). Even if the average condition of the fish caught in the fertilized bay had risen from 1976 to 1979, this does not mean, of course, that all fish have gained weight to the same extent. Some fish have obviosuly remained uninfluenced by the surplus of food present in the fertilized bay. Some may have been recent recruits to this area, but the reason might also have been that these fish have utilized food objects which have not been particularly favoured by fertilization, *e.g.*, surface fauna.

On the other hand, some fish of remarkably fine quality, for instance large brown trout and grayling, have also been caught in the reference bay—and in other parts of the lake, as well. It is, however, very difficult to judge whether these fish have actually fed where they were caught, or if they are "longdistance swimmers" feeding in more optimal reaches of the lake, *e.g.* in the larger tributaries. On the whole the migration pattern of the fish of western Lake Anjan remains unknown.

Our material suggests that climatic shifts, such as variations in the temperature regime from year to year, water level fluctuations etc. have affected, for instance, the recruitment of young year-classes of fish and the yearly growth rate of fish. Such variations could be expected and the reference bay has therefore been of vital importance in the evaluation of which effects are primarily due to the nutrient enrichment.

GRIMÅS (1961) and AASS *et al.* (1972) have stressed the importance of shallow inlet impoundments situated by the estuaries of rivers flowing into impounded lakes for the restoration of a more or less collapsed littorial bottom fauna—an approach to the problem which recalls to mind the classical work by FORBES (1887). The present proposal of using half-secluded bays of a large impounded lake for a partial restoration of dwindling fish populations is in some ways similar to the ideas presented by GRIMÅS and AASS, although on a somewhat larger scale.

VI. CONCLUSIONS

Four seasons of "partial fertilization" of the impounded Lake Anjan have verified the hypothesis that the added nutrients rapidly pass from one tropic level to the next and eventually reach zooplankton-feeding fish, among which the char populations have hitherto been most favoured.

There are considerable doubts whether the production of electric energy alone is the most rational way of utilizing the freshwater resources of northern Sweden. Normally fisheries make up a quite substantial livelihood and also stimulation for residents. In the province of Jämtland a greater proportion of the waters than elsewhere in the country are now regulated, *i.e.* presently 51.4 % of the lakes and 84.7 % of the running waters. In the western mountain region 70 % of the lake area consists of impounded lakes.

Since there have hitherto been very few biological methods at hand for compensating the most adverse effects of impoundment, small-scale applications of fertilizers would seem to be an attractive alternative. On the basis of our experience from Lake Anjan "partial fertilization" is an effective and probably also an economic way of restoring fish populations in such lakes. It is our intention to verify also the economy of the method once we have been able to do these experiments on a larger scale.

In our opinion an ideal object of restoration would have the following characteristics: In order to secure a sufficiently long retention time for nutrients the basin should be deep enough as well as fairly secluded from the rest of the lake. It is also advantageous if a stream with a fairly constant water flow enters the basin.

In the light of the indisputable advantages of applying balanced nutrient enrichment to subarctic waters for the twofold purposes of improving the condition of the fish and increasing the buffering capacity against acidification—now rapidly in progress also in northern Scandinavia—an indiscriminate application of advanced sewage treatment in these waters appears to be no less than a waste of natural resources.

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Fish Species Interactions in a Fertilized Reservoir

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ABSTRACT

"Partial fertilization" of the impounded Lake Anjan in northern Sweden gave rise to a most interesting experimental situation with dramatic changes in the intensities of interactive segregation between the fish species involved, from a situation of intense resource partitioning in the regulated phase—with little available nourishment—to a high level of niche-overlapping in the enriched phase—with a superabundance of food items (*Eurycercus lamellatus*, in particular). The possibilities of "the vacant niche space" in the latter situation being filled up by the currently depressed fish species as the three-spine stickleback—if at all present within the water system—are discussed at some length and have also made a brief discussion on specific dominance hierarchies (SVÄRDSON, 1976) motivated.

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I. INTRODUCTION

The freshwater environment would seem to be more uniform than its terrestrial equivalents and for that reason the degree of ecological differentiation could be expected to be less pronounced (ELTON 1946). That this is not necessarily the case has been shown by FRYER and ILES (1972) with remarkable examples of habitat and food specializations in cichlid fish in fairly uniform biotopes in African lakes, and, for instance, by NILSSON (1960) and SVÄRDSON (1976) and others working with niche segregation between salmonid fish in subarctic lakes in Sweden.

The study of interactions between fish species has been one of the favoured and most urgent topics in Swedish fisheries biology since the early 1950's. Fish populations in the northern countries—at least in theory—should provide numerous examples of interactive segregation in accordance with BRIAN's (1956) terminology, since it has been suggested that the fauna here, in comparison with, for instance, tropical environments, is evolutionarily young and it is likely that the ecological divergence is not yet completed (NILSSON 1967). Interactive segregation means that ecological differences between species often become magnified through the presence of competitors (or predators). Increased interactive competition, furthermore, makes the interacting populations restrict themselves around their "optima", where they have a definite advantage over their competitors (SVÄRDSON 1949). These optima do not necessarily coincide with the conditions which are preferred by the same species in allopatry (NILSSON 1960).

Cichlid fish communities in the deep, unglaciated lakes of tropical Africa, on the other hand, are considered to represent an evolutionarily old fauna association and may illustrate what Brian calls "selective segregation" meaning that species have developed very specific behavioural patterns in the selection of habit or food (NILSSON 1960). The latter kind of relationship is often misinterpreted since the species are segregated into different niches and do not appear to compete at all (FRYER and ILES, 1972). It has often proved to be difficult to demonstrate in each particular case if the segregation is a result of interaction rather than nearly complete ecological divergence (NILSSON 1967).

The freshwater fish in Scandinavia are largely non-specialists, *i.e.* the species have rather generalized feeding habits and wide habitat tolerances (LARKIN 1956). The different age-groups of each species, however, tend to have different food and habitat requirements which means that "most of the environmental resources are open to the species and is selected for" (SVÄRDSON 1976). In sympatric situations when a second — or third — fish species with nearly the same non-specialist ecology utilizes the same resources of food and shelter, a counterbalancing selection pressure is established which means that "a more specialist type of niche is selected for by the subdominant species" (SVÄRDSON 1976). These kinds of selective forces at work are illustrated in Swedish fisheries literature over the last three decades. The relation between brown trout and char is the most intensively studied phenomenon in Scandinavia. The char-whitefish relation is also a classical case in Scandinavian fisheries biology side by side with the former. The balance between fish species in a community is largely a function of interspecific population dominance (SVÄRDSON 1976). Our present knowledge about relationships of that kind makes it possible to predict the outcome of interactive segregation between species such as in situations of invasion of species, of deliberate introductions of new species into a community, of drastically changed environmental conditions, for instance in reservoirs or in waters under nutrient enrichment

II CONDITIONS PROMOTING INTERACTION RESEARCH

Invasions and introductions

Interaction research is greatly facilitated under special sets of conditions. Invasions of new predator species may offer excellent experimental situations, *e.g.* the invasions of the sea lamprey into the Great Lakes of North America (MOFFETT 1956). Even better control of the situation can be obtained by the deliberate introduction of new species. Knowledge of the date of introduction is particularly valuable in this context. Among introductions of that kind may be mentioned the redside shiner into Paul Lake in British Columbia (JOHANNES and LARKIN 1961) causing a complicated situation of interaction with rainbow trout. Other examples are the numerous, more or less controlled introductions of the European brown trout into North American waters, in many cases resulting in displacement of native species such as brook trout (*Salvelinus fontinalis*), rainbow trout, Dolly Varden (*Salvelinus malma*) and cutthroat trout (*Salmo clarki*). Brown trout is here a dominant species and the subordinate positions of the mentioned North-American species is clearly illustrated by the fact that most introductions of North-American fish into Scandinavian waters — where brown trout is a main competitor — have on the whole been unsuccessful (SVÄRDSON 1976). Besides the above-mentioned American species may be mentioned lake trout (*Salvelinus namaycush*), kokanee salmon (*Oncorhynchus nerka*) and largemouth bass (*Micropterus salmoides*). Few cases of successful reproduction (brook trout), except in fairly marginal biotopes, are known.

Elimination of species

Other conditions which greatly promote the study of interactions between fish species are the onset of heavy fishing, selectively on certain species such as on perch (*Perca fluviatilis*) in Lake Windermere (LE CREN 1959) and on pike (*Esox lucius*) in Heming Lake (LAWLER 1962) or, more unselectively, such as in the case of incomplete rotenone treatment. The gradual acidification of water systems in Scandinavia and of the Canadian shield lakes also changes the balance between the fauna components quite drastically.

Water regulation

The very high level of hydroelectric exploitation of waters in northern Scandinavia in the 1950's and the 1960's — and even earlier — and different means of compensation for damage caused by this exploitation, such as the introduction of new fish or invertebrate species etc., have brought

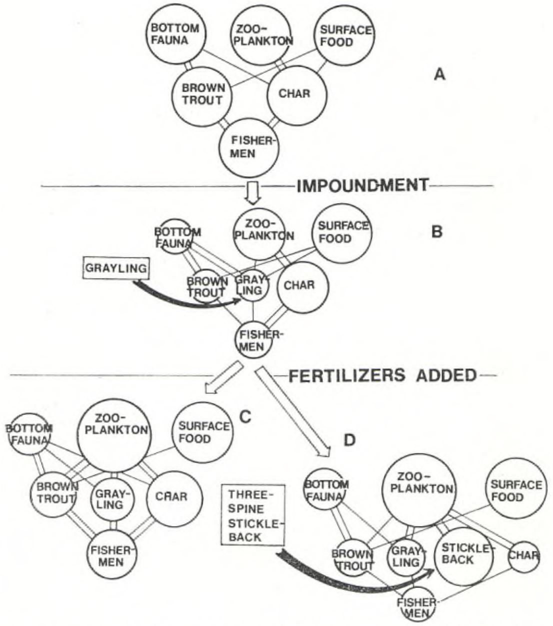

Fig. 1. Strictly simplified model of tropic relationships between food resources, fish populations and fishery in a regulated lake subjected to fertilization (C), and fertilization plus one invasive planktivorous fish species (D). Partly from Nilsson (1973). The C-situation is based upon results obtained from the "Lake Anjan study". Two to maximum four dominant fish species considered. Connecting lines between circles indicate degree of dependence.

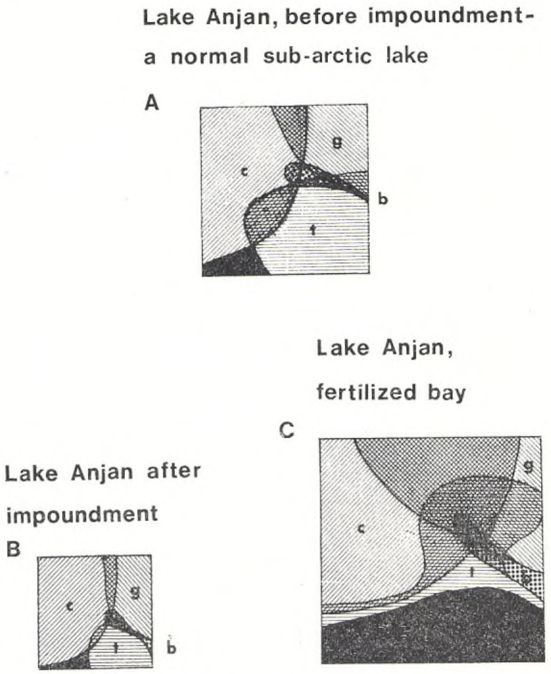

Fig. 2. Model of the "dimensions" of the feeding-niches occupied by char (c), brown trout (t), grayling (g) and burbot (b) in Lake Anjan before (A) and after (B) impoundment and some years after the start of the fertilizing activities (C). The size of each square symbolizes the availability of potential fish-food organisms (for further details, see text).

about unique experimental situations in the relatively simple ecosystems these waters represent. The list of interaction studies between different salmonid fish — and fish food organisms, in Sweden and Norway could, indeed, be made very long (*cf.* Runnström 1964, Nilsson 1964, Nilsson and Pejler 1973, Svärdson 1976).

Nutrient enrichment

Artificial nutrient enrichment of natural waters would mean the introduction of a new dimension to interaction research. Through simple dosage procedures, for instance through the method of "partial fertilization" described in Milbrink and Holmgren (1981), it is now possible to simulate otherwise large-scale and long-term processes. The strictly local character of "*in situ*" experiments of this kind makes it possible also to generate the above experimental situations in combination with nutrient enrichment — one by one or in concert.

III. INTERACTIVE SEGREGATION BETWEEN SPECIES IN A FERTILIZED RESERVOIR

The Lake Anjan study

The fertilizing experiments in Lake Anjan could be briefly summarized in the strictly idealized Fig. 1, Stages A to C (partly from Nilsson 1973). A half-secluded bay of the regulated Lake Anjan (year of regulation 1940) was enriched via a stream with commercial N- and P-fertilizers from 1976 till the autumn of 1979. The original fish fauna prior to 1940 was made up of brown trout, Arctic char — both in particularly good condition, minnow (*Phoxinus phoxinus*) and burbot (*Lota lota*) (Fig. 1, Stage A, the last two species not considered here). In 1952 grayling was accidentally introduced into the water system and successively took over as the main littoral and tributary fish species (Stage B).

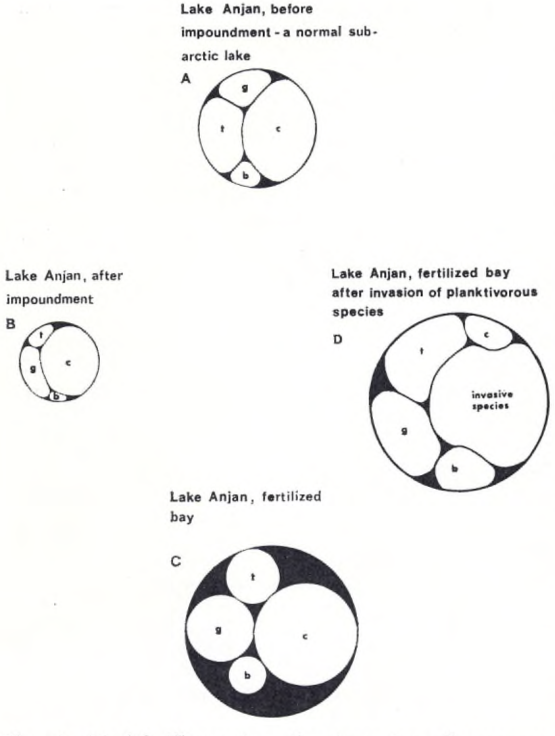

Fig. 3. Model illustrating the intensity of resource partitioning between fish species in an impounded lake under different trophic situations. The "niches" are symbolized by balls within a sphere. The size of each sphere is roughly proportional to the availability of fish-food organisms (for further details, see text).

Among the most deleterious consequences of impoundment in general could be mentioned that most of the littoral bottom fauna is eliminated (large crustaceans such as *Gammarus lacustris*, and various insect larvae). The littoral bottoms with vegetation are exposed to severe erosion due to water level fluctuations and are exposed to freezing when the water level is gradually sinking under the ice. The euplankton, however, is usually comparatively little affected. Bottom-feeding fish such as brown trout are hereby greatly disadvantaged while char is less so.

After regulation, the quality and the abundance of the fish gradually decreased in Lake Anjan (Stage B) and the species, due to lack in nourishment, became more sharply segregated into different feeding niches (Fig. 2, Stage C). Soon after the fertilizing activities had started, dense populations of euplankton (various cladocerans and copepods) and semi-zooplankton (*Eurycercus lamellatus*) developed in the bay. Within two years also the bottom fauna had increased in the fertilized bay of the lake by a factor of roughly 3. The three main fish competitors have all taken advantage of the new situation, the populations have notably increased and the condition of the fish has returned to nearly its former level.

This fertilization technique, although on a large scale, would make a fishery on at least a half-time basis meaningful, since catches have increased from a very low level by roughly a factor of 3 (Stage C). Mention can be made of a fairly similar fertilizing experiment in the regulated Lake Langvatn in Norway, which likewise resulted in a roughly threefold increase in the catches of brown trout and char (Langeland *et al.* 1977).

Fig. 2 is an attempt to model the feeding niches occupied by the main fish competitors in Lake Anjan before and after impoundment and three years after the start of the fertilizing experiments. Only the diet of fish caught in late August and in September is considered here, in accordance with the general experience that interactive segregation may be a seasonal process reaching a relative maximum in the autumn when food is not in superabundance any more (*cf.* Nilsson 1960, Milbrink and Holmgren 1981). The "dimensions" of the niches occupied by char, brown trout, grayling and burbot in sympatry are given within the total frame (partly from Nilsson and Pejler 1973). The areas in black also mark "the niche space" not occupied by the above species—or any species. The area of each square symbolizes the abundance of potential fish-food organisms. The percentage overlap of food niches is here presented in rather approximate figures.

The situation in the fertilized bay is further complicated because "drift fauna" (mostly chironomid larvae) from the stream entering the bay may at least periodically play an important role in the bay ecosystem (*cf.* Milbrink and Holmgren 1981). Drifting chironomid larvae in superabundance no doubt successfully compete with semi-zooplankton and euplankton as first rank food for all fish species involved here.

Fig. 3 is another way of illustrating the food niches of the above fish species and the "vacant niche space" (adapted partly from Svärdson 1962). Each species is here represented by a "ball"—or a "balloon"—within a sphere. Depending upon the level of food segregation each ball exerts a pressure against other balls and against the walls of the sphere. Compressed balls may in principle fill all vacant niche space.

Part A of the figures shows a situation characteristic of subarctic lakes in Scandinavia with a supposed level of niche-overlapping of 30—40 %. The balls are fairly compressed, since the level of food-segregation is considerable.

The B-part of the figures illustrates the impounded lake where food is in short supply. The balls are compressed nearly to a maximum and the level of niche-overlapping has reached a minimum.

Part C, on the other hand, shows a situation of a superabundant food supply and little competition between the species involved. The balls barely touch each other and niche-overlapping reaches a maximum.

There are different ways in which the present situation in the fertilized bay may develop further (Figs. 1, 2 and 3, Part C). It is likely that the fish populations will continue to increase and also that more fish will be attracted to the experimental area. More fish and a constant availability of fish-food organisms will lead to increased interactive segregation with a much reduced overlap of food niches—as in the case of Lakes Åsvallstjärnarna presented in Milbrink and Holmgren (1981). After some kind of equilibrium has been established a stage reminding of the A-situation is likely to develop. The "vacant niche space" will be filled up with the currently dominating fish species/alternatively by the currently depressed species such as minnows or perhaps by three-spine sticklebacks or whitefish — if the latter species are at all present within the water system.

The Norwegian fertilization experiments in the regulated Lake Langvatn (see above) eventually ended with the expansion of sticklebacks primarily at the expense of the char population but also of the brown trout population. In a large-scale fertilization project in the Great Central Lake on the Vancouver Island in British Columbia, three-spine sticklebacks likewise "exploded" and could effectively compete with young sockeye salmon (Manzer 1976).

Recent experience from the impounded Lake Torrön in Sweden has shown that the burbot is greatly favoured by the introduction of *Mysis relicta* (Dr. M. Fürst, pers. comm.). This has given rise to the suspicion that also nutrient enrichment may favour burbot, because *Eurycercus lamellatus*, which is a particularly common cladocean species on fertilized bottoms (*cf.* Milbrink and Holmgren, 1981), belongs to the burbot's most preferred food items. No indications, however, have yet been noticed of burbots being particularly favoured by the fertilizing activities in Lake Anjan.

Provided the total availability of potential food-organisms is constant, the next phase in the sequence of events following fertilization could be modelled in the following manner (Fig. 3, Part D). Each ball within the large sphere in the C-situation will probably shrink more or less. It is likely that the "char-ball" will shrink the most and a new ball symbolizing the invasive species will increase in size and press against the other balls and the sphere. This situation also leads to a reduction of the "vacant niche space".

The introduction of planktivorous whitefish or grayling into previously typical char-trout waters (such as has been the case in Lake Anjan) and the sudden "explosions" of sticklebacks, minnows, etc. make a brief discussion on specific dominance hierarchies motivated. The general pattern of development between pairs of salmonids in sympatry cold be formulated in two general rules. Firstly, one of the species of a pair of this kind tends to exploit the open water, largely depending on a zooplankton diet, whereas the other species exploits the littoral reaches depending upon benthic or semi-benthic food items. In that way the species populations are well segregated spatially during much of the year. The other rule is that the pelagic species is generally numerically dominant over the littoral species (*cf.* Nilsson and Northcote 1981).

Char is generally the pelagic species and brown trout the littoral species in sympatric situations in Scandinavia, their co-existence is also ensured by differential reproductive behaviour (Nilsson

1963). In allopatry, however, both species tend to prefer the littoral bottom fauna and their reproductive behaviour is also very similar. Among other intensively studied pairs of salmonids with a similar food and space partitioning may be mentioned whitefish and char (*cf.* SVÄRDSON, 1976), rainbow and cutthroat trout (NILSSON and NORTHCOTE 1981), cutthroat trout and Dolly Varden (ANDRUSAK and NORTHCOTE 1970) cisco (*Coregonus albula*) and smelt (*Osmerus esperlanus*) (SVÄRDSON 1976), whitefish and cisco (SVÄRDSON 1976) etc.

If the particular water into which one of the species of a pair is introduced is not deep enough, large enough, or topographically varied enough, one of the species is likely to outcompete the other (SVÄRDSON 1976, NILSSON and NORTHCOTE 1981). There is ample evidence in Scandinavia of displacements of species following the introduction of pelagic whitefish into char-trout lakes (EKMAN 1910, NILSSON 1967). While char is dominant in char-trout communities, char takes a subordinate position when whitefish is introduced. Accordingly, it has proved to be particularly difficult to introduce char into waters dominated by whitefish (SVÄRDSON 1976). Another well-known case of displacement is the grayling, which under certain conditions can outcompete brown trout (*cf.* Lake Anjan) by virtue of its capacity of utilizing the tributary resources of reservoirs or natural lakes (*cf.* NILSSON 1967).

Many species in sympatry no doubt utilize a common food supply less economically than one species alone, and the introduction of new species into a freshwater community tends to depress the individual growth of other species (NILSSON 1960). The problem of stunted populations and dwarfed fish as a result of the less competitive species being forced to select food items of a lower rank (IVLEV 1961) has been treated in SVÄRDSON (1976) and in NYMAN (1972).

CARLANDER (1955) could formulate the general rule that the standing crop of fish increases as the number of species increases — or as the niches are filled, but the maximum crop of an individual species is usually obtained with few species present. SVÄRDSON (1976) has reflected upon the fact that so many formerly char-trout lakes in Scandinavia have been "destroyed" by introductions of whitefish. The presence of the latter species has, no doubt, brought about a considerable rise in the total biomass, which was formerly of great importance for food production, and it is only in recent time that char has become more appreciated than whitefish. The same practical reason has probably underlain the decisions of introducing grayling into the watersheds of impounded lakes.

The most effective utilization of common resources is generally obtained by the combination of species belonging to different trophic strata, *i.e.* bottom-feeders and plankton-feeders. In reservoirs in northern Sweden, where the benthic fauna is largely lacking, the best efficiency would be secured by reinforcing the planktonic food chain, which is best achieved by nutrient enrichment and—if possible—keeping pelagic whitefish, sticklebacks and other potential competitors of the char out of the water system.

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The Systematics and Biology of Landlocked Populations of Arctic Char from Northern Europe

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ABSTRACT

Ecological and biochemical data from approx. 22,000 specimens of Arctic char were employed to characterize three sibling species of char. More than 250 populations were sampled, the great majority being landlocked but diadromous populations from the Canadian Arctic, Greenland, Iceland and Svalbard (Norway) were also included. All three species occur in a landlocked as well as a diadromous state. The clear-cut differences between the three species in interspecific competitive ability as evidenced by numerous sympatric populations of all three species combinations may explain otherwise seemingly contradicting results of lake regulation schemes or management measures taken. The systematic analysis yielded the following nomenclature suggestions: *Salvelinus salvelinus* (L.) is the most competitive of the three, a big, predatory fish with a predominance in large lakes, and a wide distribution in Sweden. *Salvelinus alpinus* (L.) is the least competitive species and the earliest immigrant after the recession of the last glaciation, dominating the headwater lakes of the mountain range bordering Norway. This species may also inhabit rivers and spawn in them, and also in lakes show an ecological adaptation similar to brown trout. *Salvelinus stagnalis* (FABRICIUS) seems to be of western origin, *i.e.* from the North Atlantic Ocean, and has reached Sweden only in areas where contact with Norwegian rivers must have been easy in the post-glacial period. This species typically is a pelagic planktonfeeder which also implies that it does not attain as large a maximum size as the other two species.

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I. INTRODUCTION TO THE PROBLEM

Speciation

Most modern biologists would probably agree that some amount of geographical isolation be needed to allow for a genetic differentiation of natural populations, as a starting point for the development of isolating mechanisms and a final evolutionary goal of attaining reproductive isolation and thus species rank. MAYR's excellent account of the dynamic biological species concept (*e.g.* 1969) has greatly facilitated the understanding of the process of speciation, but still there is much controversy as to the mode and rate of evolution in many species groups. One of the major problems debated among taxonomists is how much geographical isolation is needed and also how and when to consider two sympatric populations reproductively isolated. The major difference of opinion between adherents of allopatric speciation and sympatric speciation, respectively, is really only a matter of where on the time scale speciation is believed to occur, 10,000 or half a million years ago? Even if this view is an over-simplification of the problem, there are genera which are well suited for a detailed investigation of the problem.

Sibling species

Sibling species are by definition sympatric populations that are morphologically almost identical but are reproductively isolated and thus functionally indistinguishable from "valid" species. Often this morphological convergence does not imply genetic similarity, but among the basically anadromous salmonids of previously glaciated regions in the Northern hemisphere it seems likely to assume that the morphological similarity of many species groups indeed indicates both a close genetic affinity and a relatively recent aquisition of reproductive isolation (*e.g.* SVÄRDSON 1961). Whether all of these species groups in the genera *Oncorhynchus*, *Salmo*, *Coregonus* and *Salvelinus* have evolved as the result of genetic differentiation already in pre-glacial or inter-glacial lakes or rivers, or actually have attained reproductive isolation in post-glacial times may be of fundamental interest to those searching for the correct time-scale of evolution, however, what can not be disputed is the fact that populations of these species groups frequently hybridize. The frequency of spontaneous hybridization and the lack of intergeneric hybrid sterility may be taken as evidence of the incomplete isolating mechanisms and the recent event of species differentiation. The Arctic char (*Salvelinus alpinus* (L.)) is an example of one such species group, and it is the intention of this paper to discuss the biological significance of some of the numerous forms of Arctic char that have been described in northern Europe, with special emphasis on landlocked populations.

Distribution

The Arctic char has a circumpolar distribution in the Northern hemisphere, and occurs in lakes, rivers and marine coastal areas of Greenland, Svalbard, Jan Mayen, Iceland, the Faeroe Islands, northern Norway, the Arctic coast of the Soviet Union and the Arctic areas of North America, extending as far south as the Great Northern Peninsula of Newfoundland. Besides, numerous landlocked populations of Arctic char occur in inland areas, where the fish has no present-day access to the sea, such as in Sweden, Norway, Finland, the British Isles, the Alpine area of central Europe and as isolated populations far to the south of anadromous populations in the Soviet Union and North America (Fig. 1).

Taxonomy of the Salvelinus alpinus complex

Few genera of fish have attracted so many opinions on the systematic position of the various morphological forms as the Arctic char. If the entire genus *Salvelinus* is considered including the proposed separate genus *Cristivomer* a large number of species was suggested by taxonomists of the early part of this century. REGAN (1911)) named 15 species of this genus in the British Isles alone, JORDAN *et al.* (1930) recognized 14 in North America and BERG (1948) described 11 in the Soviet Union. Even though these early investigators (except BERG) sometimes reverted to a more conservative model they have recent followers (*e.g.* VLADYKOV 1954, WENT and TWOMEY 1957, TWOMEY 1960, ROUNSEFELL 1962, LADIGES and VOGT 1965). The other extreme has been held primarily by Soviet taxonomists (RESHETNIKOV and SAVVAITOVA 1962, SAVVAITOVA 1966, 1980, CHERNENKO 1969). These authors even regard *S. malma* as conspecific with *S. alpinus*, but on the other hand give specific rank to *S. leucomaenis* of the Soviet Union. At present there is little controversy as to the systematics of *S.* (*Cristivomer*) *namaycush* and *S. fontinalis*, but the *S. alpinus* complex (with or without the Dolly Varden and the Gogi char included) still shows all signs of a closely knit group of sibling species (SVÄRDSON 1961, MCPHAIL 1961, BEHNKE 1972, NYMAN 1972).

The complex taxonomy of Scandinavian chars was early realized, and specific names were suggested for a number of supposedly distinct forms as early as 1832 (NILSSON 1832). SMITT (1882, 1886) and LILLJEBORG (1891) reduced the number to three, and this number was suggested by recent authors also (*e.g.* SVÄRDSON 1961, NYMAN 1972) even though no attempt was made to correlate them with the older taxa.

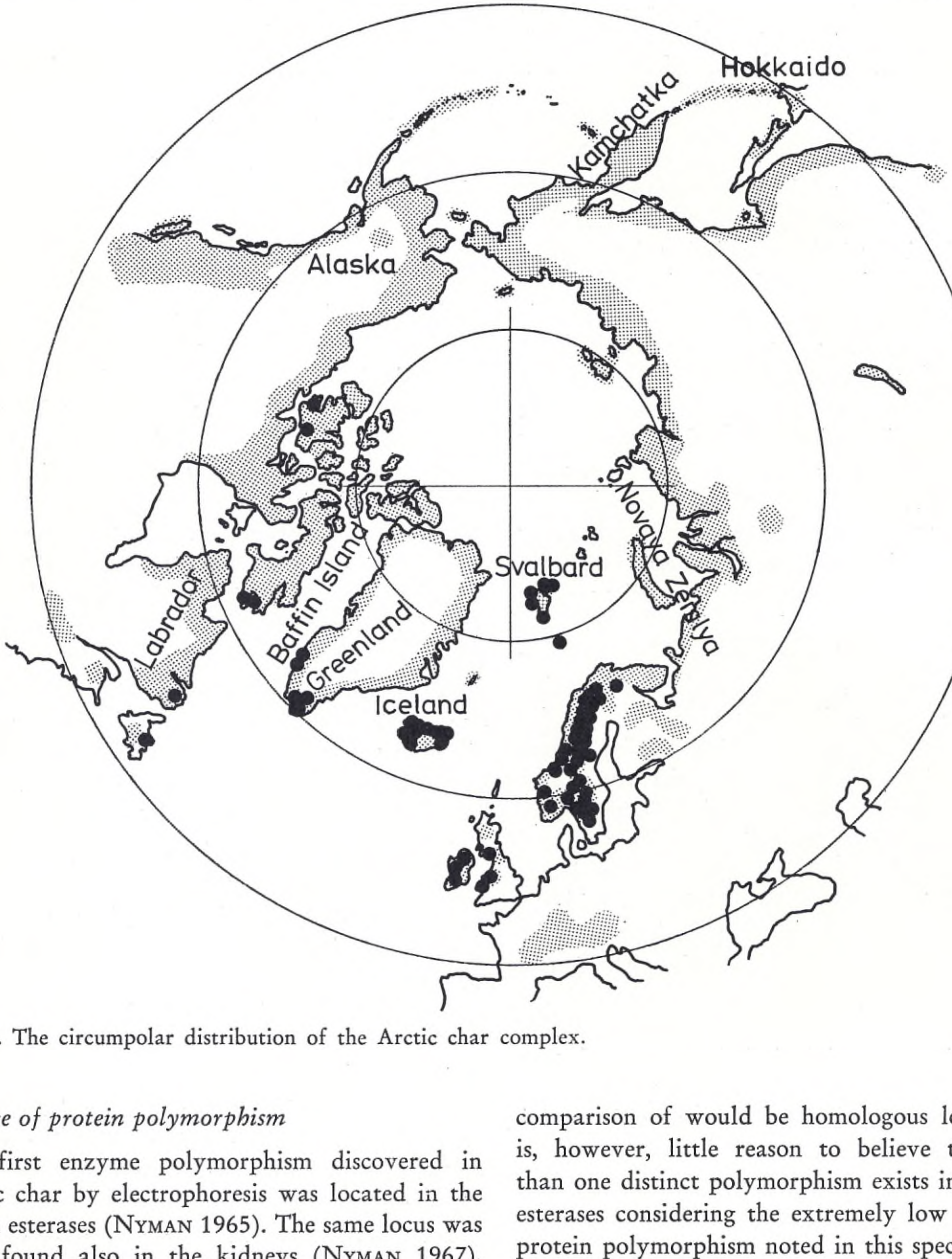

Fig. 1. The circumpolar distribution of the Arctic char complex.

Degree of protein polymorphism

The first enzyme polymorphism discovered in Arctic char by electrophoresis was located in the serum esterases (NYMAN 1965). The same locus was later found also in the kidneys (NYMAN 1967), slime (NYMAN unpubl.) muscle, liver and eyelenses (HAMMAR and GYDEMO unpubl.). Polymorphisms in the liver esterases and indeed even qualitative differences between populations of char have also been described by other authors (SAUNDERS and MCKENZIE 1971, MCCART unpubl. data, BAIN 1974) but the use of slightly different electrophoretic methods has so far precluded a direct comparison of would be homologous loci. There is, however, little reason to believe that more than one distinct polymorphism exists in the liver esterases considering the extremely low degree of protein polymorphism noted in this species group. The only additional polymorphisms so far detected were other two-allele codominant variations in the transferrin complex (NYMAN 1965) and in the muscle MDH (Nyman unpubl.). The first population data of the transferrin polymorphism, however, were evaluated when CHILD (1977) secured data from four Welsh populations of char. All early authors reporting on the variability of protein electrophoregrams in Arctic char agree that intraspecific variation is negligible (TSUYUKI *et al.* 1966, SAUNDERS and MCKENZIE 1971, NYMAN 1972). More refined histochemical staining methods have since provided far more information on the variability of protein and enzyme loci in char tissues (NYMAN, HAMMAR and GYDEMO, unpubl. data, CLAYTON and IHSSEN 1980, FERGUSON 1980) but not even these studies gave evidence of more than one "new" polymorphic locus, *viz.* the eye LDH polymorphism found in char of Nettilling Lake, Baffin Island (CLAYTON and IHSSEN 1980). As an example of the search for polymorphic population markers FERGUSON's analysis of Irish char population can be given. FERGUSON (1980) analysed in excess of 60 proteins and 27 enzyme loci, and concluded that no consistent interlake differences could be detected at any of these loci except for the serum esterases. Judging from these results alone it would seem that the sibling species group of Arctic char were on the verge of extinction considering the low level of polymorphic loci in comparison with many other salmonid fishes (*e.g.* ALLENDORF and UTTER 1979). The ecological plasticity of the species refutes such a conclusion which indicates that care must be taken when evaluating "life quality" criteria from protein data with the limitations of the present techniques. Improved techniques, like sequential electrophoresis, have already shown great promise, and enzymes which were previously thought to have little if any genetic variation were found to possess numerous alleles, so there is all reason to ask as JONES (1980): How much genetic variation is there? On the other hand, it is not self-evident that detection of numerous polymorphic loci will simplify evaluation of species and population characteristics, because increased complexity will also increase our difficulties to assign a polymorphic locus to its proper taxonomic level. This problem is already with us. Why is it, that some polymorphic loci display very little geographical variation in allele frequencies, while others in the same species show tremendous differences even between adjacent populations? Evidently because they have very different significance as population markers. With these limitations of the biochemical techniques in mind we must broaden our search for supporting ecological clues since these traits, even though they are modified by the environment, at least are certain to be under strict genetic control by polygenes.

Ecological segregation

Returning to northern Europe numerous examples of sympatric populations or Arctic char have been described (*e.g.* NYSTRÖM 1863, TRYBOM 1883, EKMAN 1912, SAEMUNDSSON 1904, 1909). These investigators realized that in fact two or three populations of char could coexist without interbreeding but the mechanisms by which they were kept apart remained secluded until ecologists and geneticists revealed both the principal isolating mechanisms and clues to an invasion theory of a limited number of allopatrically evolved sibling species. The first indication of niche specialization and thus differential natural selection was the different growth rates found in sympatric populations (OLOFSSON 1932, NILSSON 1955, NORDENG 1961, AASS 1968, ANDERSSON *et al.* 1971).

The real break-through, however, was Nilsson's discovery (1955) that the sympatric forms were segregated in terms of food. Many examples of habitat and temporal segregation during spawning were also noted. More recently, a number of ecological parameters have been added to the list of characters distinguishing sympatric populations of char (*e.g.* NILSSON and FILIPSSON 1971, NYMAN and FILIPSSON 1972, GÖNCZI 1971, KLEMETSEN and GROTNES 1975, 1980, FÜRST *et al.* 1978, HAMMAR 1980).

Mode of speciation

The invasion theory of SVÄRDSON (1958, 1961, 1970, 1979) shed light on the evolutionary process responsible for the occurrence of two or three sympatric populations of char in several bodies of water. SVÄRDSON assumes that reproductive isolation was achieved allopatrically in preglacial or inter-glacial times, and that subsequent invasions of post-glacial river systems explain the present distribution of three species. The fact that many of these populations still are capable of maintaining reproductive isolation despite few possibilities for niche specialization in many small lakes is good evidence that the ancestral species had indeed reached full rank of functional species.

On the other hand, there are many instances of present-day introgression between all three species (NYMAN 1972, HENRICSON and NYMAN 1976, NYMAN and FILIPSSON 1972, FÜRST *et al.* 1978. HAMMAR 1980) indicating that the species, even though they may have been slightly hybridized before entering freshwater, were more segregated ecologically and probably genetically during their allopatric past than at present. From a systematic point of view it is clear that no set of morphometric or meristic variables, including chromosome studies, can separate the three proposed sibling species of the Arctic char species complex of Scandinavia. In North America, however, the eastern form of Arctic char could be distinguished from the western type by the number of gillrakers and pyloric caeca (MCPHAIL 1961).

FRIDRIKSSON (1939) also found a difference in the number of vertebrae of the three different Arctic char forms of Thingvallavatn, Iceland.

On the other hand a number of ecological parameters may be used to discriminate between the species when they occur sympatrically *e.g.* habit selection, growth rate, sexual maturity, food preference causing quantitative differences in incidence of parasite infestation by a number of parasite species, and habitat and temporal segregation at spawning. Since most of these criteria form a rather fixed pattern from lake to lake with sympatric populations, and nearby allopatric populations can be used as controls of species specificity, certain generalized features of biological and thus systematic significance may be evaluated. Actually, the very presence of certain common features distinguishing the three species in all bodies of water where they occur sympatrically is in accordance with the view that only three ancestral species are involved, and that reproductive isolation occurred allopatrically.

From the above discussion it may seem quite simple to characterize the various units of this set of species, but two factors complicate things in many cases. When a body of water is inhabited by one species of Arctic char only, it typically occupies all food niches available, and for every competitive species added niche specialization becomes progressively more pronounced. Also because the gene frequency level so far is the only character that can be used to discern allopatric populations, fixation of the most common allele is likely to occur quite frequently when the effective population size is small. This latter problem may complicate the discrimination of the "N"- and "F"-char, described below, because both have high frequencies of the Est F-allele at lower altitudes.

By increasing the number of discerning gene-markers (*e.g.* transferrins and the eye LDH) the degree of fixation will probably be more easy to identify.

As a consequence of the first problem, *i.e.* lack of food segregation in allopatry, all three species may grow to a rather large size when food supplies are good. Even here, however, the maximum size attained by the three species differs, which, in agreement with the segregation of the species when they occur sympatrically, indicates that genetic factors control the range of variation.

II. MATERIALS AND METHODS

This paper is based on population genetic and ecological data from well over 22,000 Arctic char, derived from 274 bodies of water. The bulk of material emanates from Sweden, but large samples have been included from Norway, Iceland and Greenland as well. Samples of char have also been analysed from Finland, Spitsbergen, Victoria Island, Baffin Island, Labrador and Newfoundland (Table 1.) The geographical distribution of the various samples is given in Fig. 1.

All fish were analysed electrophoretically (horizontal starch gel electrophoresis) and their serum esterase phenotypes have been routinely screened. This simple two allele polymorphism is a cheap and fast method for identification of char populations. Detailed information on the electrophoretic procedures and the hereditary basis of the polymorphism is given elsewhere (NYMAN 1967, 1972).

In order to get as complete as possible information on the biology of the sibling species all kinds of ecological data were collected from the populations sampled. Principal interest has been devoted to information on age and size, since growth patterns in combination with frequency calculations of the esterase alleles is the single set of parameters most easily employed for species classification. Apart from growth data, habitat selection can be indicated by fishing in all layers of a lake,

Table 1. *The geographical distribution of the fish analysed electrophoretically.*

Country	Number of lakes/streams	Number of individuals
Sweden	194	18,163
Norway	19	1,935
Svalbard	7	173
Finland	2	84
Iceland	39	1,258
Great Britain	1	43
Greenland	6	330
Canada	6	360
Total	274	22,346

and food and parasite infestation is readily evidenced by stomach and wholefish analyses (Henricson 1977, 1978). Information on local names of the different forms of Arctic char and morphological characters are noted. Knowledge of local spawning grounds and spawning time may simplify the test of sympatric populations, since it is rather safe to assume that the great majority of fish on the spawning grounds are con-specific. This hypothesis is of course further substantiated by the good accordance with Castle-Hardy-Weinberg equilibrium in the samples, indicating that the samples are derived from panmictic populations. Any discordance indicates examples of genetic disturbance, introgression or introductions of other chars by local fishermen.

The methods used for calculating rates of gene flow and magnitude of introgression between sympatric populations have been described previously (Nyman and Filipsson 1972, Henricson and Nyman 1976). Basically the data used are esterase phenotype, age, length and comparison with allopatric fish from the same region.

III. RESULTS

Descriptive treatment of the three sibling species *Salvelinus alpinus* (Linnaeus 1758). Original description: Systema Naturae, Ed. X, 1758.

The original description is based on the views of Petrus Artedi (*e.g.* Ichthyologia, 1738) and Linnaeus' own visit to Lapland, as described in Iter Lapponicum, 1732. In the latter publication Linnaeus describes the char of high altitude lakes, above timber line, where char were the only fish species of the lakes. According to the route he describes, the type locality must have been the small headwater lakes of the Tarrejokk River, NW of Kvickjokk in Swedish Lapland. These lakes are situated at an altitude of well over 800 m above sea level. In a collection of Linnaeus' lectures at the University of Uppsala in the period 1748—52, *i.e.* almost a decade before the tenth edition of Systema Naturae, his description of this taxon is as follows (authors' translation from the Swedish): "This fish abounds in the very coldest lakes in Lapland, where no other fish ... can thrive: it is difficult to understand what it eats, because in these lakes, which almost always are frozen, there is no worm or plant ..." In Artedi's opinion this fish was "*in lacubus summis Alpium Lapponicarum frequentissimus* ..."

Type and type locality: No samples have been procured from the very lakes of the original description, but the vast majority of the headwater lakes of the Swedish alpine region are inhabited by one species of char only, and according to the diagnosis below the following type localities may be selected to cover the habitat range exhibited by allopatric populations of this species:

Jävsjön	64° 4′ N, 13° 3′ E
Lenglingen	64° 15′ N, 13° 45′ E
Tärnasjön	66° 0′ N, 15° 28′ E
Hundtjärn	66° 2′ N, 15° 58′ E
Pajeb Njuorajaure	68° 29′ N, 18° 13′ E

Synonymies: Lilljeborg (1891) makes the following suggestions after the publication of Systema Naturae, Editio Decima (1758):

Salmo alpinus,	Linné (Linnaeus): Fauna Svecica, Ed. II, p. 123, 1761.
,, ,,	A. J. Retzius: Faunae Suecicae, Part I, p. 346, 1800.
,, *ventricosus,*	
,, *carbonarius,*	
,, *alpinus,*	
,, *rutilus,*	S. Nilsson: Prodomus Ichthyol. Scand., p. 7 ff, 1832.
,, *alpinus*	
,, *carbonarius,*	
,, *rutilus,*	S. Nilsson: Skand. Fauna, 4th Ed. The Fishes, p. 426 ff, 1855.
,, *willoughbii,*	A. Günther: Contribution to
,, *cambricus,*	the Knowledge of the British

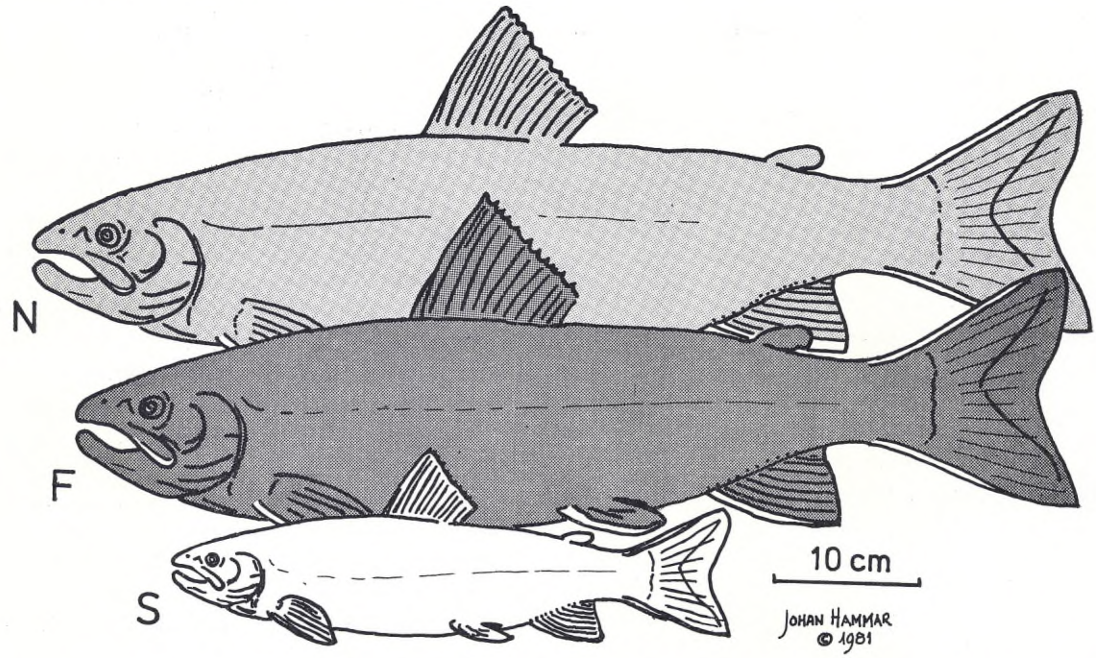

Fig. 2. Size relationships between the three species, *i.e.* maximum size in allopatry. Relative scale same as in Fig. 4.

N = *Salvelinus salvelinus* (formerly "Normal char")
F = *Salvelinus alpinus* (formerly "F-char)
S — *Salvelinus stagnalis* (formerly "S-char")

Salmo grayi, Charrs, Proc. Zool. Soc., London, p. 10 ff, 1862.
Salvelinus alpinus, A. W. MALM: Göteborgs och Bohusläns Fauna, p. 540. 1877.

Synonymous with "F-char", "F-tita", "F-dwarf", "T_F-dwarf" and "blattjen" of previous publications.

Diagnosis and description: Food niche littoral or benthic. When sympatric with either of the other two species more deepliving. May spawn in streams. Feeds on benthic crustaceans and fish, also reflected in its parasite fauna. Least competitive of the chars. Most frequent species in alpine headwater lakes in Sweden. Frequency of the most anodal serum esterase allele in electrophoresis at pH 8—9 0.90—1.0. This allele is frequently fixed. Stunted growth in sympatric populations with either of other two species of char, but may attain considerable size in allopatry (Fig. 2).

Numerical data extremely variable and not different from other two species.

Geographical range: The entire mountain range of Sweden bordering Norway (Fig. 3). Also frequent in Norway and occurs in Iceland, and probably also in Spitsbergen (Svalbard), Bear Island, Great Britain and Ireland. It is still unclear whether it is synonymous with any of the North American chars, but there are indications that it occurs in certain ponds in Newfoundland. Although primarily landlocked certain populations are still anadromous (*e.g.* in Iceland) (GYDEMO 1980).

Habitat: see above—Diagnosis and description.

Material examined: More than 100 populations of this species have been examined, approximately totalling 10,000 specimens.

Salvelinus salvelinus (LINNAEUS 1758)

Original description: Systema Naturae, Ed. X, 1758.

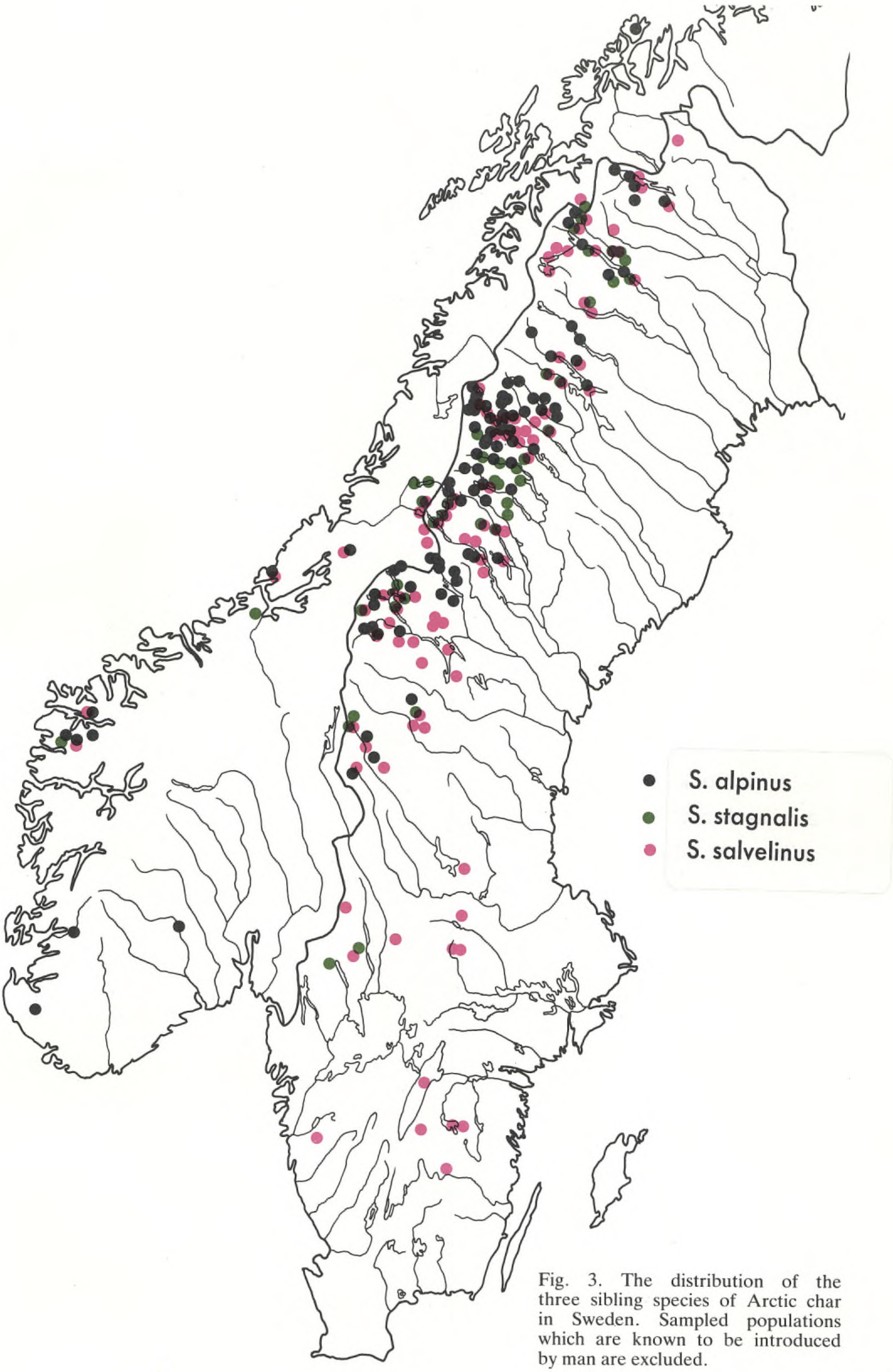

Fig. 3. The distribution of the three sibling species of Arctic char in Sweden. Sampled populations which are known to be introduced by man are excluded.

Even this description is based on Artedi's (1738) material. Artedi places the original material in a watershed in Austria outside Linz. The proper site has not been located and neither has any material from Austria been examined in order to compare with relevant Swedish material. Thus the naming of this species may seem premature, and may need revision once char from the Linz region have been examined. However, numerous authors have considered *S. salvelinus* to be synonymous with the large predatory char typical of large deep lakes, which makes it logical to follow their suggestions. Nilsson (1832, 1855) remarks that this species exists in south Swedish lakes like Vättern, Sommen and other lakes in the province of Småland. This suggestion coincides with the allopatric occurrence of the so called N-char of our earlier publications. According to F. A. Smitt (communicated in Lilljeborg, 1891) it also occurs in more northern lakes, like Lake Storsjön in the province of Jämtland and even at Spitsbergen. Collections in lakes of Spitsbergen have substantiated this view (Hammar, unpubl.).

Type and type locality: The original type locality has not been located (see above), but according to the opinions of many followers who have translated Linnaeus' classification as a large fish found in large lakes, many things talk in favour of letting it become synonymous with the so called "normal" or "N-char" of earlier publications (*e.g.* Nyman 1972). The dominating species of the large lakes of Sweden and the exclusive species of char in southern Sweden should as type and type locality have the populations of Lake Vättern. However, in order to better reflect the range of variation in habitat five lakes have been chosen to represent this species, in the same manner as for *S. alpinus* above:

Vättern	58° 15′ N, 14° 23′ E
Rösjöarna	62° 32′ N, 12° 48′ E
Sandsjøen	64° 26′ N, 13° 45′ E
Vastenjaure	67° 28′ N, 16° 33′ E
Råstojaure	68° 46′ N, 20° 27′ E

Synonymies: Again Lilljeborg (1891) has been used to sample the opinions after the publication of Systema Naturae, Editio Decima, 1758:

Salmo salvelinus,	Linné (Linnaeus): Systema Naturae, editio XII:ma, T. I, p. 511, 1766.
,, ,,	Bloch: Naturgesch. der Fische Deutschlands, 3:er Theil Tafel 99. p. 149, 1784.
,, *pallidus,*	S. Nilsson: Prodromus Ichthyologieae Scandinavicae, p. 9, 1832.
,, *Salvelinus,*	S. Nilsson: ibm. p. 10.
,, *umbla,*	L. Agassiz: Hist. nat. des Poissons d'eau douce de l'Europe centrale. Planches, tab. 9, 10, 10 a & 11, 1839.
,, *Salvelinus,*	Valenciennes: Hist. nat. des Poissons par Cuvier & Valenciennes. T. XXI, p. 246, 1848.
,, ,,	S. Nilsson: Skandinavisk Fauna, 4:e del. Fiskarna, p. 422, 1855.
,, ,,	C. Th. E. v. Siebold: Die Süsswasserfische von Mitteleuropa, p. 280, 1863.
,, ,,	F. A. Smtt: Kritisk Förteckning öfver de i Riksmuseum befintliga Salmonider; Kongl. Svenska Vetenskaps Akademiens Handlingar, Bd. 21 (8) (särsk. aftr.), p. 108, 1886.

Synonymous with "ordinary char", "normal char" and "N-char" of previous publications.

Diagnosis and description: Large; predatory with food niche littoral or pelagic (Fig. 2). When sympatric with either or both of the other two species superior in growth rate and size. May become stunted allopatrically when food is scarce. Most frequent in southern Sweden and in big, deep lakes. Spawns in fairly shallow water. Frequency range of the most anodal serum esterase allele in electrophoresis is usually 0.40—0.70, but may become fixed in low latitudes at 1.0 due to genetic drift in small populations.

Numerical data extremely variable and not different from other two species except for the normally better initial growth rate.

Geographical range: Dominates at lower altitudes and in southern Sweden (Fig. 3). Widest geographical range of the three species (in Scandinavia). Occurs frequently in Norway and Iceland, but also in Spitsbergen, Great Britain and Ireland. It is still unclear whether it is synonymous with any of the North American chars. Although primarily landlocked some populations are still anadromous (*e.g.* in Norway and Iceland) (NILSEN 1980, GYDEMO 1980).

Habitat: see above—Diagnosis and description.

Material examined: Roughly 100 populations have been examined, representing some 9,000 specimens.

Salvelinus stagnalis (FABRICIUS 1780)

Original description: Fauna Groenlandica, p. 170, 1780).

This is a provisional name which has the merit of being older than any other known scientific name from a region where the named species exists and where other classified taxa have already been lumped into either of the two species described above. It may well be that some of the taxa described by *e.g.* NILSSON, GÜNTHER or REGAN may prove synonymous with this species when examined, in which case they will have precedence over *S. stagnalis*. So far this has not been done. There are *e.g.* indications, that either of the chars of Lakes Coomasaharn and Finn in Ireland may indeed belong to this species. Both have esterase allele frequencies within the expected range (FERGUSON 1980) and both are dwarfs. It is, however, untypical of this species to become stunted in allopatry, especially when fishing pressure is low. Also, the two populations were given different specific names by REGAN (1908).

On the other hand there are additional facts that talk in favour of selecting the name *S. stagnalis* for this taxon. FABRICIUS' original species was considered of high Arctic origin, with a distribution in areas bordering the Arctic Ocean, hence its Swedish name *Ishavsröding*, meaning Arctic Ocean Char. Even if the populations of char examined by the present authors have failed to show homology of the char of the various areas mentioned by FABRICIUS, at least this species has a westerly distribution from a Scandinavian point of view, and of the three taxa distinguished by the method described in this paper, the taxon proposed to bear the name *S. stagnalis* has the most westerly distribution—at least in Sweden—thus indicating an immigration from the Norwegian coast, *i.e.* from the fringes of the Arctic Ocean.

Type and type locality: O. FABRICIUS named this species from Greenlandic waters in Fauna Groenlandica (1780), p. 175, and there are indications that anadromous populations of char from southern and western Greenland indeed may be synonymous with the Swedish populations according to the esterase frequency range (*e.g.* NYMAN 1972, HAMMAR, LINGDELL and MOSEGAARD unpubl.). As stated above there is, however, considerable controversy as to the homology of the originally proposed taxon as classified by FABRICIUS (1780) and SMITT (1886) and the present "low frequency char" of this paper, thus the provisional status of its scientific name. We have been unable to find a scientific name given to any of the populations chosen as type populations (see below) but the western predominance (from a Swedish point of view) is the main reason for using the term *S. stagnalis*. The five allopatric populations chosen as "type populations" are the following:

Fjellkjösvatnet	63° 20′ N,	9° 45′ E
Torröjen	63° 56′ N,	12° 53′ E
Namsvatn	65° 0′ N,	13° 40′ E
Västra Marssjön	65° 1′ N,	15° 23′ E
Satijaure	66° 28′ N,	18° 48′ E

Synonymies: In his treatise on the Greenlandic Fauna FABRICIUS (1780) mentions four taxa of char, with the specific names *carpio*, *alpinus*, *rivalis* and *stagnalis*. SMITT (1886) considers them conspecific under the name *S. Stagnalis*, and also suggests a broad distribution of this taxon and describes intermediate forms between *stagnalis* and *alpinus* and *stagnalis* and *salvelinus* (In: LILLJEBORG 1891). With the rather limited geographical distribution of our analysis of this taxon it has not been possible to prove the homology between *stagnalis* and any later described forms of char from the same general area. Synonymous with "S-char", "S-tita" and "T_S-dwarf" of previous publications.

Diagnosis and description: Moderately sized fish rarely exceeding 30 cm total length (in landlocked populations) (Fig. 2). Almost exclusively

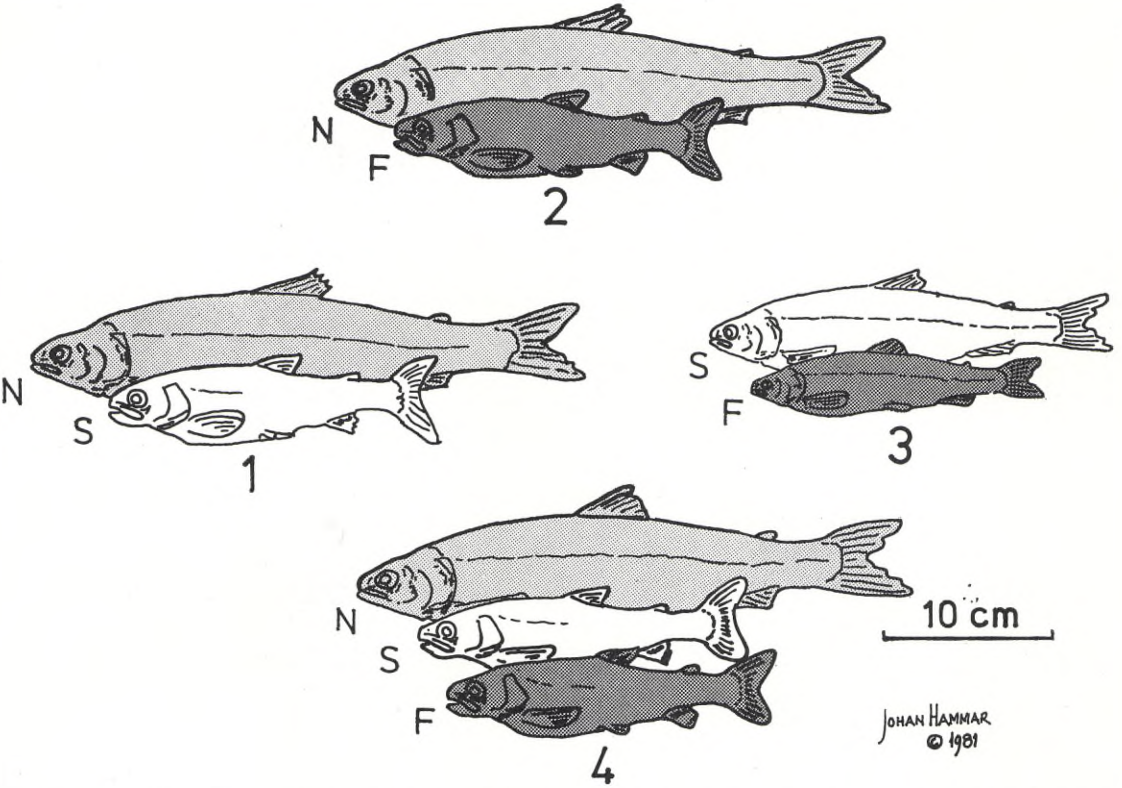

Fig. 4. Size and dominance relationships between the three species in sympatry. Relative scale same as in Fig. 2.
N — *S. salvelinus*
F = *S. alpinus*
S = *S. stagnalis*

feeding on planktonic crustaceans. Mostly pelagic, but may become deepwater living and benthic when sympatric with *S. salvelinus*. Competitively inferior to *S. salvelinus* but slightly superior to *S. alpinus* when occurring sympatrically with either of the two other char species. Pronounced western distribution in Sweden, indicating a western (Arctic Ocean) origin. Most frequent in the central areas of the alpine mountain chain forming the border between Sweden and Norway. Rarely found in headwater lakes thus indicating it arrived later than *S. alpinus* to its present distribution in central Scandinavia. Spawns in fairly deep water when sympatric. Frequency range of the most anodal serum esterase allele in electrophoresis is usually from 0.00—0.20. Fixation at 0.0 may occur even when effective population size is large, indicating that all admixture with the alternative allele (F) may indicate mutation or slight introgression with the other two species.

Numerical data extremely variable and not different from the other two species except for the smaller maximum size attained.

Geographical range: Occurs rather sporadically along the entire mountain region of western Sweden, with its southern-most distribution in the province of Värmland (Fig. 3). Dominating species only in the northern parts of the province of Jämtland (the Indalsälven water system) and in adjacent parts of Norway (River Namselva). Found in central and western Norway. Occurs in Iceland, both as landlocked and anadromous. May be synonymous with anadromous populations of west Greenland and the Canadian Arctic, but true homology has still to be proven.

Habitat: see above—Diagnosis and description.

Material examined: Some 50 populations have been examined, representing a total of approx. 3,000 specimens.

Sympatric populations exhibiting various stages of introgression.

As stated above introgression is a common feature when populations of the various char species live in the same lake. The dominance scheme indicated above in the species descriptions reflects the relative size of individual fish in sympatry (Fig. 4), what must also be borne in mind is the importance of the relative strength of the contributing species numberwise. Thus if one of the sympatric species for some reason is superior in number but in general inferior in competitive power the final outcome of the interactive process may well be that the ecologically dominant species will be swamped by "inferior" genes if there is little or no difference in spawning ecology. In such a case the dominant species will only manifest itself as fish with slightly better growth rate and slightly different gene frequency than the bulk of fish in a sample which superficially may seem quite homogeneous. Stunting, relatively speaking, may thus become the final destiny of normally large *S. salvelinus* fish as a result of longtime introgression with a more numerous and smaller char of a different species. In many instances, however, introgression is slight and the species are well separated ecologically even when sympatric. There are also many instances where human influence through hydroelectric development and/or selective fishing may have initiated introgression. This process is not necessarily irreversible.

For this reason we have chosen to present briefly a few cases with various combinations of the three species and also stated the present situation in terms of introgression and relative strength of the species present.

S. salvelinus×*S. stagnalis* (Fig. 4,1)

1) Lake Blåsjön: *S. stagnalis* dominating (f EstF= =0.07). *S. salvelinus* small and few (but still larger than most *S. stagnalis*), f EstF=0.17, versus roughly 0.50 in allopatric populations. The majority of fish have intermediate frequencies indicating their hybrid origin. (NYMAN 1972, FÜRST *et al.* 1978.)
2) Lake Yraf: Both species occur in approximately equal number, but introgression has had most impact on *S. stagnalis* which has an f EstF= =0.28 versus some 0.07 in allopatry. The *S. salvelinus* has a frequency close to that observed in allopatry (0.50). Ecologically, *S. stagnalis* occupies the littoral zone with *S. salvelinus* dominating the pelagic zone (NYMAN and FILIPSSON 1972).
3) Lake Båtsvatn: Both species occur in approximately equal number, probably with a slight excess of *S. stagnalis*. The gene flow between the species has had marginal impact, *S. stagnalis* having a frequency of 0.15 versus 0.10 in allopatry, and *S. salvelinus* having 0.51 versus 0.50. (KLEMETSEN and GROTNES 1980.)

S. salvelinus×*S. alpinus* (Fig. 4,2)

1) Lake Stora Rösjön: In the southern part of the geographical distribution of *S. salvelinus* where its allele frequency is high (0.70—0.90) there are many cases where the gene frequency is of limited value for separating sympatric populations of *S. salvelinus* and *S. alpinus*. This 100 hectare lake contains both species with a more numerous *S. alpinus* population, but probably with a larger S. salvelinus population in terms of weight. Gene frequencies are almost identical, around 0.90, but the growth rate, size and food of the two species are extremely different. The gene flow between the two is likely very small. (ANDERSSON *et al.* 1971, NYMAN 1972.)
2) Lake Övre Björkvattnet: A pelagic *S. salvelinus* with an F frequency of 0.70 and a littoral *S. alpinus* of 1.0 previously in a fairly stable equilibrium, are now being reduced by interactive segregation from a recently intruding whitefish species. (NILSSON and FILIPSSON 1971, NYMAN 1972.)
3) Lake Bjellojaure: This lake contains a marginal population of rather unaltered *S. salvelinus* in an area dominated by *S. alpinus* (F frequencies are roughly 0.65 and 0.92 respectively). *S. salvelinus* occur in the easternmost part of the lake and in the outlet region of the west end. Traces of *S. salvelinus* are found in the first lake downstream of Lake Bjellojaure, but the

two following lakes appear to be of pure *S. alpinus* stock. *S. salvelinus* has slightly better growth rate. (HENRICSON 1977.)

S. alpinus×*S. stagnalis* (Fig. 4,3)

1) Lake Fättjaure: This species combination has only been found in three more or less interconnected lakes. Hybridization has proceeded at a different rate in the three lakes, but in the least changed lake (Lake Fättjaure proper) there is still considerable difference in growth rate and feeding ecology between the two species, even though the *S. stagnalis* F frequency has become altered from roughly 0.15 to 0.46 and the respective figures for the *S. alpinus* population are 0.95 and 0.61. From these figures it can also be seen that both species have been changed in the direction of intermediacy with approximately equal force, which is good evidence that they occur in roughly equal number. The last statement is also supported by growth curve analysis. (HENRICSON and NYMAN 1976.)

S. salvelinus×*S. stagnalis*×*S. alpinus* (Fig. 4,4)

1) Lake Sitasjaure: This combination is extremely rare and has been recorded in only two bodies of water. *S. salvelinus* dominates in commercial catches because both other species are stunted in growth as a result of interactive segregation. The pelagic zone harbours the *S. salvelinus* populations whereas both dwarfed species occur littorally or in the benthic region. F frequencies indicate that *S. salvelinus* and *S. stagnalis* are most numerous because they are the least altered: observed and expected frequencies (in allopatry) are *S. salvelinus*, 0.25 and 0.41, *S. stagnalis,* 0.22 and 0.15 and *S. alpinus* 0.58 and 0.90. (NYMAN unpubl. data.)

It should be noted that the ecological characteristics presented above refer to lacustrine populations of Scandinavia. Sampling anadromous populations in a number of Arctic regions has shown that probably all three species occur in an anadromous condition also. A detailed analysis of all populations sampled will be published in the near future, in the "Information Series" of the Institute of Freshwater Research, Drottningholm, Sweden.

IV. DISCUSSION

The fact that two or three discrete populations of Arctic char may occur sympatrically was early realized (*e.g.* NYSTRÖM 1863, TRYBOM 1977) and attempts were made to describe many of the various morphological forms as species or varieties (*e.g.* SMITT 1886, LILLJEBORG 1891). The morphological plasticity of this species group has also given rise to numerous opinions on the origins and affinities of the various forms, which of course has affected nomenclature to the degree that, to cite BEHNKE (1972): "The taxonomy of the charr of the glaciated lakes of Europe provides an excellent case history to illustrate the lack of evolutionary reality in current usage of nomenclature." The methods presented in this paper to distinguish between sympatric populations of the postulated three ancestral sibling species, hopefully will facilitate not only the nomenclature problems of the entire circumpolar distribution of the species group and the postglacial zoogeographical development, but also facilitate the management of stunted populations, once information on the different environmental requirements of the three species is taken into account (FILIPSSON and SVÄRDSON 1976).

The ecological criteria and the frequency distribution of the Est-F allele may thus be combined to display the dynamic, although distinct features of a group of three morphological sibling species of Arctic char in Scandinavia. Also, there is reason to believe that some or all of these species are conspecific with the Arctic char populations of other regions of the northern Hemisphere. No qualitative differences have been found and this is still true of the Dolly Varden char (*Salvelinus malma* (WALBAUM)) as well, when it has been compared with other taxa of Arctic char biochemically TSUYUKI *et al.* 1966, NYMAN 1972, CLAYTON and IHSSEN 1980).

Finally, this enzyme polymorphism with its different frequency ranges in the three sibling species and very little intraspecific variation among neighbouring populations adds a new dimension to the view of treating all Mendelian polymorphisms as "simple" population markers.

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The Impact of Eutrophication and Climate on a Warmwater Fish Community

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ABSTRACT

A set of gill-nets was fished annually, 1955—78, during the first half of September in Mellanfjärden, a part of Lake Hjälmaren. Mesh-sizes, number of nets and annual efforts were constant.

Cyprinids and sander (*Stizostedion lucioperca*) increased during the period, while perch (*Perca fluviatilis*), pike (*Esox lucius*) and burbot (*Lota lota*) decreased in numbers. There were changes in growth rates of sander and three cyprinid species. All age groups of sander improved their growth. The cyprinids, bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*) were favoured in younger age groups but their denser populations depressed growth rate in older age groups.

The changes in the fish fauna were correlated to cultural enrichment by means of phosphate-rich detergents, increased communal waste and agricultural fertilization run-off. The strength of year-classes in sander, white bream, bream and roach was correlated to the spring weather. The positive factors were a short, intensive period of warming up, rainfall in May (bream and white bream) or April (sander and roach). A hot spell in June was also important and hot weather during the rest of the summer could improve the year-class still further.

The similarity between human eutrophication and a more favourable climate is pointed out, with regard to fish populations. Cyprinids were more wide-spread and abundant in northern areas during the warm Atlantic period some thousand years ago. In spite of a cool climate they have recently reappeared in oligotrophic lakes, as a result of eutrophication.

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I. INTRODUCTION

Lake Hjälmaren is the fourth largest lake in Sweden. It is a naturally eutrophic lake, which has been further enriched in this century by cultural eutrophication. Some general data on the lake are given by Svärdson and Molin (1973) and Rundberg (1977).

The fish fauna of Lake Hjälmaren has been described by Uggla (1786), Alm (1917) and Rundberg (1971). The sander population has been studied by Svärdson and Molin (1973) and Rundberg (1977) discussed harvest yields of sander, perch and pike.

During the period 1955—78 experimental netting for sander was performed at a fixed station. Other fish species were also caught. These years covered the period when the lake was heavily enriched by phosphate-rich detergents, increased general communal waste and agricultural fertilization run-off. As far as phosphorus is concerned, the eutrophication culminated in the middle of the 1970s, while nitrogen, now mainly from agriculture, continues to be added to the lake (Pierrou 1979).

II. MATERIAL AND METHODS

The fishing station was situated in Mellanfjärden, a western bay of Lake Hjälmaren. It belongs to

Table 1. *Age distribution for the total catch of four species.*

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
Sander	2	106	622	624	353	226	72	26	7	2	1	1	1	1	—	—	—	—	2,044
%	0.1	5.1	30.4	30.4	17.3	11.1	3.5	1.3	0.3	0.1	0.1	0.1	0.1	0.1	—	—	—	—	100.0
Bream	—	—	—	84	161	141	117	98	79	50	53	45	45	38	19	16	10	5	961
%	—	—	—	8.7	16.7	14.7	12.2	10.2	8.2	5.2	5.5	4.7	4.7	4.0	2.0	1.7	1.0	0.5	100.0
White bream	—	—	—	2	3	38	81	130	156	168	171	112	61	39	21	8	1	2	993
%	—	—	—	0.2	0.3	3.8	8.2	13.0	15.7	17.0	17.3	11.3	6.1	3.9	2.1	0.8	0.1	0.2	100.0
Roach	—	—	—	—	—	6	55	88	115	82	26	12	3	2	—	—	—	—	389
%	—	—	—	—	—	1.5	14.1	22.6	29.6	21.1	6.7	3.1	0.8	0.5	—	—	—	—	100.0

one of the most eutrophic areas of the lake. Only the westernmost bay, Hemfjärden, close to the city of Örebro, is even more enriched (Willén 1976).

The gill-nets used were of six different mesh-sizes, mostly rather coarse in order to catch the sander. The same six nets were used annually for ten nights during the first half of September. The same fisherman (G. Molin) operated them on all 24 occasions. The annual catches are thought to be fully comparable.

The fishing area was about 400—500 metres in diameter. Water depth was 1.5 metre and visibility 30—40 cm, on windy days even less. Since the station was in free water, species dwelling in the vegetation belt were not normally caught. The relative frequency of the different species is not representative for the fish fauna (eel and ruffe are known to occur but were not recorded, small fish were not caught) but only for annual fluctuations and general trends.

Only four species were aged, for various reasons, and this was done using the scale method. Back-calculation on scales was done only for the sander. All sander caught were aged. Annual samples for age analysis were taken for only three cyprinids. Time was normally short and therefore no cumbersome length measurements could be used to prove that the selected sample was representative for the total catch. It was later found that large and small specimens were probably favourably biased. Dominant year-classes of fish of similar size were thus more prominent in the population than in our aged samples.

All fish were judged to have terminated the season's growth. Age is given in whole years, *i.e.* I+ and II+ are referred to as age 2 and 3.

Scale reading is more of an art than true objective science, as anyone engaged in this activity will probably endorse. Moreover, some older fish may not grow and therefore fail to show an annulus on the scales. They are recorded as younger than their true age. Scale-reading may even add to the bias already produced by sampling methods with regard to the strength of very rich year-classes.

In order to illustrate the strength of year-classes, different methods were used. When all aged samples from 24 years were added (Table 1) a sort of standardized catch for the age groups appeared. Every single year-class could then be compared to

Table 2. *Annual catch, during ten nights, for all species, Mellanfjärden, Lake Hjälmaren 1955—78.*

Year	White bream	Bream	Sander	Roach	Perch	Pike	Rudd	Zope	Crucian carp	Tench	Asp	Burbot	Smelt
1955	125	123	36	8	18	32	6	—	2	1	3	4	—
1956	273	165	136	17	30	8	1	—	—	—	—	—	—
1957	152	63	75	5	45	4	—	—	—	—	—	2	—
1958	114	132	63	18	163	5	—	—	—	—	—	—	—
1959	79	132	74	6	154	12	4	2	—	—	—	1	—
1960	62	67	44	2	16	9	—	—	—	—	—	—	—
1961	200	106	38	18	30	1	1	—	2	—	—	—	—
1962	85	70	44	9	15	6	—	—	—	—	1	—	—
1963	216	219	101	17	12	2	—	—	—	—	1	—	—
1964	233	319	111	26	34	1	3	—	—	—	—	—	—
1965	515	192	69	126	28	6	2	—	—	—	—	—	—
1966	572	175	121	308	128	6	—	—	—	—	—	—	—
1967	835	189	51	402	117	6	17	—	1	1	1	—	—
1968	893	318	132	181	182	9	—	5	—	—	—	1	—
1969	1,059	113	123	43	37	4	—	2	—	—	1	—	—
1970	447	173	95	56	11	5	—	2	—	3	—	—	—
1971	409	372	92	26	13	8	—	3	—	—	1	—	—
1972	631	988	88	46	8	—	—	2	—	2	—	—	—
1973	1,039	659	82	91	9	1	—	4	4	—	—	—	—
1974	711	380	93	183	163	1	1	8	2	3	—	—	—
1975	873	223	160	69	125	3	—	—	6	—	—	—	—
1976	388	345	113	11	13	12	—	—	1	—	—	—	—
1977	661	538	46	16	26	7	1	3	3	2	—	—	—
1978	435	251	75	10	9	2	—	1	—	1	—	—	3
Total	11,007	6,312	2,062	1,694	1,386	150	36	32	21	13	8	8	3

this standard (Svärdson 1961). An index was thereby obtained, allowing each year-class a percentage of the standard. This percentage could be based on all available age groups or on only some of them.

All sander specimens caught were referred to year-classes. For the cyprinids the aged sample, though often small, was taken as representative of the total annual catch, which was then split up into year-classes.

III. TRENDS OF POPULATION CHANGE

The total catch is given in Table 2. The fish community is dominated by cyprinids. The predatory percid fish, sander and perch, as well as pike, are the economically important species. Smelt is a numerous and important forage fish. It was taken only occasionally, when entangled in the net by its teeth.

There are strong annual fluctuations in the catch, suggesting the passage of rich or poor year-classes. There are also more general trends. Rundberg (1971) summarized the unanimous opinion among the commercial fishermen of Lake Hjälmaren (some 50 people) that cyprinids had increased very much in numbers during recent decades. Even over such a short period as 24 years, this tendency is clear. Fig. 1 gives the linear trends of white bream (*Blicca bjoerkna*), bream (*Abramis brama*) and roach (*Rutilus rutilus*), all of which have increased, two of them markedly. The scarcer species such as tench (*Tinca tinca*), crucian carp (*Carassius carassius*) and zope (*Abramis ballerus*) appear to have been caught more often during the later part of the fishing period. Two cyprinids show a trend towards decreasing numbers, *i.e.* the rudd (*Scardinius erythrophthalmus*) and the asp (*Aspius aspius*). The rudd is known to live in the vegetation belt, where it may be dominated by crucian carp and tench.

The predators also display trends (Fig. 2). The sander is known to be favoured by eutrophication, where increased turbidity suits its hunting behaviour. It is also known (*cf.* Svärdson and Molin 1973) that the sander dominates pike and perch, both of which have become fewer in Mel-

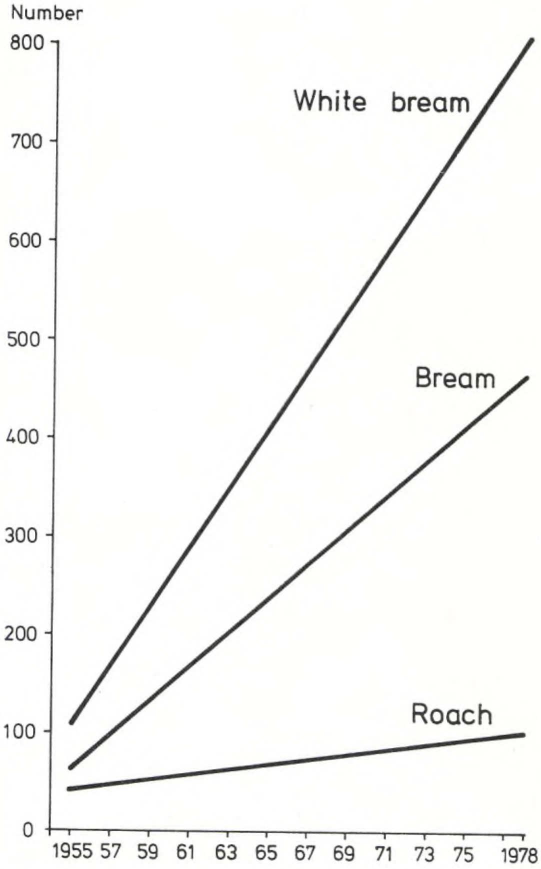

Fig. 1. Trends of change in annual catch.

lanfjärden. The burbot (*Lota lota*) was reported by RUNDBERG (1971) as dwindling in numbers and even in our material this trend was noted (Table 2). It is not known if this trend is caused by turbidity, some other physical parameter or, what seems rather more probable, by predation by the sander.

IV. EFFECTS ON GROWTH RATE

The growth data are given in Table 3. Younger fish were caught more often in the later half of the study period, suggesting an improved growth rate.

During the first twelve years, sander, 1—3 years of age, composed 20 % of all sander caught. In the second half of the period, however, sander of the same age groups made up 48 % of the total sander

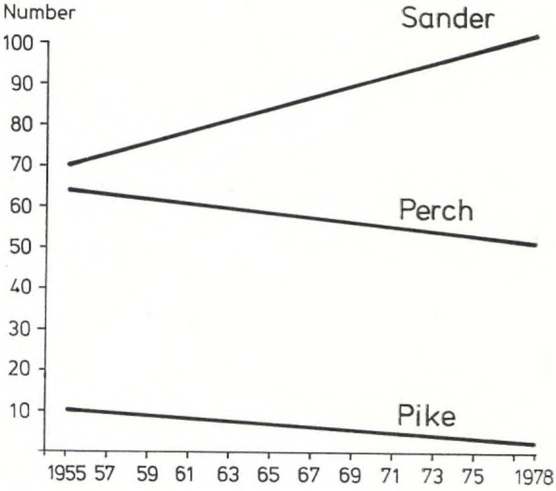

Fig. 2. Trends of change in annual catch.

catch. The length-to-age data confirms that growth rate had improved.

At an age of 3, the sander of the first half-period had a total length of 312 mm compared to 321 mm for those caught later. In the next age groups the length difference was 22 mm, followed by 26 mm and, for the six-year olds, the difference had widened to 41 mm. Sander of 7 years were actually 70 mm longer during the latter half of the peirod. Thus, during the study period, the sander had become more vulnerable to overfishing.

The white bream is certainly not overfished, since it is of no commercial value but is thrown back into the lake, moribund or dead after having clotted the gill-nets. The nets used by us were highly selective and only caught white bream of over roughly 185 mm total length (Table 3). During the first half of our study, age groups 4—8 constituted 18 % of the total catch, while later on this percentage increased to 31 %. Age group 9 seems to confirm the better growth rate of the younger white bream caught during the later half period: 191 mm compared to 188 mm.

Later on, however, growth rates were reversed. From 12 years onwards the earlier white bream specimens were larger than those caught later. Our interpretation is, that all young white bream, up to the age of 9, had improved their growth rate. Older fish had on the other hand slowed down their growth.

Table 3. *Change in length-for-age data between period I (1955—66) and II (1967—78). Note that most age groups of sander have improved their growth while older cyprinids grew more slowly in the second period.*

Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
Sander																			
I length, mm	—	205	312	360	398	404	421	441	652	—	—	—	—	—	—	—	—	—	—
II length, mm	139	251	321	382	424	445	491	516	642	—	—	—	—	—	—	—	—	—	—
I number	—	6	177	306	210	148	41	8	2	—	—	—	—	—	—	—	—	—	898
II number	2	100	441	328	131	78	31	17	5	—	—	—	—	—	—	—	—	—	1,133
Bream																			
I length, mm	—	—	—	189	203	212	236	261	283	294	322	346	356	365	371	367	384	—	—
II length, mm	—	—	—	192	213	232	253	267	279	289	314	332	347	358	377	382	386	398	—
I number	—	—	—	20	60	62	58	70	50	29	30	45	19	13	5	3	4	—	448
II number	—	—	—	64	101	79	59	28	29	21	23	20	26	24	14	13	6	5	512
White bream																			
I length, mm	—	—	—	—	—	197	186	185	188	195	200	217	236	240	253	245	—	—	—
II length, mm	—	—	—	180	197	186	185	185	191	194	200	207	214	218	229	234	—	—	—
I number	—	—	—	—	—	6	19	46	66	62	78	55	34	20	10	6	—	—	402
II number	—	—	—	2	3	32	62	84	90	106	93	57	26	20	11	2	—	—	588
Roach																			
I length, mm	—	—	—	—	—	—	211	222	220	220	237	210	302	—	—	—	—	—	—
II length, mm	—	—	—	—	—	205	209	210	216	221	233	233	252	—	—	—	—	—	—
I number	—	—	—	—	—	—	14	21	23	19	10	2	1	—	—	—	—	—	90
II number	—	—	—	—	—	6	41	67	92	62	26	9	2	—	—	—	—	—	305

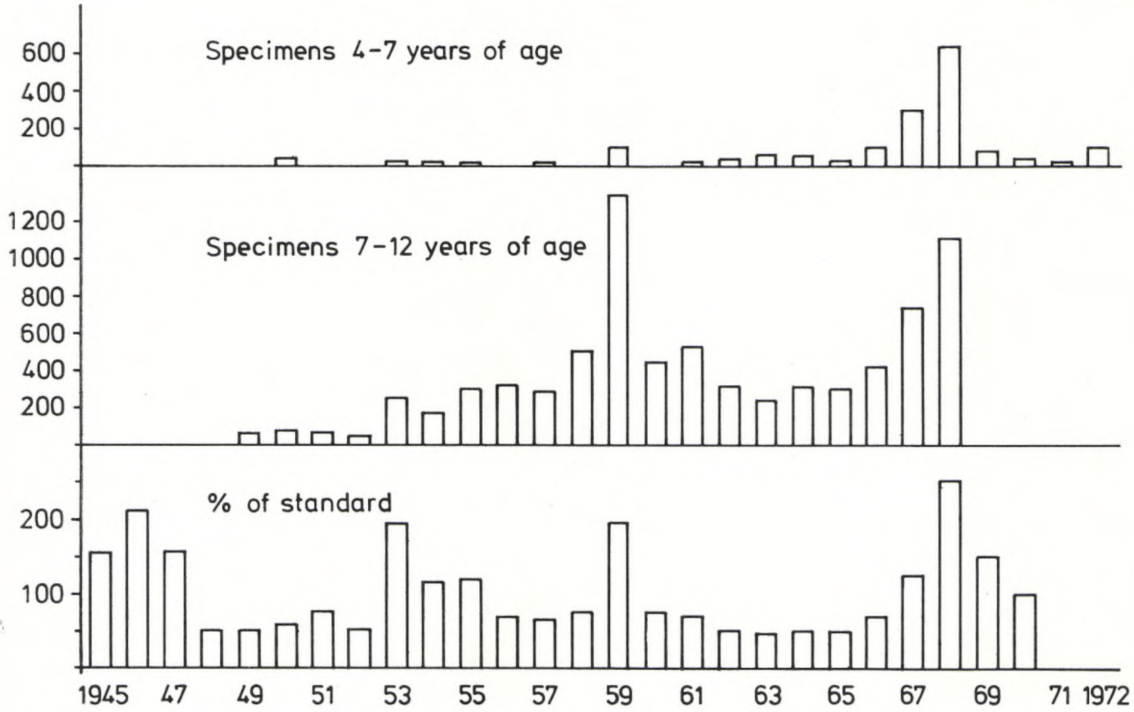

Fig. 3. White bream (*Blicca bjoerkna*). Strength of year-classes 1945—72.

For bream the growth changes were very similar. Age groups 4—6 made up 32 % (out of 448 fish) during the first half period and 48 % (out of 512) in the second. The length data confirm the better growth suggested by these figures. Bream, 4—6 years of age, were 3, 10 and 20 mm longer during the last twelve years. However, the trend was again reversed for older fish. Age groups 9—14 all had shorter total lengths than corresponding age groups of bream during the first half period.

Even for roach the growth rate changes were similar, although not quite as evident. All the 7—11 age groups for which sufficient data are available, indicate a deteriorating rate of growth. Age groups 6—8 were relatively unchanged in numbers, being 39 and 37 % respectively for each half of the study period. Since roach increased in numbers during the 24 years (Fig. 1) there was probably an improved growth rate for the youngest age groups, which was not recorded in our wide-meshed nets.

Increased intra- as well as interspecific competition for benthic food might explain the slower growth rate of older cyprinid fish. Younger age groups, however, especially the very youngest, feed on algae, which is not normally in such short supply. It seems as if competition pressure is stronger among the older specimens in the cyprinid fish community. In some way this competition may influence the roach in a more detrimental way than white bream and bream, which tend to become more dominant with increasing amounts of eutrophication.

V. YEAR-CLASSES AND SPRING WEATHER

Figs. 3—6 give the strength of the year-classes, as recorded by the different methods.

Svärdson and Molin (1973) discussed sander year-classes of Lake Hjälmaren up to 1967 and found those of 1953 and 1959 to be dominant. The material was the same as that recorded in this paper. It can now be verified that the classes 1966—69 were quite good, that of 1969 probably being the very best. The summer of 1969 was the

Table 4. *Deviation from average temperature readings, Örebro 1953—75. Centigrades.*

Year	May	June	July	August	Total deviation
1953	+0.4	+2.6	—0.4	—1.2	+1.4
1954	+1.4	—0.3	—1.6	—0.8	—1.3
1955	—2.7	—1.1	+2.3	+2.8	+1.3
1956	+1.1	—0.4	—0.8	—2.7	—2.8
1957	—1.3	—0.9	+0.3	—0.9	—2.8
1958	—0.8	—0.7	—0.9	—1.2	—3.6
1959	+0.6	+0.7	+1.4	+2.5	+5.2
1960	+1.4	+1.6	—1.4	—0.9	+0.7
1961	—0.3	+1.5	—1.2	—1.3	—0.3
1962	—1.9	—0.9	—2.7	—2.6	—8.1
1963	+1.7	+0.5	—0.5	—0.3	+1.4
1964	+2.0	—0.3	—1.4	—1.0	—0.7
1965	—1.0	+0.5	—2.8	—1.2	—4.5
1966	+0.5	+3.1	+0.2	—0.5	+3.3
1967	—0.6	+0.1	—0.1	+0.5	—0.1
1968	—1.8	+2.9	—0.8	+1.1	+1.4
1969	—0.4	+3.2	+1.1	+2.4	+6.3
1970	+0.2	+3.8	—1.6	+0.5	+2.9
1971	+1.5	+0.3	+0.2	—02	+1.8
1972	—0.1	+1.4	+2.0	—0.1	+3.2
1973	+0.5	+2.5	+2.1	±0.0	+5.1
1974	+0.2	+0.4	—2.1	±0.0	—1.5
1975	+0.9	+0.1	+1.3	+3.9	+6.2

warmest on record (Table 4) confirming the correlation between year-class strength and summer climate. The exceptionally hot spell in August of 1975 also influenced the sander survival, accelerating the growth and producing good year-classes for 1974 and 1975 (Fig. 6).

In our earlier paper (Svärdson and Molin 1973) we reported that the very rich 1959 year-class was found to depress the growth rate from 1961—64 and the forage fish, smelt, were very scarce. It now appears that the poor year-classes of 1964 and 1965 were also probably caused by heavy cannibalism by older sander on younger ones. When this predatory pressure terminated, a series of good classes appeared 1966—69.

The white bream had as rich year-classes as the sander, not only in 1953 and 1959 but also in 1968 (Fig. 3). The percentage index suggests at least one rich year-class in the 1940s. Since back calculation on old specimen scales was the only method available for judging the 1940s, the result is rather uncertain. The best class may have been

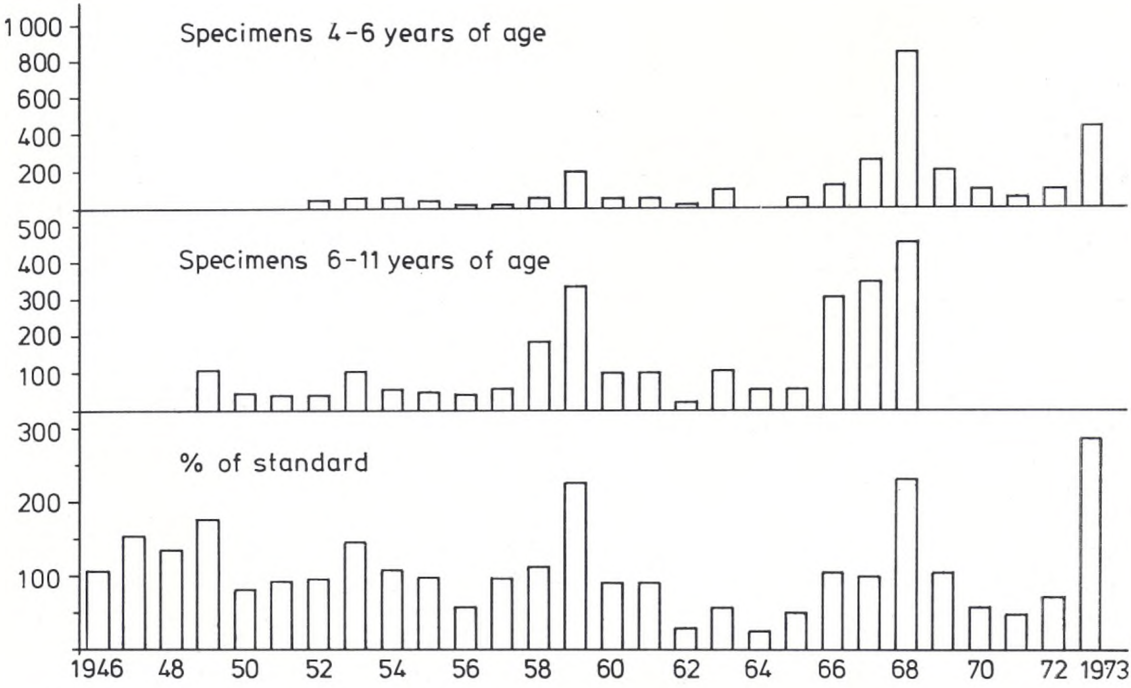

Fig. 4. Bream (*Abramis brama*). Strength of year-classes 1946—73.

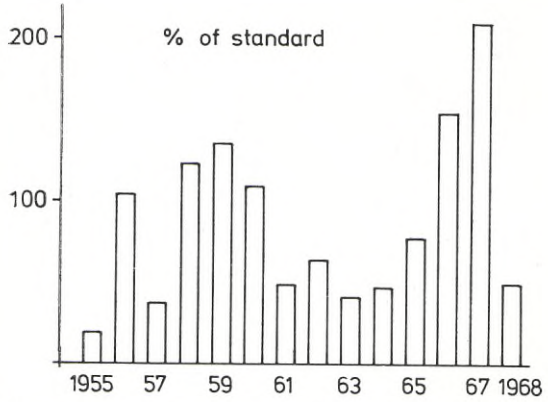

Fig. 5. Roach (*Rutilus rutilus*). Strength of year-classes 1955—68.

Table 5. *Rainfall (mm) as deviation from average values, Örebro 1953—75.*

Year	March	April	May	June	Total deviation
1953	—28	+15	— 3	+19	— 3
1954	+27	—17	—11	± 0	— 1
1955	— 7	+14	+13	—32	—12
1956	—21	—21	—26	+ 5	—63
1957	+ 7	—21	± 0	— 1	—15
1958	—10	+13	+46	+11	+60
1959	+40	+ 1	+ 4	—32	+13
1960	—19	+ 1	— 8	+ 3	—23
1961	— 4	— 6	+38	— 8	+20
1962	+11	+28	+21	+ 5	+65
1963	—22	— 5	+13	+27	+13
1964	+10	—17	— 6	— 4	—17
1965	—25	+ 1	—32	+ 3	—53
1966	+17	—15	— 4	—24	—26
1967	+ 4	+ 7	+27	—22	+16
1968	— 1	—17	+23	—27	—22
1969	—16	+13	+ 4	—49	—48
1970	— 2	+13	—15	—26	—30
1971	+14	—21	—21	—12	—40
1972	+ 5	+26	+32	—14	+49
1973	—24	—10	+16	—41	—59
1974	± 0	—35	—27	+ 3	—59
1975	— 2	± 0	+ 8	—29	—23

produced in 1947, a year known to have produced strong year-classes of other fish (Svärdson 1951).

The percentage index only takes into account the relative strength of classes close to each other in time and it is independent of the catch of non-aged specimens. When the total catch is also considered, the estimate based on 7—12-year-old fish is probably the best, while that based on 4—7-year olds is biased by the improved growth rate of young fish.

The bream (Fig. 4) presents a rather similar picture. Again, 1953, 1959 and 1968 produced rich year-classes. Due to the low age of bream caught, the 1973-class could also be studied and was found to be rich. The improved growth rate of young fish gives a biased impression of the strength of the 1968 class compared to that of 1959. The true relation between the two classes is probably best indicated by the analysis based on 6—11-year olds.

The material on roach is scanty and uncertain (Fig. 5). It suggests, however, that 1959 was also a good year for this species. The classes of 1966 and 1967 seem to have been rich as well. In this respect the roach resembles the sander. Both spawn earlier (May) than the white bream and bream (June).

The city of Örebro is the closest meteorological station to Lake Hjälmaren. Data on air temperature and rainfall are given in Tables 4 and 5.

Above average rainfall in April and May coupled with high June temperatures are suggested as common factors for the interesting years 1953, 1959, 1968 and 1973. A closer inspection of the day-to-day variations reveal that spring in these years was short with low temperatures and heavy rainfall in early May when agricultural fertilization takes place. Later in June anticyclones gave rise to hot spells with peak readings of 30.2° C (1953), 31.0° (1959), 30.2° (1968) and 31.0° (1973). These June temperatures are high, according to average air readings at Örebro and even for the country as a whole.

A limnological survey was in progress in Lake Hjälmaren during 1966—73 (Willén 1976). She found the highest values for total nitrogen in 1968 and 1973 for the Mellanfjärden area. Again for phosphorus, the peaks occurred in 1968 and 1973. In both cases the organic fraction was quite dominating. These are two of the years when white bream and bream had attained exceptional year-classes.

The spring and early summer of 1966 is of special interest. The white bream and bream showed no reaction in contrast to the sander and roach. Elsewhere, 1966 gave rise to a rich year-class of whitefish in Lake Vättern (Svärdson 1976 a), of sander in Lake Mälaren (Svärdson and Molin 1973) and of sander in Lake Roxen (C.

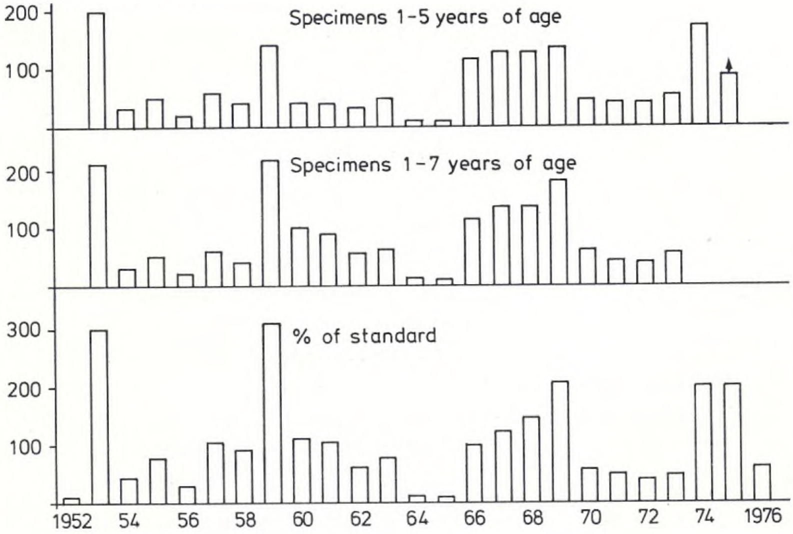

Fig. 6. Sander (*Stizostedion lucioperca*). Strength of year-classes 1952—76.

Lindhé, pers. comm.). Pike had the best year-class thus far recorded in Lake Mälaren for a period of more than 30 years (Svärdson and Molin, unpubl.).

April 1966 was very cold, more than 3° C below average in the southern and eastern parts of Sweden. Heavy snow-falls in the middle of the month produced a snow cover of some 20—30 cm, persisting for several days — most unusual weather conditions. In late April, when the ice finally broke up, the water levels of lakes in the eastern fringe of southern Sweden were very high. May temperatures were just average but June was warm with a hot spell culminating at 29° C. The spring of 1966 therefore could be described as very short and intensive with a rapid warming up. A similar situation in Lake Erie produced rich year-classes of walleye (Busch *et al.* 1975).

The water retention period is only 35 days in Mellanfjärden. The enrichment from rainfall or snow melting in April might thus produce an abundance of algae or zooplankton at the optimal time for fish spawning in May, while rainfall in May is more important for June spawners. In both cases a warm June seems to be important for securing a rapid growth rate and a decreasing instant mortality in the fry. Above average temperatures during later summer months may even further improve the year-class which has had a good start in favourable spring weather.

VI. DISCUSSION

Nikolskii (1961) pointed out that bream, zope and rudd were more wide-spread in the north during the warm Atlantic period, some thousand years ago. The evidence comes from archeological studies of old human settlements. Archeologists have also found in Scandinavia similar indications. The abundance of cyprinids in northern areas was later reduced and some species withdrew from the White Sea region. Filipsson (1980) pointed out the significance of isolated populations of roach and other southern fauna elements in the mountain region of Scandinavia. The remnants of relict populations live in shallow or otherwise warm lakes, *e.g.* roach in small lakes within the Idijoki system of the River Torne Älv drainage (Svärdson 1976 b).

Both the cyprinids of northern Europe and those of the alpine lakes are regarded as indicators of eutrophication, since they generally increase synchronously with an enrichment of their home lakes. An increase of nutrients could therefore be said to compensate for the detrimental impact of low temperature.

The Mellanfjärden study illustrates how eutrophication may create progressively richer year-classes of cyprinids and that temperature effects may also be involved. When both factors cooperate a very strong year-class may appear.

Regional surveys suggest that white bream and bream are more dependent on eutrophic conditions than roach. This ecological profile of the species shows that the roach is more dominant than the other two in moderately rich waters while the dominance relation is reversed when eutrophication improves. The roach then constitutes a lesser biomass within the cyprinid total. The general consequences of enrichment on a certain species should therefore be judged with regard to other sympatric species (*cf.* SVÄRDSON 1976 b).

Within a species the competition between age groups may also switch. In Mellanfjärden the life conditions for younger cyprinids were generally improved while those of older specimens deteriorated. Growth curves were thus flattened out and the results support the opinion that the growth rate should generally be regarded as extremely flexible.

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