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Contents

On the Morphological Differentiation of Juvenile Whitefish (0+, 1+), *Coregonus sp.*, and Juvenile Char (1+), *Salvelinus sp.*, with Particular Regard to Population Ecology of Closely Related Species

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Abstract

The early development of young of closely related species should give information as to how their cohabitation is possible. In this paper the development of some morphological characters are studied in order to explore some possible means of ecological differentiation. The development of the dorsal fin, number and size of gillrakers and size of gill arch, gonads and size and shape of otoliths in young (0+ and 1+) whitefish and young (1+) char is studied and compared, between species, within each genus.

Species differences in growth and reproductive strategy the second and following years are two very likely factors that could facilitate cohabitation between species within these two genera. These events occur in whitefish after an initial year with pronounced similarities between species in growth and in certain morphological and other characters correlated with total length, in gill structure and diet, in dorsal fin structure.

The material from juvenile char is much less conclusive. A greater latitude for differentiation between char species in such characters that are correlated with total length can be envisaged.

Introduction

There are a number of papers on the morphology of larval coregonids which also deal with the juvenile stage (Schnakenbeck 1936, Faber 1970, Mähr et al, 1983). The organization of the juvenile body can be understood as a development from the larval body as described in the anatomical study of Nagieć (1977). Our knowledge of the morphological development of the young of the char is summarized by Balon (1980 a, b) and Pavlov et al. (1987). The description of the larval morphology of the closely related grayling is also of great value when studying juvenile coregonids (Penaz 1975, Scott 1985). The anatomy of the adult whitefish and grayling is described by Norden (1961).

There is a particular purpose behind this present morphological investigation. The char studied here are from two high mountain lakes, above the range of whitefish (the Fulufjäll lakes), while the whitefish are from a region close to the Swedish chain of high mountains, a region where whitefish is the most important fish and char populations are small or non-existent. Both genera consist of groups of species which can live sympatrically and are prone to introgression within the genus (Svärdson 1979, Nyman et al. 1981, Hammar 1988). The purpose of the present paper is to discuss how the different species within the respective genera solve the problems of cohabitation.

The genera can be described in a very cursory manner by stating that the whitefish and char take care of much of the resources in their respective districts, whether represented by one or more species in the different lakes, as their ecological plasticity allows their feeding niches to be broad (one species) or narrow (more than one, Nilsson 1967, 1978). The ecological potential in each genus also includes spawning in flowing water, near lake shores and in deep water.

The consequences of the parents' choice of spawning site for the hatching of the larvae and the survival of the juveniles of the char and

whitefish are no doubt quite different. The whitefish and char belong to separate groups within the salmonoids, groups which differ in their fundamental morphological, physiological and behavioural characteristics during their embryonal, larval and juvenile stages. For a group of closely related species within a genus, the larval and juvenile period is a time when a species cohort has to explore the possibilities for living without competition from larvae and juveniles of other species within their genus or facing the necessity to compete with these. The differentiation of morphological characters can give some information on this period.

One objective of this work is thus to study the differentiation of certain characters during the juvenile period:

1) The number of rays in the dorsal fin, a meristic character assumed to be important for swimming and known to be affected by temperature during early development, (Tånig 1952, Lindsey 1981).

2) The size of the otoliths. According to Blacker (1974) and Love (1980) these vary in shape and size in different environments. Their size is an allometric character related to the size of the daily rings. This feature is sensitive to metabolism and temperature (Mosegaard et al. 1988).

3) The number and length of gillrakers, known to be important for feeding, and characters which vary between populations in a manner which suggests short time selection (Lindsey 1981). Number can be used as species marker. Some notes are also provided on the allometric growth of the gill arch.

4) The morphological development of the gonads in juveniles in the period when the young of different populations are starting to use different strategies for taking advantage of available resources.

A second objective is to faciliate comparisons of data on older fish caught with ordinary gear for population surveys with data on catches of juvenile whitefish and char.

Material and methods

The material is classified according to the systematic presented by Svärdson (1979), Nyman et al. (1981) and Hammar (1984, 1988). The number of gillrakers is used as a species marker for the whitefish and dress, age, maturity and body shape for the char. A translation from the old to the new taxonomy in the present lakes has been published in a paper on the whitefish diet (Lindström 1988).

Most of the samples of fish material have also been included in earlier studies of whitefish and char ecology (Lindström 1988, Lindström and Andersson 1981 b, 1984), but some new juvenile char samples from fine-meshed gillnets are also included, Table 10. It was difficult to obtain young char in their first year from nature for the present purposes and some interpretations were facilitated by the examining of one-year-old juveniles from a hatchery.

In order to obtain precise descriptions of the dorsal fins, gillrakers and scales, methods such as in vitro staining and/or radiography would have been desirable (Dunn 1983), but ordinary field surveys of fish populations depend on samples comprising numerous specimens and are often carried out without optical accessories for gonad descriptions, for example. Binocular microscopes with low magnification are regularly used for classifying grillrakers, fin-rays and scales.

The method employed here for examining the juveniles involved a binocular microscope with a 4× objective and 8× ocular, and a 8× objective for scales.

Counting the total number of rays under a dissecting microscope with the aid of needles and with the fins spread out flat on the microscope table will also give the correct number of small cranial rays, even though they may be densely packed, and may be better than radiography. It also speeds up the analysis in population surveys. It is nevertheless important to consider the methods used when comparing the results with those of serial sectioning, for example.

Smitt (1895) distinguished between unsplit and Y-split rays, the majority belonging to the

latter group. All rays are formed by two lepidot-richia, one from each half of the body (cf. Pot-hoff 1975 or textbooks e.g. Goodrich 1930), completely joined at the top in unsplit rays and separated in Y-split ones, with the apical parts spread out cranio-caudally. Discrimination be-tween Y-split and unsplit rays is not always reli-able, particularly when the fins have been ex-posed to stress (in the lifetime of the fish or afterwards).

The gillrakers in a whitefish must stand out as protrusions regardless of the stage of develop-ment they have reached when doing so. They are generally much lower in the char, and alizarin staining was used in most samples studied. The rakers were counted on the anterior left arch in both genera, and the raker in the angle between the upper and lower leg was measured together with length of this gill arch. The space between neighbouring rakers was estimated.

Otoliths were studied in both the whitefish and char, scales being used to check the aging of the whitefish otoliths.

The otoliths were viewed under reflected light against a dark background and were either dry or immersed in propylene glycol. The degree of opaqueness decreases with time in this treatment and the time is usually set at one day. Even very protracted treatment does not make "difficult" otoliths sufficiently transparent, however. One, two and three-summer-old fish have otoliths that can be analyzed without grinding or cut-ting, with the following restrictions:

1) White material in the opaque shell of the sec-ond summer in whitefish and approx. the third summer in char can often conceal some details in the first year otolith.
2) The simple structure of the dwarfed F-char otolith during the first and second summer becomes more complicated in specimens caught at a higher age in periods when their growth has changed (see page 25) e.g. they may aquire the perpendicular opaque needles typical of older normal char otoliths, which makes their otoliths very difficult to read with increasing age.

"Height" and "width" do not refer to the anatomical position of the otoliths.

Significance tests: significance at the 95 %-level is estimated by doubling the standard errors of the means in the tables.

Description of certain develop-mental stages in the whitefish

This description will establish the premises for the discussion of metamorphosis.

The gross terminology for the early life his-tory of fish remained confusing for some time. The terminology to be used here is that pro-posed by Blaxter (1969), which recognizes larvae and juveniles. The description of the morpho-logical stages of many fish species on the other hand, is very exact, even though intraspecies variation in development patterns is possible. The schedule first presented in an earlier paper (Lindström 1962) is now based on populations of six species of whitefish in 15 lakes in a region covering one third of the length of Sweden, and it is not violated in that area, at least, by the fact that fish larvae can hatch at different degrees of development (cf. Braum 1974, Brooke 1975, Zilúkas et al. 1983, Penaz 1983, Casselman et al. 1981) or the possibility that different organs may not always keep pace with one another in their development (Hayes et al. 1953, Braum 1974, Govoni et al. 1986). There are some de-tails, however, that call for minor changes in the earlier schedule (op.cit. 1962, Table 6).

The first occurrence of rays in the dorsal and anal fins seems to be slightly variable, or at least it is not so easy to pin it down at the early, mesenchymatic stages. More serious for the schedule is the late developement of the pelvic fins as compared with the caudal fin in some lakes (part of the material from lakes Landösjön and Kallsjön), and the schedule has been modi-fied at this point. Pavlov et al. (1987) reports on a similar case in the char.

Much emphasis must be placed on the de-velopement of the constriction of the pylorus and the occurrence of the first pylorus appendices, as these characteristics are tied to the metamor-

phosis, page 25. From its start as a simple tube, a part of the gut, the midgut (O'Conell 1981, Govoni et al. 1986, Norden 1961), gains a ventral expansion in the cranial part. The first sideways bend in the gut is taken as a stage separation (pictures in Mähr et al. 1983 and Dabrowski 1981). Both the caudal part of the foregut and this expansion of the midgut are involved in the loop which is formed afterwards. The oesophagus and stomach develop from the foregut, which has longitudinal ridges and a very narrow lumen almost to the stage when the pylorus is constricted. The expansion of the midgut is displaced laterally, and the plica of the intestine are mainly transversal (cf. general characteristics of fish larvae, Govoni et al. 1986). The constriction of the pylorus and the first pyloric appendices are taken as a stage separation.

The first scales occur early (Hoagman 1974) and may easily be overlooked or lost in preparation, so that the distinction between E and F juveniles in the old schedule has been abandoned. The first scales occur at approx. 3 cm total length, i.e. in very early juveniles, in accordance with observations of Hogman and others.

Schedule, description of stages, formol preservation.
Stage A. Yolk-sac visible in the profile of the body.
Limit A/B. Pelvic fins protrude from the body surface.
Stage B. For some time there is an inner remnant of the yolk. The end of the chorda points straight caudally at first, but bends upwards later (the caudal fin becomes obviously asymmetrical dorsoventrally). Mesenchymatic rays become visible in the caudal, dorsal and anal fins and ossify later (cf. Nagiec' 1977). The timing of the development of these characters varies between populations.
Limit B/C. The unpaired dorsal finfold is divided in the dorsal and adipose fin primordia. It is no longer one bimodal finfold, but a very low remnant remains between the two fins for some time. This may detract from the exactness of application of this definition. Fin rays are visible over the whole

length of the caudal fin at approx. this point.
Stage C. The alimentary canal is still a straight tube, although expanded behind the foregut. The nasal openings are simple or dumb-bell shaped. The colour is vividly whitish and greenish and the larvae are more easily observed in lakes than the more transparent younger stages. The first stage of advanced schooling behaviour (Lindström 1970) includes this and the following D stage, the total length being 15–30 millimetres (rather than 15–25 millimetres).
Limit C/D. The alimentary canal begins to bend in the cranial part of the visceral cavity, and a loop starts to develop in which both the foregut and midgut are involved (see above). The hind end of the air bladder reaches the cranial part of the dorsal fin, and is often supplied with an ampulla.
Stage D. The nasal openings are dumb-bell shaped or double. The adipose fin primordium dwindles and becomes smaller than the anal fin. The ventral finfolds between the pelvic fins and the anal opening are successively reduced and the last vestiges occur caudally to the pelvic fins and cranially to the anal opening. The caudal fin is still clearly asymmetrical (heterocercal). Fin rays become visible in the pelvic fins. Total length some 20–30 millimetres.
Limit D/E. The rounded caudal fin becomes slightly forked at stage D and is now homocercal, i.e. secondarily symmetrical when viewed from the outside (the location of the urostyl can often be spotted for some time by virtue of the pigmentation). Shortly after this the pyloric constriction and the first pyloric appendices are formed. The cranial part of the midgut remains expanded and there is a cuff-like constriction of the straight intestine tube somewhat caudally to this.
Stage E. Juveniles.

Black pigment is not used in the stage descriptions, nor for distinguishing between whitefish species, but it is of decisive importance for the identification of a larva as whitefish larva. Techniques for distinguishing between vendace and

whitefish larvae by means of black pigment have been published by Schnakenbeck (1936), and between ciscoe and whitefish by Cucin and Faber (1985). The dorsal black pigment is also of importance for distinguishing between very early whitefish and grayling larvae. (If these pigments are highly expanded and the pattern is blurred, however, it is possible to use the size of the dorsal fin and the number of lepidotrichia of the dorsal fin at stage C and later.)

Results

The dorsal fin

The numbers of rays in the dorsal fin have been reported for some Swedish whitefish populations by Smitt (1895). He distinguished between unsplit and Y-split rays, the majority belonging to the latter group (ten to twelve out of a total of thirteen to sixteen, also referred to as branched, e.g. by Norden 1961). The numbers of rays in the present juveniles fall well within the range reported by Smitt (op.cit.), when all rays are counted and the last, the V-split, is counted as one.

The mean number of dorsal fin rays in very recently metamorphosed juveniles from Lake Sällsjön caught on June 27th fell one short of the number observed in August. There is no significant differences between 0+ in August and 1+ in August (=two-summer-old young), nor is there any difference between juveniles of "älvsik", *Coregonus lavaretus*, from two lakes on the River Indalsälven and "planktonsik", *C. nilssoni*, in one of these lakes and "sandsik", *C. acronius*, and "aspsik" *C. pallasi*, in a lake on the River Ume älv, all of which have a mean value of 14 rays (Fig. 1, Table 1).

The Arjeplog lakes
Uddjaur
Storavan
Fjosokken
Ö & N Björkvattnet
Rönnösjön
Landösjön
Kallsjön
Sällsjön
Storjuktan
Storuman
River Ume älv
River Indalsälven
The Fulufjäll lakes
St Rösjön
N Särnamannasjön
St Harrsjön
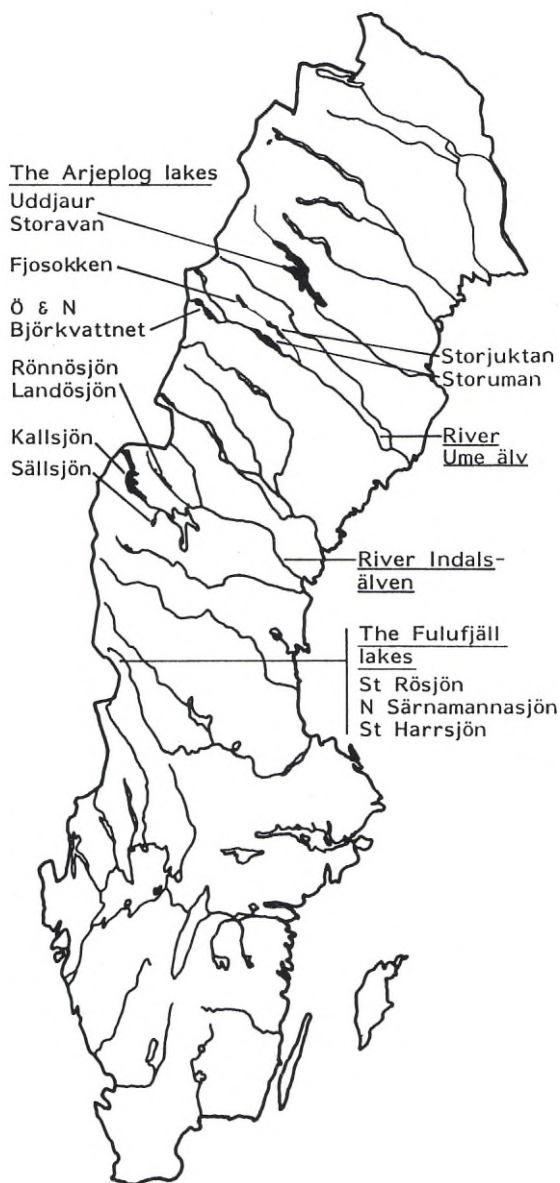
Fig. 1. Survey map of the district.

Table 1. Number of rays in the dorsal fins of juvenile whitefish in August of the first (stage E) and second summer (1+). The lakes are arranged according to river systems, Fig. 1, in all the tables.

	Sällsjön C.lavaretus E, Aug.	1+, Aug.	Landösjön C.lavaretus E, Aug.	C.nilssoni E, Aug.	1+, Aug.	Storuman C.acronius E, Aug.	C.pallasi E, Aug.
Number	25	14	16	15	13	8	12
Mean	14.25	14.21	13.88	14.07	14.08	14.13	13.83
Standard error	0.20	0.15	0.18	0.21	0.18	0.23	0.27

Table 2. Number of rays in the dorsal fins of juvenile normal char and F-char in late August and early September of the second summer or later in the year and at higher ages, in recently introduced populations in Lakes N. Särnamannasjön and St. Harrsjön and in the donor population in Lake St. Rösjön. "Char (cf. text)" is explained in full on p. 19 and 24. Mean age denotes age attained in the previous spring – the number of summers is one unit higher.

Species	Normal char	Char (cf. text)	F-char		
Lake	St.Rösjön St.Harrsjön	St.Rösjön	N.Särnamanna- sjön	St.Rösjön	St.Rösjön
Stage	juvenile	juvenile	maturing	mature	mature
Mean age	2.9	2.5	1.2	3.4	3.4
Number	17	23	55	13	13
Mean	12.41	12.39	12.95	13.00	12.62
Standard error	0.15	0.17	0.15	0.23	0.18

The number of Y-split rays in certain Swedish char populations, according to Smitt (op.cit.) is 8–10 (occasionally 11 or 12) out of a total of 11–14 (occasionally 14–16). Two-summer-old (= 1+) maturing F-char from Lake N. Särnamannasjön had 13 rays, as did mature four-summer-old F-char from Lake St. Rösjön, while longer but still not mature four-summer-old normal char from this lake had 12 rays (Table 2). No developement after the age of two summers is indicated and no significant difference between species.

Gillrakers

The numbers of gillrakers of the whitefish juveniles are used to identify the different populations (Fig. 2). The period covered is from metamorphosis to the age of 1+ in August. Means for the adults of the same populations are also shown in the figures. In the middle of the first summer the gillraker numbers have almost attained their final values in Lake Sällsjön (Fig. 2), with only one whitefish species, and there is no increase between the August values of the first and second summer in this lake, an insignificant decrease in the mean number even occurring in the sample of older fish of this population. It is more difficult to see the trends in a lake with more species, but material from the Arjeplog lakes (Lindström 1962) implies that the number in the middle of August of the first summer is close to the final number, with the number still missing being highest for the species with the highest final number, *C. pallasi*.

Two local problems have not yet been satisfactorily solved:

1) Lakes Fjosokken and Storjuktan, Fig. 2: it is difficult to draw a borderline between 0+ juveniles of "sandsik", *C. acronius*, and "planktonsik", *C. nilssoni*.

2) Lake Storuman, Fig. 2: the gillraker number distribution relates to two species. The upper cluster is still far from the final number of the adult "aspsik", *C. pallasi*, on August the tenth. There have been suspicions of a third whitefish species in Lake Storuman (*C. nilssoni*?) since the early part of this century, but this has not so far been verified in spite of extensive sampling (Lindström et al. 1982b). The steep inclination of the regression in the present sample indicates *C. pallasi*.

The lengths of the central raker in whitefish juveniles in the August of their first and second summer and the lengths of the first left gill arch are correlated with total length (Fig. 3a, b). Information on older whitefish from Lake Sällsjön is also shown. Gill arch sizes together with gillraker numbers give a crude estimate of the opening between the rakers (Table 3). This is further elaborated for *C. lavaretus*. The opening between the rakers in the angle between the ventral and dorsal members of the gill arch (where the central raker lies) is less than 5 ocular units in one-summer-old, 10 o.u. in two-summer-old and 15–20 o.u. in older whitefish from lakes Sällsjön and Landösjön (30 o.u. = 1 mm). There are differences between species and within the same species between lakes in the length of the central
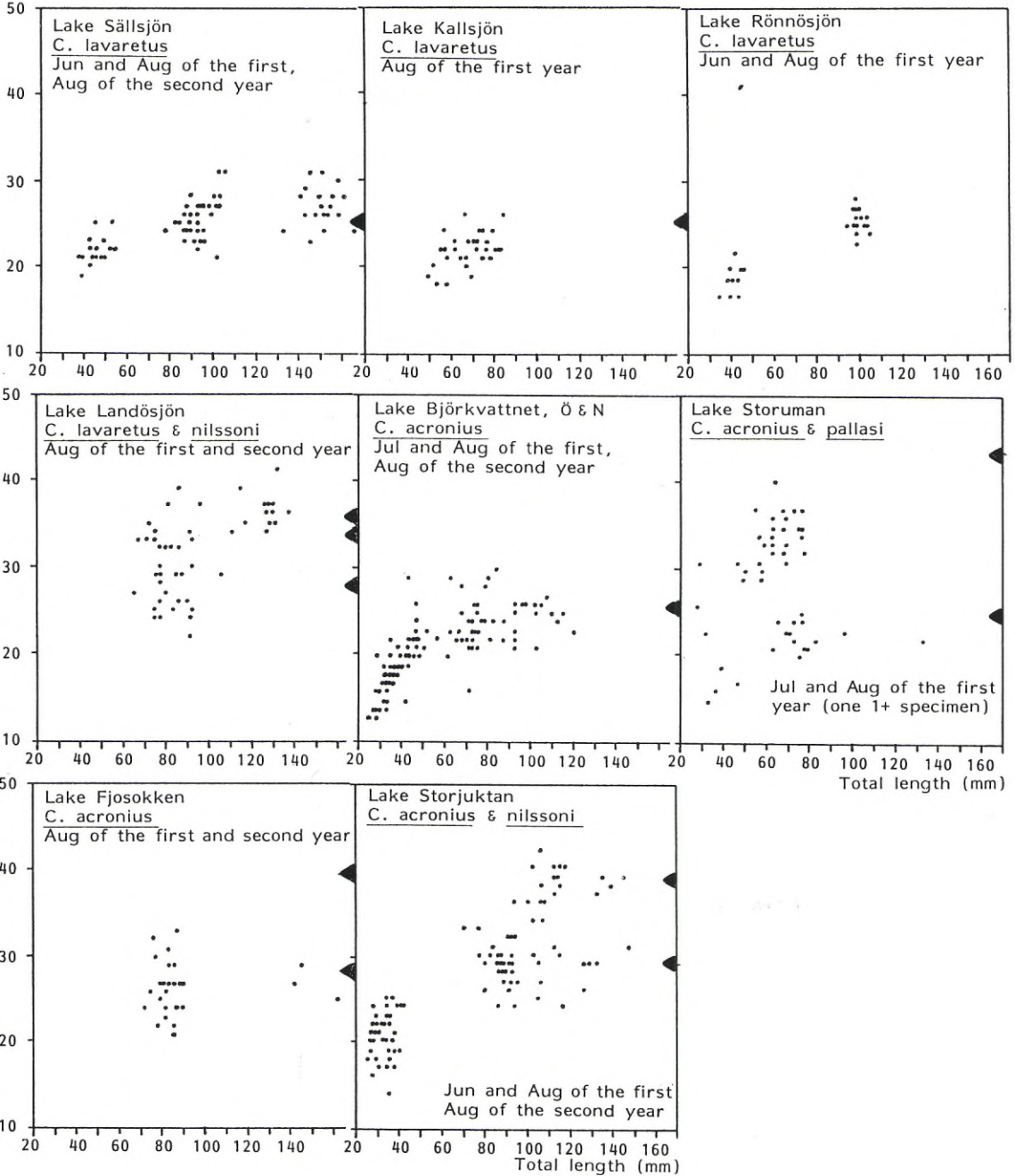
Fig. 2. Identification of whitefish species. Distribution of gillraker numbers in relation to total length in juvenile whitefish. The mean in adult fish is indicated in the right-hand margin, and in Lake Landösjön also that of *C. wartmanni* although juveniles of this species do not occur in the samples.

Length of central raker (ocular units)
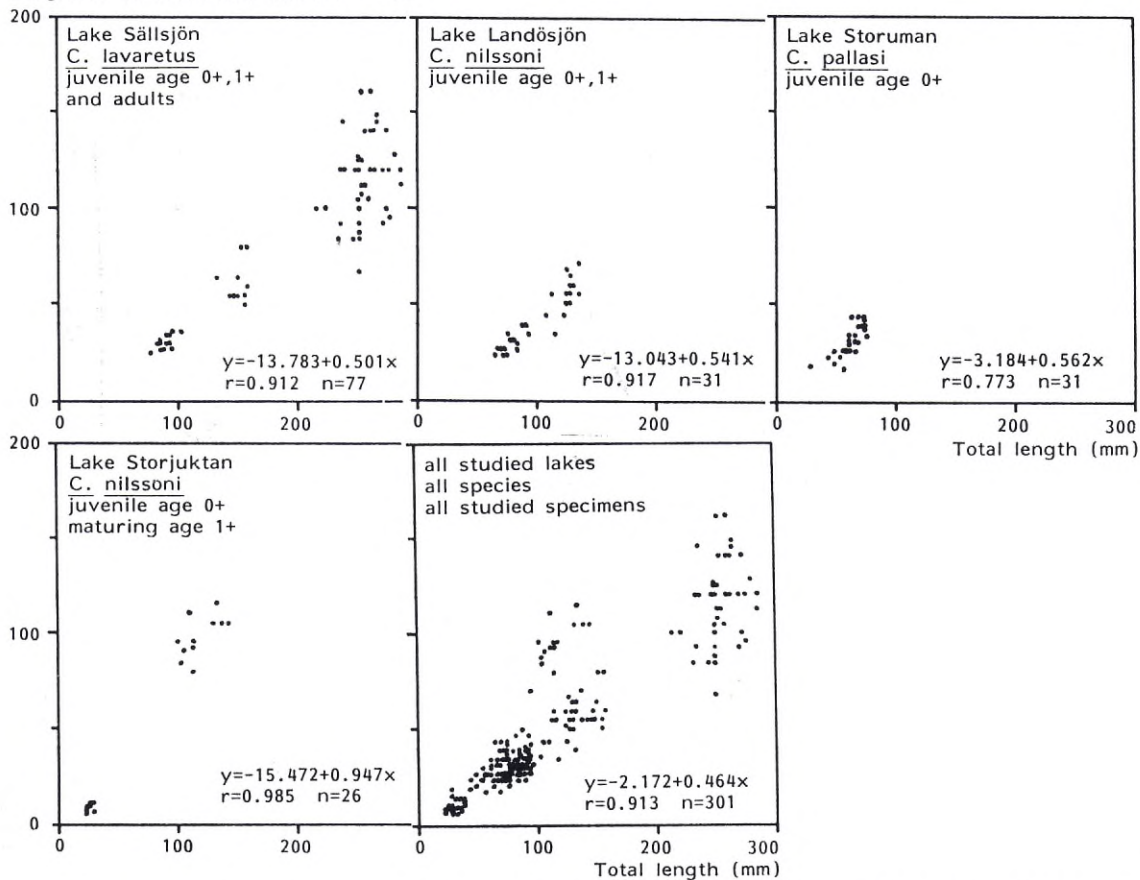
Fig. 3a. Regression of the length of the central raker in the first left gill arch on total length. Y-axis in ocular units (30 o.u. = 1 mm). In addition to 0+ and 1+ there are some old juveniles from Lake Sällsjön.

Length of first gill arch   (ocular units)
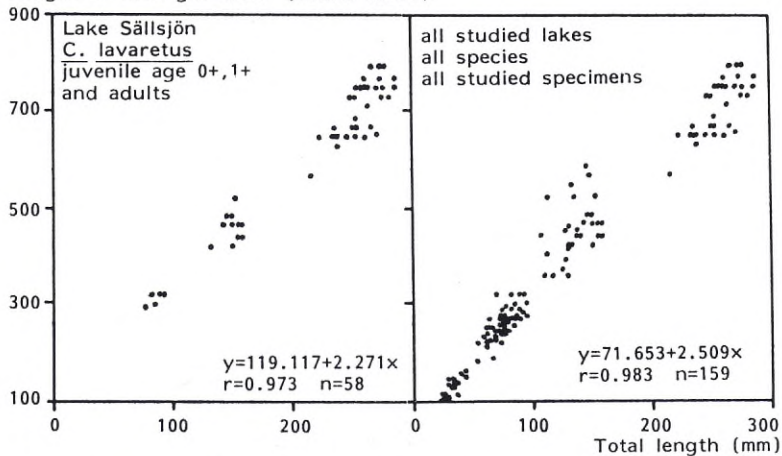
Fig. 3b. Regression of the length of the gill arch on total length. Y-axis in ocular units.

Table 3. Length of the first left gill arch in ocular units (30 o.u. = 1 mm) divided by the number of gill-rakers in juvenile whitefish in June or August of the first (stage E) and in August of the second summer (1 +) and also adults from Lake Sällsjön.

| | Sällsjön C.lavaretus | | | Landösjön C.lavaretus | C.nilssoni | |
	E, Aug.	1+, Aug.	adults	E, Aug.	E, Aug.	1+, Aug.
Number	5	14	39	16	14	13
Mean	12.48	17.43	27.84	9.94	8.00	11.23
Standard error	0.27	0.49	0.47	0.28	0.28	0.28

| | Storuman C.acronius | C.pallasi | Storjuktan C.acronius | C.nilssoni | |
	E, Aug.	E, Aug.	E, June selection of large	E, June selection of small	1+, Aug.
Number	8	12	23	14	7
Mean	11.43	7.13	6.97	5.48	13.07
Standard error	0.37	0.39	0.27	0.16	0.56

Table 4. Number of rakers on the first left gill arch (left part of the table) and length of this gill arch in ocular units (o.u.) divided by the number of rakers (right part) in normal char and F-char in Lakes N. Särnamannasjön, St. Rösjön and St. Harrsjön, cf. caption to Table 2.

Gillraker, number

Species	Normal char	Char (cf. text)	F-char		
Lake	St.Rösjön St.Harrsjön	St.Rösjön	N.Särnamanna-sjön	St.Rösjön	St.Rösjön
Stage	juvenile	juvenile	maturing	mature	mature
Mean age	2.9	2.5	1.2	3.4	3.4
Number	25	7	33	9	13
Mean	25.72	25.29	24.99	24.00	24.00
Standard error	0.30	0.84	0.29	0.65	0.41

Gill arch length/raker number

Species	Normal char	Char (cf. text)	F-char		
Lake	St.Rösjön	St.Rösjön St.Harrsjön	N.Särnamanna-sjön	St.Rösjön	St.Rösjön
Stage	juvenile	juvenile	maturing	mature	mature
Mean age	2.9	2.5	1.2	3.4	3.4
Number	25	7	23	9	13
Mean	26.72	23.14	16.52	21.33	20.62
Standard error	1.37	1.03	0.33	1.38	0.76

raker, which seem mainly to be explained by differences in total length, although the *C. nilssoni* in Lake Storjuktan and probably also the *C. pallasi* in Lake Storuman deviate from the other populations, t-test for difference between the regression coefficients of lakes Storjuktan and Sällsjön in Fig. 3a, t = 8.99.

The numbers of gillrakers in the Fulufjäll char populations were reported in Andersson et al. (1971), being 25 rakers for F-char and 26 for normal char.

Table 4, the left-hand side, shows that two-summer-old maturing F-char from Lake N. Särnamannasjön and four-summer-old mature F-

Length of central raker (ocular units)

y=5.006+0.265x
r=0.83 n=26

y=25.647+0.189x
r=0.389 n=53

Length of gill arch (ocular units)

y=49.953+2.895x
r=0.899 n=26

y=199.856+2.037x
r=0.597 n=54
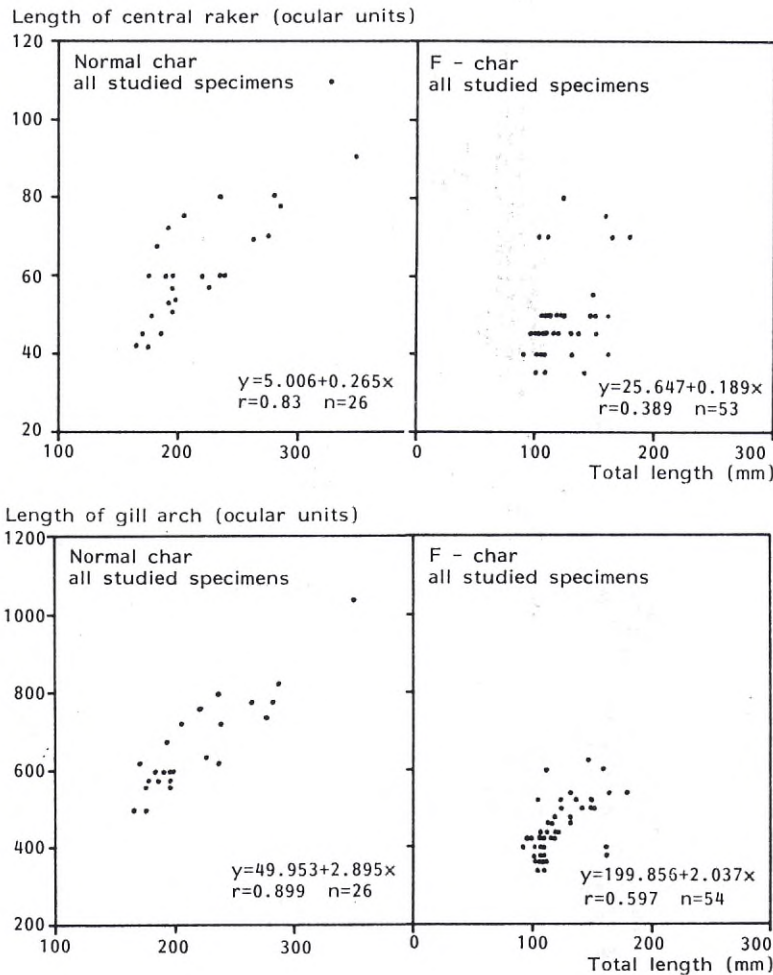
Total length (mm)

Fig. 4. Regression of the length of the central raker in the first left gill arch on total length (top) and of the length of this gill arch on total length (bottom) in normal char and F-char in August/September of the second summer and later, in recently introduced populations in Lakes N. Särnamannasjön and St. Harrsjön and in the donor population in Lake St. Rösjön. Y-axis in ocular units (30 o.u. = 1 mm).

char from Lake St. Rösjön had 24 rakers, while longer four-summer-old immature normal char from Lake St. Rösjön had 26 rakers. The high error in the "Char" sample renders identification of this group difficult (p. 19 and 24).

The length of the central raker on the first left gill arch of char and the total length of the gill arch both increase with the total length of the fish (Fig. 4). The ratio between length of the gill arch and the number of rakers is shown in Table 4, the right-hand side, as a measure of the distance between the rakers. The opening between the central rakers is estimated to be 10–15 ocular units in two-summer-old char and over 20 o.u. in four-summer-old char at a total length of 109 and 253 mm respectively (1 mm = 30 o.u.).

Otoliths

Otoliths and scales were obtained from juvenile whitefish in their first and second years and from some older fish. The ageing of young whitefish was fairly simple, as otoliths and scales from juveniles were sampled successively during their first year together with the growth and stage development data.

The otolith of a 0+ whitefish juvenile in the August of its first year consists of a hyaline nucleus (kernel in the terminology of Panella, 1980) surrounded by a broad and then a narrow opaque zone, separated by a narrow hyaline "strip", the broad zone showing a radial structure. (It is in reality three shells, of course.)

Otolith width (ocular units)
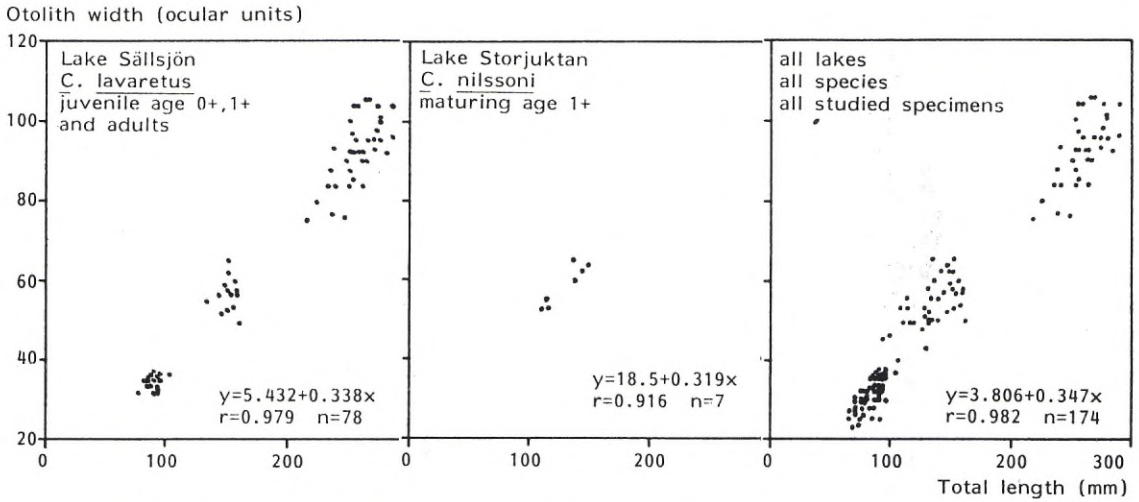
Fig. 5. Regression of otolith width on total length in whitefish. Y-axis in ocular units (30 o.u. = 1 mm). In addition to 0+ and 1+ there are some old juveniles from Lake Sällsjön.

These structures are not discernible in all samples or all specimens, although the opaque structure of the first year never forms a uniformly coloured structure (volume).

One year later, the otolith of a 1+ (=two-summer-old) juvenile whitefish has a new broad opaque zone at the periphery, and the inner details are somewhat obscured in uncut otoliths by increased opaqueness.

The widths of the otoliths of the juvenile whitefish are correlated with total length (Fig. 5), and the width of the otolith is also correlated with its height (Fig. 6). The height-width ratio is increasing. In natural whitefish populations the precise number of weeks since hatching in the first year is not so well known, as juveniles can easily belong to different cohorts within one year-class, but comparison between the first and second-

Otolith width (ocular units)
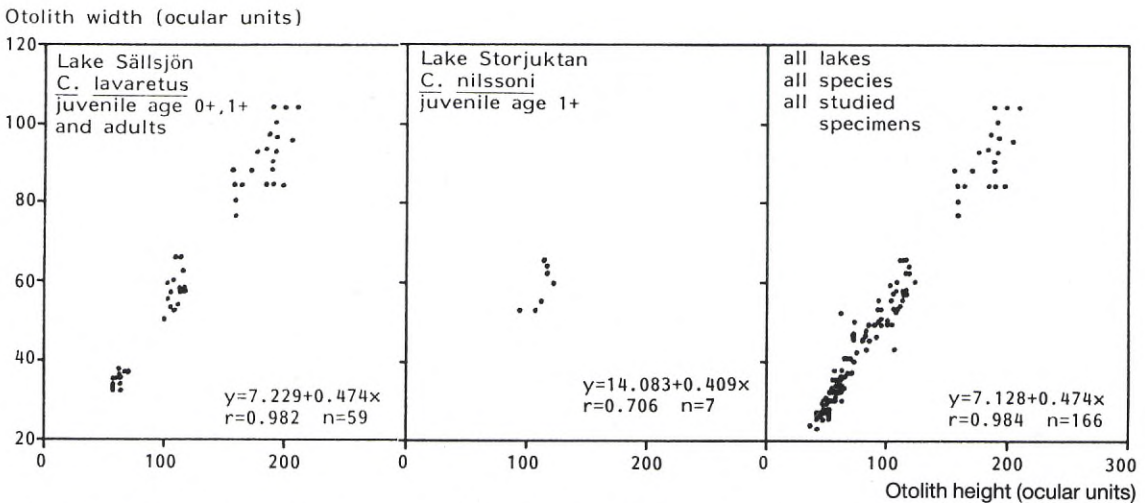
Fig. 6. Regression of otolith width on otolith height in whitefish. Both axes in ocular units.
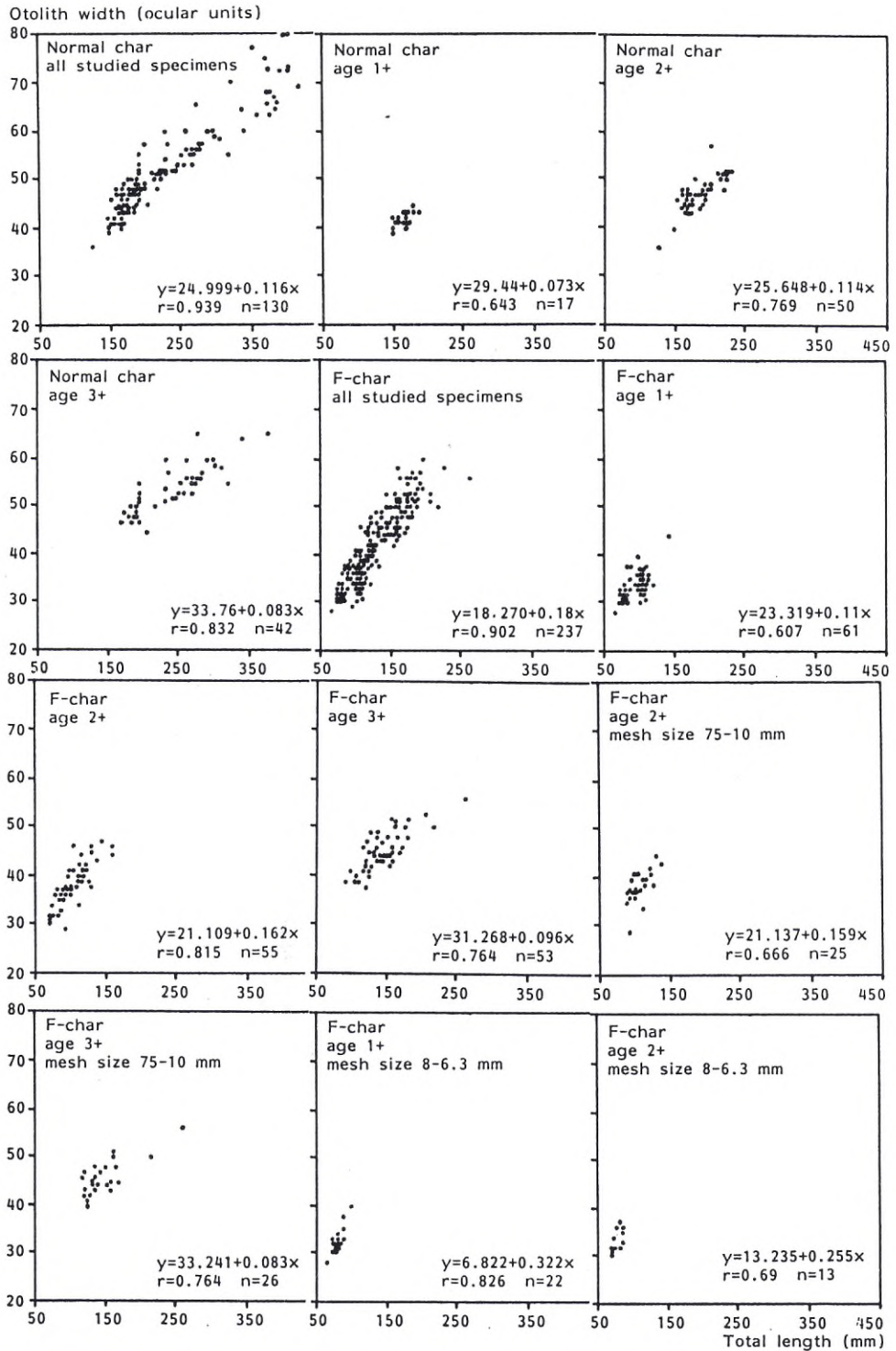
Fig. 7. Regression of otolith width on total length in normal char and F-char. Results from the complete material and separate reports for different ages and different gillnets used. Y-axis in ocular units (30 o.u. = 1 mm).

Otolith width (ocular units)
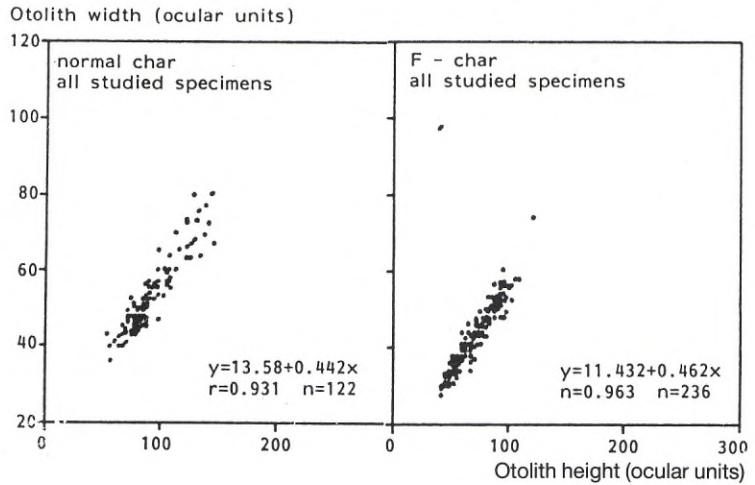
Fig. 8. Regression of otolith width on otolith height for normal char and F-char. Both axes in ocular units.

year fish can give better information on the effect of age. The otolith width-total length correlation coefficient is high, even though samples with good as well as poor growth in the second year are included. Three whitefish species and six populations from four different lakes are contained in the material, and only the "planktonsik" from Lake Storjuktan differs from the others in the otolith width-total length regression, t-test for difference between regression coefficients, Fig. 5, $t=1.14$, $P=0.2$.

The structure of the otoliths of young F-char up to and including the second or even third summer are similar to those of normal char, and the two could not be distinguished (they are sometimes quite different later). The otoliths of both species during the first few years contain:

1) A fairly hyaline nucleus (kernel) and outside this the opaque material belonging to the first year. It is not abruptly surrounded by hyaline material peripherally, as markedly "coloured" opaque sectors protrude into the hyaline zone, and probably out to the limit of the first year ring.

2) The opaque zone in the second year ring may also be a rather complicated structure, e.g. in some year-classes a very narrow opaque zone follows immediately outside the main opaque zone of the second year (not to be mistaken for a split ring in the sense usually employed

in the literature, Lindström and Andersson, 1981 a).

The positive relation between otolith width and total length of the char is depicted in Fig. 7, and that between otolith width and height in Fig. 8. The different diagrams show the variation in otolith size and fish growth within ages and the variation due to gear effects (different mesh sizes). t-test for the difference between the F-char and normal char regression coefficients, $t=9.91$.

The material of char otoliths on which these conclusions are based caused significant hesitation at a number of points, however, particularly when a specimen had to be assigned to an age of $1+$ or $2+$ and a narrow outer opaque zone was "partly" or "almost" joined with the opaque zone of the second summer.

Morphology of the immature gonad

The gonad classification is based on schedules presented by Dahl (1917) and Sømme (1941) for brown trout, *Salmo trutta*. Some morphological characteristics used for female whitefish and char were described by the present author in papers published in Swedish, but a safe classification could only be obtained after histological

2

studies published by Zawisza and Backiel (1970) for the vendace and Flumé (1978) for the char.

The eggs are densely packed and the ovary has sharp edges in the juvenile female. When the thickening of the ovary extend beyond the middle of the abdominal cavity and the diameter of the larger eggs exceed one millimetre in the char and approach one millimetre ($>1/2$ mm) in the whitefish in late summer or the beginning of the autumn, the fish is going to spawn that year. An unripe mature female has loosely packed eggs and a sac-like ovary without sharp edges. Atretic eggs are not so common in the summer after spawning. An immature male cannot be easily distinguished from a mature, unripe male on cursory inspection of the gonads, and one has to rely on observations that fish below a certain age are never observed to ripen in a particular population. When the testis is ripening, it is not only the cranial part that shows a thickening, but the testis is lobated along its whole length.

Much emphasis has been placed on the size of the eggs (Flumé 1978). Although there is variation in egg size within and between classes (Toots 1951, for the whitefish), the general impression is that the variation is small. It has also been shown that salmonid eggs pass through a stage of rapid growth in ripening females (Henderson 1963, Zawisza and Backiel 1970, Bagenal 1976). The applicability of the same, loosely defined egg size classes quoted above to both dwarfed F-char and a sympatric population of normal char and another such size class for all whitefish populations was checked in the present study. Smallsized char have relatively large eggs (Flumé 1978).

Additional observations are that males have a cranial expansion of the testis very early, in the first year in the case of whitefish which will not spawn for the first time until several years later. This expansion is not observed so early in normal char.

Habitus at maturity

The thickening of the gonads of whitefish juveniles can reach the middle of the abdominal cavity in the second summer, although it is still often difficult to distinguish between males and females without any kind of preparation. In one population of "planktonsik", *C. nilssoni* from Lake Storjuktan they were more advanced on August 5th in their second summer, however, and the lobated testes of the males extended well over the middle of the abdominal cavity. They would have spawned later that autumn. No colour or shape characteristics have been observed to separate these ripening 1+ fish from other whitefish of the same age.

In the two char populations in Lake St. Rösjön (Lindström and Andersson 1981b) two-summer-old young could not be separated as to species by form or colour, and had a yellowish-rose dress with parr marks and some degree of silvery glow during that year.

No F-char were then found maturing below the age of 2+. They still carried the dress described above at that age i.e. in their third summer, even though some were maturing. During ripening at higher age their dress went quite blackish, including the parr marks. The colours of the F-char were always less pronounced in spring.

The normal char were still not maturing at the age of 4+ years. In the intervening time the juvenile normal char had as 2+ and older an entirely silvery dress, easily distinguishable from that of the mature F-char and that of the young.

The development of the dress characters in these two populations is indicated by the catches with fine-meshed gillnets from 1984 to 1987. The catches are identified in Table 10 by year and mesh size of the gillnets. Total catches are reported on lines designated "sum" while the selected fractions show dress and variation in maturity stage with age etc. There are still rapidly growing normal char which remain silvery and immature to the age of over four summers. There are also two- and three-summer-old char carrying the yellowish-rose dress with parr marks, and this group now included some F-char males with lobated testes aged 1+ in 1984 that had spawned the just finished spawning period for F-char, and such males were more frequent in 1986. Some 1+ and 2+ females of F-

char had also spawned earlier in 1986. (Table 10, 1984 mesh size 12.5, 1986 mesh sizes 16.7 and Ö 8.0–6.3 and Ö 75.0–10.0 mm). It may be that the cumulating sampling and the more fine-meshed gillnets only disclosed more extraordinary specimens, but there was another trend: slow-growing, immature 3+ juveniles with silvery dress were quite common in 1987, and might have been classed as younger normal char without any knowledge of their age (Table 10, 1987 silvery small char).

This recent developement will be considered in the discussion, but the following detailed observations may contribute to its explanation. While searching for better species markers in the years 1971 and 1984, it became possible to distinguish between 1) paler, and 2) more intensely coloured juveniles within the group of yellowish-rose 1+ young with parr marks (Table 10, 1971 mesh size 10.0 and 1984 mesh size 12.5 mm, pale and sombre).

This separation resulted in:

1) a group consisting of juveniles/females with very slight thickening of the gonads in the anterior abdominal cavity and males with very narrow testes, and

2) a group consisting of females with a thickening amounting to 1/3 or 1/2 of the abdominal cavity and males with a marked thickening in the anterior part or lobated testes.

Growth

The pattern of growth during the first summer can only be presented for whitefish.

Three lakes with different break-up of the ice.
Starting point and early development.
Cohort problems when studying whitefish

To exclude the possibility of very early hatching, the habitat of *C. pallasi*, "aspsik", larvae in the Arjeplog lakes – one of four sympatric species – was examined on April the 3rd and May the 7th in 1970, that of *C. acronius*, "sandsik", larvae in Lake Ö. Björkvattnet on June 17th 1982, and that of *C. lavaretus*, "älvsik", larvae in Lake Sällsjön

on May 8th and 9th in 1970. No larvae were obtained. The spawning site for "aspsik" is clear of ice early, as it is located in flowing water, but the adjoining lakes are ice-covered until the end of May or beginning of June. Of the lakes with only one whitefish species, the ice broke up on Lake Ö. Björkvattnet, in a harsh climatic region, in the beginning of June in 1982, while the survey was performed in Lake Sällsjön during the dispersal of the ice in May.

The early development in the Arjeplog lakes has been treated in two earlier papers (Lindström 1962, 1970). In Lake Ö. Björkvattnet the early survey in 1982 in the present material was followed by catches on July 15th and 16th. The small size of the young confirmed that the year-class was late in this lake and this year (a more normal year will be referred to below). Length distribution was bimodal.

A sample with a bimodal length frequency distribution can raise the suspicion that larvae of two species may be involved, e.g. as it occurred in the habitat from which the *pallasi* larvae were eventually obtained (op.cit. 1970). A sample from a lake with one whitefish species, e.g. Lake Ö. Björkvattnet may apparently also show a bimodal length-frequency distribution. The examination of rate of growth and development at one station is always hampered by the fact that cohorts of larvae of one or more species with different hatching times may pass through the station or habitat in the course of time. This implies a number of methodological difficulties. Identification of whitefish fry to species by means of length frequency tables is not possible if there is no supporting evidence. Another problem is that growth details at the beginning of the first year are obscured. Growth stanze (Cucin and Faber 1985) may exist in the present material too, but none has so far been demonstrated.

The problems raised by cohorts can only be neglected in lakes with one whitefish species and a fairly uniform habitat for their larvae. These conditions may be encountered in the third lake, Lake Sällsjön, where early surveys with no observed larvae were followed by a fairly extensive survey in 1970 (Table 5). The withefish larvae in Lake Sällsjön develop rapidly.

Table 5. Fresh total length and development of "älvsik", *C. lavaretus* larvae from Lake Sällsjön in different years. The lake contains no other whitefish species. Stage A(B) means mainly stage A specimens, A/B means about equal numbers.

Date	Mean larval length, mm	Stage	Sample size	Beach temp.°C	Date of icebreak
69					0525
700521-0530	13.2	A	69	5-10	0526
700601-0603	13.5	A(B)	26	5-10	
700605-0607	14.3	A/B	15	8-13	
700613	16.7	C	15	8-11	
710604-0608	15.5		29		0515
710609	16.9	B/C	14	9-11	
710610-0614	16.3		52		
710616	18.3	C	15	10-11	
720606-0607	17.4		74	10-12	0523
730604-0606	19.3	C	26	10-13	0515
730607	22.6	D	15	10-14	
740515	13.1	A	8	6	0512
830606	21.3	B(C)	20	7	0516

Early larval development in different lakes and years

The Table 5 gives lengths and stages of larvae in Lake Sällsjön in different years with differences in the breaking up of the ice. Less conclusive observations can be obtained from a larger lake with several whitefish species by comparing a number of years (Table 6). The occurrence of cohorts may e.g. explain why there seems to have been hardly any development at all between May 26th and June 12th in 1970 in Lake Landösjön, where the samples were taken from one fixed point.

Table 7 brings together information from the spring of 1983 from various lakes with differ-ences in whitefish species fauna and the break-up of the ice. The results do not support the idea that the ice and the shore temperature distribu-tions can be used to obtain a very detailed prog-nosis for early development when studying a compound material.

Whitefish: juvenile growth and first year total length

The juveniles from Lake Sällsjön in the midsum-mer series for 1984 (Table 8) are far ahead of those from the other lakes. The differences be-tween species and lakes occurring in spring and early summer are, however, reduced in August in the present material (Table 9), by which time

Table 6. Fresh total length and development of whitefish larvae from Lake Landösjön in different years, catches from a fixed point. Indica-tion is given of cohorts of larvae with different hatching times in 1970.

Date	Mean larval length, mm	Stage	Sample size	Beach temp.°C	Date of icebreak
660618	14.6	(B)C(D)	29	(12)	0523
670606	10.2	A	11	5- 6	0526
670615	11.7	A	98	6-10	
670703	18.1	C	7	12	
690607	10.6	A?	7		0524
690614	14.2	(A)B	59	9-11	
700520	10.3	A	5	4	0524
700604	10.3	A	10	5-10	
700612	11.8	A(B)	15	6-11	
71					0516
72					0513
73					0514
740523	11.4	A	5	8	0514
830609	11.8	A	25	7- 8	0515

Table 7. Differences in fresh total length and development of whitefish larvae in 1983 between lakes with one (Lakes Sällsjön and Kallsjön) or more whitefish species.

Lake	Date	Length in mm	Stage	Sample size	Beach temp. in °C	Date of icebreak
Sällsjön	830606	21.3	(B)C	20	7	0516
Kallsjön	830607	16.9	(A)B	25	(8)	0512
Landösjön	830609	11.8	A(B)	25	7- 8	0515
Storuman	830608	13.7	(A)B	26	9-11	0528

Table 8. Fresh total length of whitefish young just before (stage D), during or shortly after metamorphosis in lakes with the ice breaking up on various dates.

Lake	Date	Mean length in mm	Sample size	Stage	
Sällsjön	840627	46.3	22	Early juvenile	
Rönnösjön	840628	40.7	18	"	
Ö.Björkvattnet	820715	29.4	22	D	
"	820716	28.2	18	D	
"	840630	30.7	22	Metamorphosing	
"	660715	47.0	36	Early juvenile	
N.Björkvattnet	660704	37.3	20	"	
Storjuktan	840630	31.5	51	"	
"	selection large	36.3	12	"	low
"	" small	28.0	14	"	high

Table 9. Fresh total length of whitefish juveniles in August of the first year and after one and two full years (back calculated length). Estimates of full length after one or two years are mainly from material published earlier; for references cf. Lindström (1974). A whitefish species in Lake Landösjön that is not discussed in this paper is also included in the table.

Lake		Date	Number	Length mm	Standard error	Length at an age of one full year	two full years
Sällsjön,	C.lavaretus	830818	31	98.2	0.85		
"	"	840817	2	104.5			
"	"	860808	5	87.8	2.71		
"	"					97.2	163.3
Kallsjön,	"	830819	26	77.0	1.44		
"	"					96	169
Rönnösjn,	"	840817	18	101.7	0.58		
Landsjön,	C.lav. & nilssoni	830817	38	84.2	1.37		
"	C.lavaretus	"	21	85.3			
"	C.nilssoni	"	18	81.0			
"	C.lavaretus					100	158
"	C.wartmanni					57	78
Ö.Björkv.,	C.acronius	830821	37	75.2	1.35		
"	"	840815	45	81.4	1.68		
Storuman,	C.acr. & pallasi	830810	25	69.8	1.92		
"	C.acronius	"	14	75.1			
"	C.pallasi	"	19	65.8			
"	C.acronius					93	143
"	C.pallasi					98	140
Fjosokken,	C.acronius	830815	5	88.8	1.28		
"	"	840813	21	85.0	1.10		
"	"					85	141
Storjuktan,	"	830816	16	92.6	2.40		
"	"	840814	17	91.2	1.04		
"	"					90	147
"	C.nilssoni					85	103

Table 10. Development of the maturity stages in char of different ages and from nets of different mesh sizes in Lake St. Rösjön from 1971, 1984 to 1987. "Dress" refers to a description in Lindström and Andersson (1981 b; catch 1971 is presented in that paper and all total catches with fine-meshed gillnets from 1984 and up to 1987 are reported in this table).

A catch is identified by year and mesh size of the gillnet. The whole catch is listed in the lines designated "sum", but the distribution into maturity stages concerns only two-four summer old fish (1+–3+), most often from samples.

Ö indicates sections of multimesh gillnets.

Catch year	Mesh size in gillnet/number of nets	Dress and species if identified	Number	Age	Mean total length, mm	Otolith size in ocular units	Juveniles	Females, juv.	Females, ovary = 1/2 of the visc.cavity	Females, spawning or spent	Males, testes a narrow string	Males, testes cranially exp.	Males, testes irreg.expanded	Males, spawning
1971	10.0/1	Sum, F-char	21	2-7+										
		Sum, pale yellow parr	30	1+	106.2	34.96	1	19	1		8	1		
		Sum, sombre yellow parr	34	1+	96.8	33.56	2	4	2		5	21		
1984	12.5/1	Sum, F-char	119											
		Sum, yellow parr	78											
		F-char	1	2+	123.0	48.0				1				
		Pale yellow parr	17	1+	137.2	39.9	17							
		Sombre yellow parr	18	1+	113.8	38.2		6	5			3	5	
		Yellow parr	2	2+	110.5	39.5			1					
1984	16.7/2	Sum, silvery normal char	16											
		Sum, F-char	89											
		Silvery normal char	3	1+	175.0	42.3					3			
		Silvery normal char	6	2+	171.5	45.3		1			5			
		Silvery normal char	3	3+	221.0	56.7		3						
		F-char	4	3+	176.3	48.8				2				2
		Yellow parr	2	1+	102.0	33.0		2						
1985	16.7/2	Sum, silvery & adult norm.char	13	2-5+										
		Sum, F-char	34	2-6+										
		Sum, yellow parr	4		111.5									
		Silvery normal char	10	2+	190.6	47.3	3	6		1	1			
		F-char	4	2+	174.5	46.8				1				3
		F-char	2	3+	170.0	48.5								2
1986	16.7/2	Sum, silvery & adult norm.char	34											
		Sum, F-char & yellow parr	16											
		Silvery normal char	29	2+	192.2	45.0		15			14			
		Silvery normal char	3	3+	244.0	52.7		3						
		Yellow parr	1	1+	85.0	35.0	1							
		Yellow parr	5	2+	116.8	42.2			1		3			1
		F-char	9	3+	151.1	45.0					4	1		4
1986	8.0-6.3/4	Sum, yellow parr	70											
		Yellow parr	22	1+	80.3	32.6	11				2		3	6
		Yellow parr	13	2+	79.8	33.4	2				1		3	7
1986	75.0-10.0/4	Sum, silvery & adult norm.char	55											
		Sum, F-char & yellow parr	129											
		Silvery normal char	5	3+	322.6	59.4			2		2			1
		F-char & yellow parr	26	2+	106.2	38.5	3	3	2		6	1	8	3
		F-char & yellow parr	26	3+	147.3	45.5					6	1	4	15
		Yellow parr	1	1+	101.0	34.0		1						
1987	16.7/2	Sum, large silv.&adult norm.char	11	2-5+										
		Sum, small silvery normal char	24	2-4+										
		Sum, F-char	14	2-6+										
		Silvery, large normal char	10	3+	277.3	55.8			3	1	6			
		Silvery, small char	13	2+	164.2	44.1		4	1		8			
		Silvery, small char	10	3+	181.3	50.0			5	2	3			
		F-char	3	2+	122.0	44.0					2			1
		F-char	6	3+	128.0	42.8					2		1	3

the relative differences in length among the juveniles are less, although the order established in the spring still broadly holds good in August when comparison is made within years (Tables 7, 8 and 9).

Escape through the meshes of the seines (mesh size 27 and 59–65 mm inner perimeter in the bags) is possible up to a certain fish size, and escape in front of or below the floating seine is always possible (length is not the only and best indication of performance). Length data obtained by back-calculation are subject to other sources of error. Here first year growth is estimated by considering both actual length in August and the

backcalculated length from older fish (Lindström 1974). The material is described in Table 9. The August samples are obtained from seine catches. The length data at one full year are from gillnet catches and different year series.

Second year growth in whitefish

The information available from 1+ juveniles on second year growth matches existing growth curves (op.cit.). Starting from a fairly uniform length, the growth curves separate out during the second year (different K-values).

Second year growth in the two species of char

The use of gillnets with mesh sizes of 16.7 and 10.0 mm knot to knot, and a few of 12.5 mm, gave the bimodal catches of small char analysed in the earlier paper (Lindström and Andersson 1981b). It was tentatively suggested that this bimodal length distribution indicated young of normal char and F-char.

In later catches sections of multi-mesh gillnets with 8.0 and 6.3 mm mesh sizes knot to knot indicated a high variation in growth of the F-char (Fig. 7 and Table 10). Either the use of a more varied set of gillnets revealed an existing spread in the growth variation, or else the growth variation is a new development. In view of the uncertainty in identifying the group of silvery juveniles with slow growth reported on p. 19 and 24, no new growth curve is presented. The curves in op.cit. 1981b are still generally valid.

Discussion

Before dealing with the main theme of the paper, the juvenile will be introduced by discussing taxonomical notes and the development of some meristic and morphometric characters and by making a survey of the metamorphosis of whitefish up to the juvenile stage.

Species identification and taxonomical notes

The material was not collected with the purpose of solving taxonomical problems. The taxonomy followed is discussed in Material and methods.

Genetic set up, environmental factors working during the embryonal stages and short-term selection may all influence the meristic and morphometric characters and their variation within and between lakes, a subject recently discussed by Lindsey 1981, Ihssen et al. 1981 and Casselman et al. 1981 for North American whitefish and by Klemetsen (1984), Nordeng et al. (1985) and Dempson (1985) for European and North American char respectively. It is generally accepted that the number of rays in the fins are easily influenced by the environment in early stages, and changes in numbers of whitefish gillrakers have been achieved in experimental environments (see references above and Kliewer 1970 with references), while selection in combination with prey fauna transformations may change the gillraker length over some generations according to Kliewer (1970), Magnan (1988).

Of the meristic and morphometric characters studied, only the gillrakers of whitefish juveniles are used for species identification. The numbers of gillrakers in char and the numbers of rays in the dorsal fins in whitefish and char almost entirely overlap for different species within each genus. The pyloric caeca are said to be only an enlargement of the adsorbing surface of the alimentary canal, and is highly sensitive to the size of the fish and to its nutritional state (Fänge and Groves 1979, Bergot et al. 1976). A combined gillraker-pylorus caeca analysis gives valuable information for distinguishing between some other char populations in Sweden, but as the number caeca is so sensitive to environmental influences, this part of the present survey was abandoned.

Growth and gillraker length are not useful for species identification, as seen in the densely-rakered whitefishes. The "aspsik" *C. pallasi* of the Arjeplog lakes is large and has long rakers, while the "aspsik" from Lake Storuman in the

present material is a small-sized population (the same sample was once tentatively identified as *C. nilssoni* (Lindström 1988, Table 7)). Svärdson (1979) writes: "aspsik . . . the Swedish populations grade into a series with an increasing amount of introgression". The "planktonsik" *C. nilssoni* from Lake Storjuktan has a growth that changes with depth. Hammar (1988) writes: "The possibility of a subpopulation . . . cannot be excluded". The present sample of small-sized "planktonsik" from this lake has long gillrakers while the rakers of the fairly large "planktonsik" from Lake Landösjön deviate from what one would expect of a plankton specialist, p. 12. This seems to corroborate Kliewer's conclusion that raker length is easily modified, perhaps by the adult diet in the present case.

Body shape, dress and size and age at maturity have been used as field characters for the Fulufjäll char since 1968. There is only a very small interspecies difference in mean raker numbers in the char but it was noted both in 1968 and in the present samples. The occurrence of some small immature silvery young fish in ages of 2+ and 3+ in 1987 raised the question of whether the growth of normal char is now very variable or whether some F-char have postponed maturity and resemble young normal char, assuming that a change in hormone action has caused the silvery dress and different body shape. The occurrence of variability in growth and in dress in relation to maturity of F-char observed since 1971 (section on Habitus at maturity, and Lindström and Andersson 1981b, the growth curves) argues for the latter hypothesis. No recent change in mortality in F-char is noted that would be compatible with the four models described by Stearns and Crandall (1984). The problem remains unsolved.

Development of dorsal fin and gills

The number of rays on the dorsal fin and the number of gillrakers are generally not so useful for identification of fish larvae, as they are late to ossify (Dunn 1983), but they are useful for identifying juveniles of the salmonoids and studying their ecology.

There is probably a slight increase in the rays on the dorsal fin in whitefish juveniles during the first summer, and there is also a slight increase in gillrakers from the August of the first summer to that of the second summer in the present material. The ossification of rays and gillrakers is highly advanced before the second summer (Nagieć 1977).

There is no difference between 1+ maturing fish in a F-char population introduced into Lake N. Särnamannasjön and the adult char in the donor Lake St. Rösjön.

When the increase in whitefish and char gillraker numbers has almost ceased, the length of the central raker continues to grow with fish length, in agreement with the observations of Lindsey (1962) and Kliewer (1970). The central raker is taken as an indicator of the whole set. Meanwhile the gill arch also grows and the distances between the rakers increase.

Allometric growth of otoliths

The otolith size increases with fish length (Figs. 5 and 7) (Templeman and Squires, 1956, Mosegaard et al. 1988, Härkönen 1986), and the height-width ratio increases with fish length (Figs. 6 and 8). The second year ring of the otolith (in the sense of Blacker 1974) is narrow when growth is poor the second year. In some single 1+ whitefish and char specimens the size of the fish and the otoliths equals that of ordinary 0+ juveniles, as does the height-width ratio. Experiments have shown that there is a complex relationship between otolith size, fish age and length, temperature and nutritional state of the fish (Panella 1980, Brothers 1981, Marshall and Parker 1982, Campana 1983, Mosegaard et al. 1988).

There is no easily observable factor that is responsible for the complexity of 0+ whitefish otoliths. Their 1+ rings are fairly simple. The 0+ ring in the char is not so complex in structure, but beyond the first ring, however, the structure of F-char otoliths changed in certain years (Lindström and Andersson 1981a) and as the char started to grow better (Material and

methods). Indications of such environmentally induced changes are as follows. Instead of a simple opaque annual ring, one can see a ring consisting of a band of pearl-like components, or a double ring. The otoliths of young F-char have sometimes acquired signs of a structure with opaque, radial needles, typical of older normal char otoliths. These structural peculiarities emphasize that otolith structures are sensible to the environment (Blacker 1974, Love 1980) and that they should be used for species identification with precaution.

Metamorphosis of whitefish

Metamorphosis is not, at least in many cases, a short-term event with simultaneous changes, as might be suggested by the name. O'Connell writes: ". . much of the development . . . . can be characterized as initial differentiation and then continued recruitment of specialized cell arrays" . . . . . "pattern and tempo of development must differ among species". The term 'transformation' has been suggested by Kendall et al. (1984). In this paper juveniles start with stage E, p. 8.

Rate of development should refer to some scale. Age, length and weight are used by different authors to describe the development of fish larvae. Length is used in the present context in accordance with the statement by Ehrlich (1974), concerning the development of herring larvae, that ontogenetic changes are dependent upon larval size rather than age. Luczyński (1987) and Luczyński et al. (1988) elaborates this point further for coregonid juveniles. A close relation between total length and stage was also inherent in the present material (Lindström 1962, Table 3, and 1970, p. 474) and is further examplified in the section about developmental stages, p. 8.

Early signs of metamorphosis in coregonid larvae, as recognized here, are advanced schooling behaviour and a silvery and greenish dress which begin to develop at approx. 15 mm (see Developmental stages, and Lindström 1970). Zilúkas et al. (1983) report an interval of 15–

29 mm for the change in dress in *C. peled*. They probably become easier for predators to detect at this stage (Blaxter 1969). Improved performance, on the other hand, could compensate for the increase in the risk of detection, for Volkova (1976) in Dabrowski (1981) states that the larvae of Omul whitefish *C. autumnalis migratorius* of about this size, 17–19 mm, efficiently escape from predators. This illustrates what metamorphosis is: a series of changes aimed at adapting the young to a new ecology in the course of their ontogeny.

Changes in fin structure form the first point in the present survey of metamorphosis. The differentiation of the fins from the finfold primordia takes some time, and the final external appearance of the caudal fin, which is important for effective propulsion, occurs at the period of transition from larva to juvenile. The length is specified to between 25 and 30 mm in the present material, 15–29 mm in *C. peled* (Zilúkas et. al. 1983) and 25 mm in the *C. lavaretus* studied by Nagieć (1977), although his detailed anatomical survey shows that the number of bone elements increases up to a length of 40 mm. The late changes are probably also of importance for the performance of the tail fin.

The present material shows the swimbladder to gain a small ampulla at 20–30 mm, but the occurrence of gas cannot be ascertained in the preserved material. Judging from the pictures, *C. pollan* and the Lake Leman whitefish, *C. schinzi palea*, have a more advanced swimbladder at this size (Dabrowski 1981, Dabrowski and Kaushik 1985). Gas in the swimbladder is reported at 15–29 mm, in *C. peled* (Zilúkas et al. 1983).

The developement of the alimentary canal in fish larvae is characterized by periodically rapid changes rather than continuous gradation and one of the changes occurs at metamorphosis, when the stomach and pyloric caeca develop (Govoni et al. 1986). The foregut has a very small storage capacity in whitefish larvae and a small lumen until the late D stage, just before the metamorphosis. There may already be some storage capacity in the midgut at stage C (cf. section about development of stages) even though

the contents should pass pass through rapidly (discussed by Govoni et al. 1986). Early whitefish juveniles have both this expansion and a stomach. The occurrence of *Proteocephalus* (Cestoda) larvae in the hindgut of whitefish larvae and juveniles and just behind the pylorus in juveniles may indicate the food storage pattern, and a similar occurrence is reported for laboratory raised *C. pollan* larvae (Dabrowski 1981, cf. Scott 1985, grayling). The *pollan* and Lake Constance *Coregonus* sp. gains a stomach with some storage capacity at about the same stage as in the present material (Dabrowski 1981, Mähr et al. 1983). The development of the enzyme system is possibly a more prolonged process, particularly the development of protein digestion with pepsin in an acid environment (Mähr et al. 1983, Lauf and Hofer 1984, Govoni et al. 1986; a new approach in Segner et al. 1989. Cf. also Dabrowski and Kaushik 1984).

Zilúkas et al. (1983) report better manoeuvring capacity for *C. peled* at 13–15 mm, and better swimming capacity generally follows development in the present material, too, although it cannot be precisely pinned down. Swimming capacity generally increases with body length within certain length intervals, according to Hogman (1970) and Dabrowski and Kaushik (1985). To allow more versatile swimming, a change in the performance of the musculature is needed. The larva soon abandons the undulating swimming of newly hatched individuals, but increasing of the performance at metamorphosis requires changes in the histology and physiology of the muscles and a general enhancement of energy metabolism (Forstner et al. 1983). This and the complicated relation between metabolism and performance reported by Dabrowski (1986) imply a discontinous development at metamorphosis. The change in the alimentary canal is at least in some respects a rapid change and would in those respects fit with a sudden improvement in performance. Forstner et al. (1983) also report a change in diet, a widening of the food spectrum, at metamorphosis. The changes in diet observed in the present material, and the development in the capacity to catch chironomid pupae and imagines, are not sudden events (Lindström

1988). Improvements in behaviour (Marcotte and Browman 1986) do perhaps not keep pace with other processes during metamorphosis.

Metamorphosis is in some respects a protracted process, with effects extending over the autumn, and this period of turbulence would be a very likely time for ecological differentiation between species e.g. by differences in timing of the processes involved and differences in general performance. Diet and growth in the first year of whitefish juveniles and in the second year of whitefish and char will be discussed. The transformation to silvery char occurs in normal char at higher ages than those referred to in the conclusions.

Cohabitation of juveniles within each genus

Cohabitation of juveniles may be faciliated if, e.g.:

1) Different species use different habitats.
2) There is a difference in the acquisition of food.
3) There is a difference in allocating available resources on growth, migration, maturation etc.

The actual solutions to cohabitation problems for two or more species within the same genus might be inferred from their morphological development.

Winter habitat and dorsal fin structure

Four whitefish species in three lakes are involved. The temperature at the spawning sites after the spawning period is close to zero degrees centigrade. (Other habitat characteristics will be discussed in Conclusions). In St. Rösjön, a shallow, high mountain lake, the two char species show very few tendencies towards habitat differentiation. These two species were recently transferred to the similar lakes N. Särnamannasjön and St. Harrsjön. The F-char spawns one month ahead of the normal char in Lake St. Rösjön, which means that the temperature is higher at the spawning sites during the first month, but this is mainly before the deci-

Table 11. Most frequent sizes of *Bosmina* in stomachs of *Coregonus lavaretus* and mean sizes of *Bosmina* in plankton samples from the same lakes. Plankton formed only a small fraction of the stomach contents of the "adults" (the sample included old juveniles and adults). Plankton size data in ocular units (30 o.u. = 1 mm), mesh size in the plankton sampler = 0.070 mm = 2.1 ocular units.

Lake	Date	Most frequent sizes of Bosmina				Mean size in plankton samples	Standard error
		in early juveniles	in 0+ juv. in August	in 1+ juv. in August	in adults in August		
Sällsjön	840627	10-15					
"	830818		15-20				
"	860807			10-15	10-15		
Landösjön	830817		15-20	15-20			
Sällsjön	730827					13.2	0.17
"	730606/07					14.0	0.72
Landösjön	860808					15.3	0.73

sive period. The variation within the genera in numbers of rays in the dorsal fin is very slight in the present whitefish and char material. Although the species may have different temperature reactions, there is no positive indication of any differential influence of temperature during the decisive period.

Present diet, fish species, total length and gill structure

A difference in diet between species might be expected in the juvenile whitefish in August of the first year when the number of gillrakers approaches the final one. This could only be confirmed in a case when both a species difference and a difference in total length were involved (Lindström 1988).

As the addition of new rakers slows down in the first summer, the sizes of the gill arch and the rakers continue to increase with total fish length. The consequences are that the gill structures of the juveniles of different whitefish species are more similar in absolute measures than are those of the juveniles and adults of one species. This is in accordance with the small differences in juvenile diet between species during the first year. Table 11 shows one case in which the sizes of the prey object *Bosmina* in the stomachs of the juveniles and adults do not correspond to the increase in body size. The general size is similar to or higher than the mean size of *Bosmina* in plankton samples. The plankton samples from Lake Sällsjön show a size distribu-

tion typical of *Bosmina longispina* in the whole district, with a peak just over 10 o.u. and another just below 20 o.u. (1 mm = 30 o.u.). The ratio between plankton and insects in the diet, however, differed considerably between juveniles and adults. For a model of the effect of gillraker in food choice see Kliewer (1970), Seghers (1975), Hartmann (1986).

In five samples of two-summer-old juveniles of two whitefish species (*C. acronius* and *C. nilssoni*) from three of the lakes in August, *Bosmina* was the dominant food, followed by chironomid larvae and pupae and *Polyphemus*. The fish were caught in the afternoon, when 0+ juveniles also prefer *Bosmina*. Two samples of two-summer-old *C. lavaretus* from Lake Sällsjön in August were different. Mean total length in both these samples was 15.0, while in the five samples from the other lakes mean lengths were 12.7, 11.7, 10.9, 10.4, and 9.0 centimetres. *Bosmina* was also the most important food in Lake Sällsjön (12 1/2 specimens with mainly *Bosmina* and 6 1/2 specimens with mainly insects, by volume), but the corpus part of the stomach contained mainly insects (12 out of 14 specimens). As the Sällsjö samples were caught around sunset, the switch to insects is expected from the model of the diel feeding pattern (Lindström 1988) and not an effect of the larger size of the Sällsjö juveniles. No difference was found in the diets of different whitefish species in these samples of two-summer-old juveniles, but the results are not quite conclusive as samples were taken only during one season.

One whitefish population with a high number of gillrakers also had long rakers (*C. nilssoni*, "planktonsik" from Lake Storjuktan). The food of the 1+ young seemed to be rich in lipids, and the lymphoid ducts on the belly were very obvious. Some males were already maturing in this population, cf. p. 24.

The difference in gillraker number between the two species of char is very small but possibly real, p. 24. The small raker size and slow increase in their size with total body length suggest that true plankton is of minor importance, as shown by a study of the diet of the char in the Fulufjäll lakes (Hanson 1976, Lindström et al. 1982a). The diets of normal char and F-char were never very different as regard the major prey groups. The smaller the fish, the smaller the food items, but even the 1+ normal char accepted mainly insect larvae and *Eurycercus*. Maturing 1+ F-char from Lake N. Särnamannasjön, the smallest fish in the whole size range studied (referred to in Tables 2 and 4 in the present paper), had mainly consumed *Eurycercus* (2 juveniles consumed mainly true plankton food, 7 consumed *Eurycercus* and 3 consumed insect food in terms of volume, mean volume percentage of *Eurycercus* = 74).

A high similarity in gill structure between juveniles of the two species at the age of one summer may be inferred from the material (Fig. 4, Table 4).

Diet, time series, stability in gill structure, plasticity in food choice

It has sometimes been assumed that the number of gillrakers may change with the composition of the prey fauna and the diet. If so, there would have been excellent opportunities for such events in the present lakes. Both the whitefish and char lakes are subject to certain important environmental changes. Some of the whitefish lakes are now used as lake reservoirs, with corresponding changes in their prey fauna, and the char lakes in the Fulufjäll region have become acidified to such an extent that some fish populations are extinct. The Fulufjäll lakes studied here have been limed.

Apart from "noise", no changes have been documented in the number of gillrakers in the different species in Sweden other than those due to introgression (Svärdson 1979, Hammar 1988). The whitefish gillraker numbers presented by Svärdson (1957) may be compared with those found in some of the same lakes later (Lindström 1974, Fig. 2 in the present paper). The char gillraker numbers reported in 1968 have not changed significantly up to the present (see Gillrakers). There is thus considerable stability in the number of gillrakers in spite of the changing environment.

One change in the environment is effected by the fish themselves. The populations of "sandsik", *C. acronius*, and "älvsik", *C. lavaretus*, studied here seem to do well without daphnids in their diet (Lindström 1988), as also do the char in the Fulufjäll lakes. This does not exclude the possibility that a char or whitefish species, when first populating a lake, may reduce certain prey populations and thus "set the stage" for future cohabitation with other species. Whitefish reduce the abundance and/or species composition of Cladocera when populating a char-trout lake (Lötmarker 1964, Nilsson and Pejler 1973), and char affect the species composition (Nilsson and Pejler 1973). There are, of course, other factors controlling Cladocera populations. Daphnids are absent or sparse in the Fulufjäll lakes (acid water) and in the char lakes of the Långan River system above lakes Rönnösjön and Landösjön (Lundquist 1936, Lötmarker 1964, Quennerstedt 1955), which indicates that the water quality in this river system is unusual. Daphnids are absent in the diet of whitefish young in lakes Rönnösjön and Landösjön.

In conclusion, the quoted papers on the diet of whitefish and char contribute to the long series of studies on the ecological plasticity of these two genera. This plasticity may have been important for the survival of the species in an environment that has changed radically in some respects. The plasticity does not involve differentiation in the feeding habits of the 0+ whitefish juveniles, and in 1+ char, it is only observed in connection with a size difference between groups.

Variability in growth

Many morphometric characters are correlated with growth and so also is food choice in whitefish and char juveniles and the occurrence of metamorphosis in whitefish.

The break-up of the ice, or rather events coupled with this, triggers the hatching of the whitefish larvae. Their further development for some time to come will be dependent on whether the starting point was early or late. Lake Ö. Björkvattnet and Lake Sällsjön are examples of an "early" and a "late" lake, and this may explain the growth differences that occur up to midsummer in ordinary years. The time of occurrence of the first juveniles also varies with early summer temperatures, and may occur at variable dates in different lakes and years, but the juveniles are of similar total length (Lindström 1988). This is in accordance with the concept that development of the larvae is related to size rather than age (p. 25).

Variation in the total length reached towards the end of the first year is not great in different whitefish populations, although a ranking of lakes, established at the beginning of the summer, is broadly retained in terms of first-year length (Table 9). Considering the very important growth capacity of whitefish young shown in some experiments at rearing stations, and the total length reached in warmer climates (*C. autumnalis*, Wilson 1984, "lavarello" and "bondella", Berg 1970), it is interesting that the present variation in August was so slight. Some factors controlling growth in late summer replace or concur with the factors controlling growth in spring and early summer. These new factors are probably involved in the strategies of the different populations for distributing the available resources between growth, migration and other energy consuming activities.

The significance of a partial release from the conditions of the spring environment at hatching time should be that the importance of egg size is relaxed during the summer, a situation that has been discussed by Thorpe et al. (1984), Ware (1975) and others. Strong emphasis is placed in some other papers on an assumed connection between size at hatching and first year length, resulting in the highest qualities being attributed to the largest one-year-old juveniles ("once a size advantage, always in the winning class"), but fitness during the first year no doubt depends on many other properties. Optimal growth up to the end of the first year is a more relevant concept than a maximal growth (Ware 1975, 1980, 1982, cf. also Miller et al. 1988).

It is in the second year that the growth curves of different whitefish populations diverge.

The young of the char also reach very different first-year lengths in different districts (Balon 1980a, b, Sandlund et al. 1988). There is no information on the growth in length of char during the first year in the present material, but assuming a linear regression between otolith size and total length, a cursory back-calculation using otoliths of adult fish was performed. It showed little difference between the first-year lengths of F-char and normal char in the Fulufjäll lakes. This conclusion is, however, contradicted by the high variation in the length of 1 + F-char caught by fine-meshed gillnets (Fig. 7).

The growth of the two species diverge markedly later as is confirmed by the growth curves (Lindström and Andersson 1981 b).

Maturation

One explanation for reduced growth in some whitefish and char species in the second year is that preparation for spawning is added to their energy-consuming activities. Early maturation is the reproductive strategy of *C. nilssoni* in Lake Storjuktan (cf. Results and Hammar 1988) and the F-char in Lake St. Rösjön. This may be a response to high adult mortality, as suggested by one of the four models described by Stearns and Crandall (1984). In this case, adult mortality would be high due to predation by trout in Lake Storjuktan and normal char in Lake St. Rösjön.

The otolith size-fish length regression differs between F-char and normal char in the Fulufjäll lakes and between the "planktonsik" *C. nilssoni* from Lake Storjuktan and all other studied whitefish populations. Experiments have shown that temperature and metabolism influence the

size of the daily rings in the char (Mosegaard et al. 1988). It is perhaps only a coincidence that the early maturing populations have a deviating otolith size-fish length regression, but it may also indicate that the otolith structure is affected by the metabolic activity caused by maturation.

Conclusions

Differences in the growth and reproductive strategy the second and following years of life are likely to faciliate cohabitation between species within the two genera, as are characters correlated with length e.g. the diet of char (here only studied in samples from one season).

Changes in growth and reproductive strategy in whitefish occur after an initial year during which there were pronounced similarities between species in growth and in certain morphological and other characters correlated with total length, in gill structure and diet, and in dorsal fin structure.

The material from juvenile char provides much less conclusive evidence, e.g. because the identification of juveniles as to species is tentative in some cases and because 0+ char have not been obtained. There are almost no differences between species in the meristic characters studied. Changes in growth have occurred lately (Lindström and Andersson 1984) and the variation in the total length of 1+ juveniles seems important at present (Fig. 7). A greater latitude for differentiation between char species in such characters that are correlated with total length can be envisaged already in 0+ juveniles as the variation in growth is more important in char.

The juvenile whitefish seem to pass through a period of high similarity in morphological and ecological respects. Such a period of high similarity is less obvious in char but the life history, e.g. the occurrence of metamorphosis, also differs markedly between species. A similarity does not necessarily indicate a superabundance of food, by analogy with situations in which adults of different species share the same diet. It may e.g. be a case in which a population benefits from using the same habitat as the dominating

population of another species, as described by Frank and Legget (1983). More information on the distribution of different species on different habitats is lacking for a final evaluation. Any similarity in diet within a genus concerns only those specimens of different species that occupy the same lake strata (which is defined by the fishing gear in use), and the partial divergence in distribution between different habitats is still far from sufficiently well understood.

Addendum: application to routine population analysis

The present work highlights some of the problems one encounters when population surveys include studies of young fish. The technique described here provides a correct and reasonably rapid procedure for investigating the meristic and morphometric characters. The difficulties entailed in reading the otoliths of char, as reported on p. 17, makes the reading of daily rings highly desirable in order to distinguish safely between two and three-summer-old individuals. As a minor proportion of the char population in Lake St. Rösjön now forms either an immature slowly growing fraction of normal char or an F-char population that has postponed maturation to a higher age, the separation of species by field characters is rendered difficult. Protein analysis or other relevant technique is a necessary complement.

Acknowledgments

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Effects of Hatchery Environment on Three Polymorphic Loci in Arctic Char (*Salvelinus alpinus* Species Complex)

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Abstract

Three polymorphic loci in Arctic char (*Est-2** and the duplicated *MDH-4,5**) are used routinely as genetic tags in Sweden. Studies on possible effects of hatchery environment on the three loci included temporal stability, allele frequency dependency on size of fish, relation between effective population size and allele frequencies, mortality conditions in hatchery and Hardy-Weinberg allele frequency equilibrium. The tests performed seem to indicate that only a small effective population may cause deviations between allele frequencies found in natural populations and those of the same stocks kept in hatcheries. Implications of these results to management of hatchery populations of Arctic char are discussed.

Introduction

Genetic tags are frequently used to characterize fish populations, both in hatcheries and in natural environments (e.g. Philipp et al. 1981, Taniguchi et al. 1983, Murphy et al. 1983, Koljonen 1986, Taggart and Ferguson 1986). Indiscriminate use of any polymorphic locus may, however, lead to erroneous conclusions. This is usually attributed to the use of too few parental fish when founding a brood stock (e.g. Ryman and Ståhl 1980, Taniguchi et al. 1983, Nyman 1986, 1988, Ring and Hanell 1987). Two major types of deviations may be found, viz "distorted" allele frequencies and even loss of rare alleles because of the low number of parents on the one hand, and, as a consequence, significant differences between field and hatchery data, and even between hatcheries, on the other hand. Another source of possible importance about which we today know very little is the role of selection for the artificial hatchery environment that may occur. Unless we know that the gene markers we use to track specific populations are not affected by the atypical environment, and unless we know how many parents of each sex are employed to build up a hatchery population, there will always be a risk that we are misinterpreting data.

Another possible source of misinterpretation is to affix too much attention to electrophoretic data alone. Lack of genic variation as expressed by e.g. low heterozygosity is often interpreted as a sign of inbreeding or, when applied to comparisons of populations or species, as close relatedness. In general, large animals have the least protein variation whereas small invertebrates has the most (Nevo 1978, Wayne et al. 1986). Thus, the remarkable lack of protein polymorphism and hence electrophoretic similarity between and within populations and subspecies of moose (Wilhelmson et al. 1978) is unlikely the result of population bottlenecks but rather implies that the distinguishing genetic differences either are manifest at other loci than those ordinarily polymorphic in other species, or that ecological specialization has led to genetic uniformity. Such explanations seem to fit the ecologically very complex, but from an electrophoretic standpoint uniform chars of the northern hemisphere (*Salvelinus alpinus* species complex). Several surveys of a large number of loci have shown only three to have any widespread polymorphisms (Ferguson 1981, Kornfield et al. 1981, Andersson et al. 1983, Hindar et al. 1986, Hammar et al. 1989). These are the *EST-2** locus (Nyman 1965) and the duplicated *MDH-4,5** loci (Andersson et al. 1983). Other polymorphisms

occur, but generally at low frequencies or in populations outside Sweden.

This means that so far the *EST-2** and the *MDH-4,5** loci are the most important for use as genetic tags in Sweden. This situation calls for more detailed knowledge of how the artificial hatchery environment affects gene frequencies. What deviations from values evaluated in the natural spawning stock will occur as a result of artificial spawning, stripping procedure, use of limited number of parents, and adaptation to the hatchery environment with above-normal survival of fry and older fish, standardized food, temperature and population density conditions? What can be learned from the results of controlled tests of the mechanisms of these polymorphic loci that may have bearing on conservation issues?

These are the issues addressed in this paper, where a number of char stocks that have been bred and followed under controlled conditions in hatcheries for several years and even generations are compared with samples of the wild ancestral populations.

Material and methods

A total of 869 char were sampled. Some data on the stocks, including analysis of the *EST-2** locus, is given in Table 1. All experiments were conducted at the Kälarne Experimental Station (operated by the Swedish National Board of Fisheries), province of Jämtland, in central Sweden.

Electrophoretic analyses were performed using horizontal starch gels and visualization of zymograms were according to Nyman (1965) for the *EST-2** locus and according to Andersson et al. (1983) for the *MDH-4,5** loci.

Table 1. Some data on the stocks used in the tests, with particular reference to the *EST-2** locus.

| Population/year class | N | f(F) | *EST-2** genotypes | | | χ^2 | Hatchery generation | Number of parents ($\sim N_e$) | |
			FF 100/100	FS 100/90	SS 90/90			♀♀	♂♂
Hornavan −83 (HO)	45	0.378	Obs 3	28	14	4.71*	F 3	?	?
			Exp 6.422	21.156	17.422				
Hornavan −84 (HO)	48	0.417	Obs 11	18	19	2.51	F 2	?	?
			Exp 8.333	23.333	16.333				
Hornavan −85 (HO)	100	0.590	Obs 29	60	11	5.77*	F 2	?	?
			Exp 34.380	48.380	16.810				
Rensjön −83 (RE)	136	0.842	Obs 94	41	1	2.39	F 1	6	5
			Exp 96.399	36.202	3.399				
Rensjön −84 (RE)	45	0.844	Obs 31	14	0	1.53	F 1	95	95
			Exp 32.089	11.822	1.089				
Rensjön −85 (RE)	180	0.822	Obs 122	52	6	0.03	F 1	90	90
			Exp 121.689	52.622	5.689				
Rensjön −86 (RE)	60	0.817	Obs 39	20	1	0.77	F 1	75	75
			Exp 40.017	17.967	2.017				
Ottsjön −83 (OT)	45	0.678	Obs 20	21	4	0.21	F 1	6	5
			Exp 20.672	19.656	4.672				
Ottsjön −84 (OT)	47	0.628	Obs 19	21	7	0.09	F 1	20	15
			Exp 18.156	21.968	6.516				
Torrön −83 (TO)	75	0.113	Obs 0	17	58	1.23	F 1	6	5
			Exp 0.963	15.073	58.963				
Torrön −86	88	0.176	Obs 2	27	59	0.29	F 1	52	26
			Exp 2.730	25.540	59.730				
Total	869								

Table 2. Population data on the stocks used in the tests at the *MDH-4,5** loci.

Population/year class	N		MDH-4,5* phenotypes					χ^2	Estimated number of gametes Estimated gamete frequencies			f(S) Estimated allele freq.
			S_4	S_3F	S_2F_2	SF_3	F_4		SS	SF	FF	(number of var.)
Hornavan −84 (HO)	48	Obs	11	26	10	1	0	0.81	48.8	45.4	1.8	0.745 (2)
		Exp	12.389	23.094	11.662	0.839	0.016		0.508	0.474	0.018	
Hornavan −85 (HO)	100	Obs	13	44	27	14	2	2.86	78.5	95.0	26.5	0.630 (2)
		Exp	15.422	37.274	32.946	12.596	1.761		0.393	0.475	0.133	
Rensjön −83 (RE)	51	Obs	47	4	0	0	0	0.08	98.0	4.0	0.0	0.961 (1)
		Exp	47.078	3.843	0.078	0.0	0.0		0.961	0.039	0.0	
Rensjön −84 (RE)	45	Obs	40	5	0	0	0	0.16	85.0	5.0	0.0	0.944 (1)
		Exp	40.139	4.722	0.139	0.0	0.0		0.944	0.056	0.0	
Rensjön −85 (RE)	180	Obs	169	11	0	0	0	0.18	349.0	11.0	0.0	0.969 (1)
		Exp	169.168	10.664	0.168	0.0	0.0		0.969	0.031	0.0	
Rensjön −86 (RE)	24	Obs	24	0	0	0	0	−	48.0	0.0	0.0	1.00 (1)
		Exp	24.0	0.0	0.0	0.0	0.0		1.00	0.0	0.0	
Ottsjön −83 (OT)	45	Obs	45	0	0	0	0	−	90.0	0.0	0.0	1.00 −
		Exp	45.0	0.0	0.0	0.0	0.0		1.00	0.0	0.0	
Ottsjön −84 (OT)	47	Obs	47	0	0	0	0	−	94.0	0.0	0.0	1.00 −
		Exp	47.0	0.0	0.0	0.0	0.0		1.00	0.0	0.0	
Torrön −83 (TO)	40	Obs	40	0	0	0	0	−	80.0	0.0	0.0	1.00 (1)
		Exp	40.0	0.0	0.0	0.0	0.0		1.00	0.0	0.0	
Torrön −86 (TO)	84	Obs	79	5	0	0	0	0.08	163.0	5.0	0.0	0.970 (1)
		Exp	79.074	4.851	0.074	0.0	0.0		0.970	0.030	0.0	
Total	664											

Since the true allele frequencies for the duplicated *MDH-4,5** isoloci are not calculable, the frequencies of the MDH gametes (SS, SF, FF) and allele frequencies were estimated from the observed phenotypic distributions with a maximum likelihood method (Imhof et al. 1980). When all five possible MDH phenotypes were found in a population, both loci were assumed to be equally variable. When only two of the possible MDH phenotypes were found in a population, all variation was assumed to be restricted to one locus, the other being invariable. Data is given in Table 2. Nomenclature of the three loci studied follows the guidelines proposed by Shaklee et al. (1989).

level. The mode of segregation of alleles was verified by controlled crosses, which also disclosed whether there existed any dependency on the hatchery environment. Atypical high mortality may sometimes occur in hatcheries. In such cases the fish may be subjected to severe selection for the hatchery environment. Will such selection influence the resulting allele frequencies? A very pertinent question when establishing brood stocks in hatcheries relates to the number of parents used. Thus, the effective population size was compared to the outcome with respect to allele frequencies and so were tests of possible hatchery-induced deviations from Hardy-Weinberg equilibria expected under panmictic situations in natural populations. The results below are presented in that order.

Results

The results are centered around a number of tests. The first deals with the temporal stability of the loci studied in natural and hatchery populations. Tests were also conducted to find out if there is any correlation between size/age of the fish and allele frequencies at the population

Temporal stability of allele frequencies

The temporal stability of the loci studied (Nyman 1972, 1984) was primarily evaluated on natural populations, frequently with a background in a hatchery environment. There
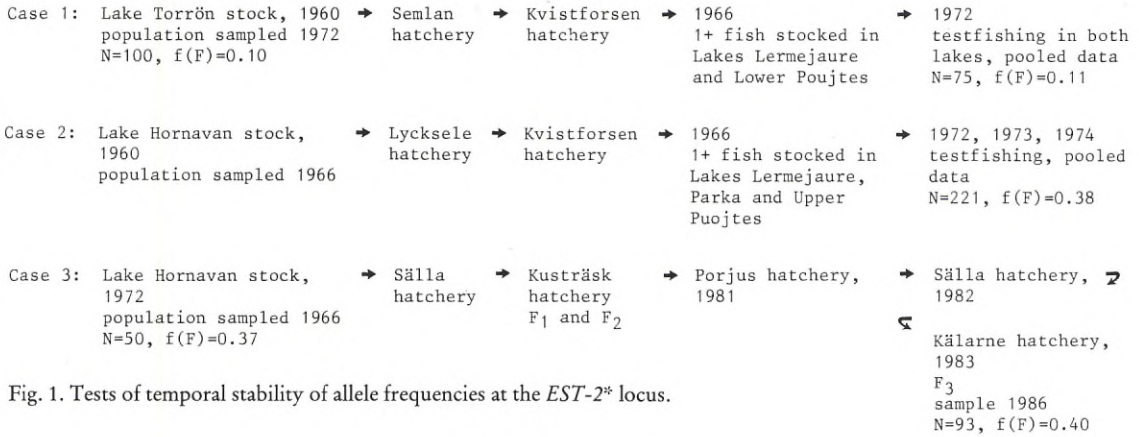
Case 1: Lake Torrön stock, 1960 → Semlan → Kvistforsen → 1966 → 1972
population sampled 1972   hatchery hatchery   1+ fish stocked in   testfishing in both
N=100, f(F)=0.10   Lakes Lermejaure   lakes, pooled data
                                                       and Lower Poujtes   N=75, f(F)=0.11

Case 2: Lake Hornavan stock, → Lycksele → Kvistforsen → 1966 → 1972, 1973, 1974
1960   hatchery   hatchery   1+ fish stocked in   testfishing, pooled
population sampled 1966   Lakes Lermejaure,   data
                                                          Parka and Upper   N=221, f(F)=0.38
                                                          Puojtes

Case 3: Lake Hornavan stock, → Sälla → Kusträsk → Porjus hatchery, → Sälla hatchery, ↗
1972   hatchery hatchery   1981   1982
population sampled 1966   F₁ and F₂   ↘
N=50, f(F)=0.37   Kälarne hatchery,
                                                                          1983
                                                                          F₃
                                                                          sample 1986
                                                                          N=93, f(F)=0.40

Fig. 1. Tests of temporal stability of allele frequencies at the *EST-2** locus.

was thus indirect evidence that no changes in gene frequencies takes place at one of the loci (*EST-2**) when a population passes through an unnatural environment.

Three such cases of mixed natural environment/hatchery environment histories are presented above (Fig. 1).

Case 1 spans a twelve-year period, where a natural population is sampled, passes through two hatcheries and is subsequently released as 1+ fish in formerly fishless lakes in a natural environment vastly different from the lake where the fish originated.

Case 2 spans fourteen years after the natural population was sampled. After an initial hatchery phase the original batch of fishes was transferred to another hatchery and then released into a natural environment where it was sampled in three consecutive years.

Case 3 also spans fourteen years after spawning the natural population. It was hatched in one hatchery, some of the progeny were transferred to another hatchery where a second generation was created. Some progeny from this were brought back to the original hatchery where it was spawned again and a third generation was created. Eggs from that spawn were transferred to the Kälarne Experimental Station in 1983, where it hatched and has since then been reared.

Fig. 2 shows the effects on the *EST-2** locus of hatching and rearing several samples of spawn from three wild populations of char. Samples were taken at different times during rearing, and all samples representing the same year class of each population were pooled in the analyses. One population of each char taxon as proposed by Nyman et al. (1981) was sampled.
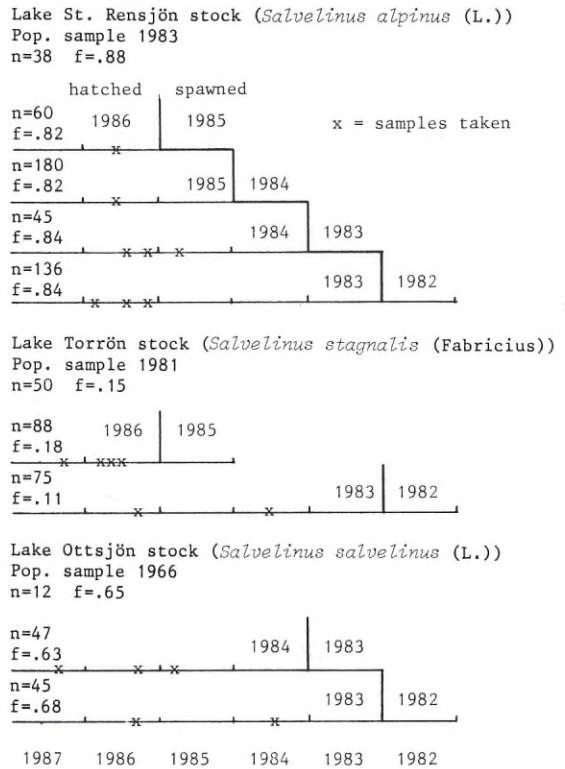

Fig. 2. Tests of temporal allele frequency stability at the *EST-2** locus under prolonged hatchery rearing.

Table 3. Tests of allele frequency dependency on size of fish at the *EST-2** and *MDH-4,5** loci.

Stock	*EST-2** FF	FS	SS	N	*MDH-4,5** S$_4$	S$_3$F	S$_2$F$_2$	SF$_3$	F$_4$	N
RE −85 small	33 f(F)=0.820	16	1	50	45 f(S)=0.950	5	0	0	0	50
RE −85 big	34 f(F)=0.830	15	1	50	47 f(S)=0.970	3	0	0	0	50
Test of allele frequency differences	χ^2=0.03				χ^2=0.52					
HO −85 small	15 f(F)=0.620	32	3	50	8 f(S)=0.635	20	14	7	1	50
HO −85 big	14 f(F)=0.560	28	8	50	5 f(S)=0.625	24	13	7	1	50
Test of allele frequency differences	χ^2=0.74				χ^2=0.02					

Table 2 shows the estimated gamete and allele frequencies at the *MDH-4,5** loci in four spawning samples which were all sampled in 1987.

Conclusions: The basic allele frequencies at the *EST-2** locus were not significantly altered despite several generations of alternating natural and artificial reproduction and environments. The *EST-2** and *MDH-4,5** loci showed no significant deviation from expected allele frequencies when compared with the natural spawning stock.

Test of allele frequency dependency on size of fish

The progenies of two stocks that were spawned in 1984 were sampled in early 1987, thus after two years of rearing. One hundred fish were taken from each of the batches and divided subjectively according to length in two classes each – small and large. A conventional contingency test for allele frequency differences was applied to each pair of classes (Table 3).

Conclusions: No significant allele frequency differences were recorded at the *EST-2** and *MDH-4.5** loci, i.e. there was no difference between small and large fish of the same stock.

Test of allele segregation and possible dependency of hatchery environment

Spawning pairs of three stocks (all three taxa) were typed electrophoretically for *EST-2** and *MDH-4.5**. Their progenies were hatched and sampled at age 1+ in 1984. All results are given in Table 4.

Conclusions: No significant differences between observed and expected values were recorded.

Atypical high mortality in hatchery

The fish mortality normally occuring in a hatchery is much lower than in nature. There is thus a greater likelihood that gene combinations that may be selected against in natural conditions may survive in the hatchery. The opposite situation may, however, occur, e.g. after a disease outbreak. In such instances the mortality may approximate that of natural conditions but of course in a vastly different environment. Table 5 displays the allele frequencies at the *EST-2** locus in three stocks when the hatchery-reared fish are 1+ old and with cumulative mortalities around 90 %.

Conclusions: No significant allele frequency differences at the *EST-2** locus were recorded.

Table 4. Phenotype/genotype distribution at the *EST-2** and *MDH- 4,5** loci in parents and progenies with controlled mating.

Parents spawning 1982

Stock	Sex	Length mm	Weight g	Phenotypes EST-2*	MDH-4,5*
RE	♀	340	390	FS	S_4
RE	♂	260	198	F	S_4
TO	♀	280	260	S	S_4
TO	♂	290	320	S	S_4
OT	♀	275	238	F	S_4
OT	♂	325	435	FS	S_4

EST-2*
phenotypes
S   FS   F

MDH-4,5*
phenotypes

SS   FS   FF
genotypes

F_4 SF_3 S_2F_2 S_3F S_4
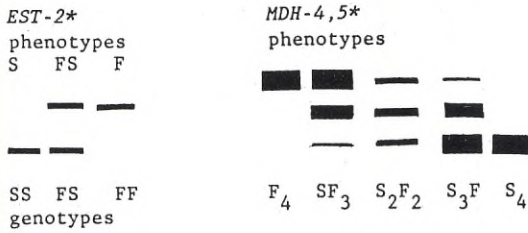
Observed genotype distribution in offspring

Stock	O/E	FF	FS	SS	N	S_4	S_3F	S_2F_2	SF_3	F_4	N
RE	Obs	24	24	0	48	12	0	0	0	0	12
	Exp	24	24	0	48	12	0	0	0	0	12
TO	Obs	0	0	35	35	17	0	0	0	0	17
	Exp	0	0	35	35	17	0	0	0	0	17
OT	Obs	16	14	0	30	30	0	0	0	0	30
	Exp	15	15	0	30	30	0	0	0	0	30

Table header note: *EST-2** genotypes / *MDH-4,5** phenotypes

Expected genotypes in offspring

RE: *EST-2**   *MDH-4,5**

TO:

OT:
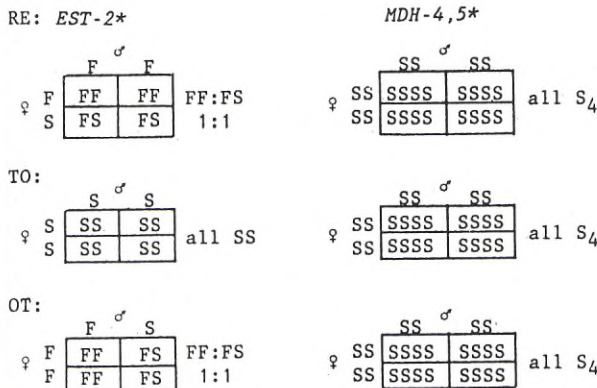
Table 5. Tests of allele frequency dependency on high mortality under hatchery conditions at the *EST-2** locus.

Stock	Total fry mortality June 1984	Initial allele frequency	N	Resulting allele frequency	N	Test of allele frequency differences χ^2
TO -83	90%	0.150	50	0.113	75	0.74
OT -83	96%	0.650	112	0.678	45	0.39
RE -83	82%	0.882	38	0.842	136	0.75

Relation between effective population size and allele frequencies

A low number of parental fish in a founding population will reduce the number of rare alleles. The likelihood that such losses will occur can be calculated. For practical reasons the offspring from three sets of three different populations were compared at the *EST-2** locus (Table 6). The effective population sizes were approximately 2, 10 and from 35 to 200, respectively. Because two of the populations are homozygous at the *MDH-4,5** loci only one could be evaluated (Lake St. Rensjön). The 1982 spawners were 11 (6 + 5), those fish contributing to the 1984 year class were some 200 and so were those of 1985. The resulting S allele frequencies at the *MDH-4,5** loci were .96, .94 and .97 respectively, ie no elimination of the rare F allele in either case (Table 2). Although 150 spawners contributed to the 1986 year class in Lake St. Ren-

sjön (Table 6) the rare variant allele (f(F)=0.03) was not found. This result can easily be explained by the fact that too few fish were sampled (N= 24). With so few fish sampled there is a 23 % risk that you will not be able to find the rare allele according to the equation given by Tave (1986): $P=(1.0-q)^{2N}$, where N is the number of fish examined. Using the same equation you will find that with a desired probability of e.g. P= 0.05 you will need 49 fish in the sample to obtain a 95 % chance of locating the rare allele.

Conclusions: Only at an effective population size of 2 there was any loss of the rare allele or significant difference between the initial frequency of the founding population and the offspring. Effective population sizes over 10 yielded no instance of deviation from expected allele distribution.

Table 6. Tests of deviations from original allele frequencies and loss of the rarer allele in progenies resulting from parental populations with differing N_es.

Stock	Number of parents ♀♀	♂♂	Initial allele frequency	N	Resulting allele frequency	N	Test of allele frequency differences χ^2
TO -83	1	1	0.150	50	0.00	35	11.52***
OT -83	1	1	0.650	112	0.767	30	2.95
RE -84	1	1	0.882	38	0.750	48	4.77*
TO -83	6	5	0.150	50	0.113	75	0.74
OT -83	6	5	0.650	112	0.678	45	0.39
RE -83	6	5	0.882	38	0.842	136	0.75
TO -86	52	26	0.150	50	0.176	88	0.31
OT -84	20	15	0.650	112	0.628	47	0.14
RE -84	95	95	0.882	38	0.844	45	0.50
RE$_2$ -85	90	90	0.882	38	0.822	180	1.62
RE$_3$ -86	75	75	0.882	38	0.817	60	1.48

Hardy-Weinberg allele frequency equilibrium, or not?

Three of the lines kept at Kälarne Experimental Station are derived from parents originating from two hatchery brood stocks. Samples of two of those lines display heterozygote excess, the third homozygote excess. This disequilibrium is thus characterized by high chi-squares, 4.71, 2.51 and 5.77, respectively, with a mean of 4.33. In contrast, eight stocks originating from wild parents but kept in the hatchery for up to three years show significantly better accordance between observed and expected values with a mean chi-square of only .82, the highest value recorded reaching 2.39.

Conclusions: There are indications that stocks originating from brood fish with a hatchery background display deviations from the normal Hardy-Weinberg equilibrium usually found in samples of wild fish or fish that are offspring from wild parents.

Discussion

It is very difficult to estimate the effects of natural selection on genotypes at specific loci. Thus we normally fail to prove if an allelic variation visualized by electrophoresis of polymorphic proteins is the result of natural selection or simply reflects genetic drift at selectively neutral loci (Allendorf and Phelps 1981). It is equally evident that polymorphic loci that are subjected to highly variable selection forces from generation to generation must possess the virtue of selective neutrality in order to be employed as genetic tags in population research. The results obtained by the tests described in this paper have given evidence of selective neutrality at the three loci analysed. Temporal stability of allelic frequencies irrespective of the environment in which the fish had been kept was evident. A novelty was indicated by the apparent genetic disequilibrium of hatchery fish originating from parents also with a hatchery background when compared with the panmixia displayed by fish emanating from wild parents. Deviations from

Hardy-Weinberg equilibrium, both shown as heterozygote excess and homozygote excess, may render a word of caution necessary. A straighforward heterozygote excess could have been construed as "preparedness" for an unnatural environment by heterozygote superiority, but the only case displaying homozygote excess refutes such generalization.

It seems as if the single factor affecting allele frequencies after a fish population has passed through a number of different environments is the initial effective population size. A single bottleneck of more than 10 parents with roughly equal sex ratio did not produce any loss of the rarest alleles and the correlation between observed and expected numbers according to the Hardy–Weinberg criterion was equally good at 11 parents as at roughly 200. If founding populations, irrespective of the number of generations they are to be retained in a hatchery, are initiated with an effective number exceeding 50 there is thus very little risk that the three loci routinely screened as population markers in Arctic char will display deviations from expected allele frequencies. This number is the population size where the reduction in heterozygosity per generation (inbreeding) will reach 1 %.

There is some controversy concerning the harmful effects of population bottlenecks. The vast majority of data indicate that loss of genetic information, as evident by reduction of heterozygosity and the number of rare alleles, will affect the performance of captive populations with regard to fitness, both on a short term basis and with regard to the evolutionary potential of the population (e.g. Falconer 1981). Other recent information (Goodnight 1987, Lewin 1987) points in a somewhat different direction. With quantitative data from houseflies it was shown that crosses with a limited number of parents displayed an increase in variance, not a decrease as statistical models would suggest. The loss of rare alleles at highly variable loci cannot be refuted nor can the reduction in heterozygosity encountered, but the results show that once we leave the welltrodden steps of predictable additive variance analysis behind we reach a level

where mathematical representations of biology simply may go wrong (Lewin 1987). It may well be that nonadditive gene interactions like dominance, overdominance and epistatic variance may actually account for the majority of gene interactions, and they are progressively more complex. It is also possible that part of the increased variance stems from influence of harmful recessive alleles. This in turn will lower the average fitness of the population after the bottleneck, but the increased variance also implies "a greater opportunity for selection to act on new and fitter genetic combinations". The essence of this new information might be that the increased quantitative variance despite the bottleneck reflects a shift in the value and work done by the different alleles.

Both heterozygosity and the number of alleles at various loci are, however, good measures of genetic variation (e.g. Allendorf 1986). In the short run, heterozygosity is only little affected but the number of alleles may be severely reduced. Consider e.g. the extreme case where only one pair of fish is used to found a new population. If we have a locus containing 200 alleles a maximum of 4 will "survive" the initial bottleneck, but the overall heterozygosity will only be reduced to 75 % of the initial value. In the long run, however, allelic diversity might be of more importance for the longterm survival of the population.

Conclusions

1) The polymorhic loci *EST-2** and *MDH-4,5** in Arctic char (*Salvelinus alpinus* species complex) may be employed as genetic tags both in natural and hatchery populations, provided N_e is adequately high. These data will be routinely employed as genetic tags in the National Strain Registry.

2) From a general standpoint it has frequently been suggested that (e.g. Nyman 1988) 50 parents should be employed when founding hatchery populations or other broodstocks of fish, to reduce the risk of deviations from natural stocks in allele frequencies. This number is validated for Arctic char also.

3) It should be emphasized that studies on genetic isolation between populations or closely related species should not be performed on fry or fertilized eggs (e.g. Allendorf and Phelps 1981) because they may be the progeny of a few parents only. Only sexually mature fish or spawners should be sampled for natural population comparisons.

4) Despite the fact that no "hatchery selection" appears to have taken place at the polymorphic loci studied, this does not necessarily imply that the fitness of the population studied has not decreased.

Acknowledgments

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Liming Increases the Catches of Atlantic Salmon on the West Coast of Sweden

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Abstract

The potential smolt production of Atlantic salmon (*Salmo salar*) on the west coast of Sweden was estimated using an empirical production of 0.2 smolts/m² of rearing habitat and year. As a result of field studies more precise estimates were available for several streams and estimated annual production ranged between 0.12–0.40 smolts/m² rearing habitat. In addition to the former estimate, a conservative estimate of 0.1 smolts/m² was used for the whole watercourse area. The total area of the swedish Atlantic salmon rearing habitats was 1.3 km², with a potential smolt production ranging between 124,300–200,700 smolts/year.

Using the criterion that an annual mean alkalinity of less than 75 μeq/l is deleterious to Atlantic salmon, due to low pH and metal fluxes during high flow, it was estimated that nearly 60% of the available rearing habitat was acidified before liming operations started. These areas, which would have lost most salmon production if liming had not been carried out, were estimated to produce approximately 39–46 % of the wild salmon smolts. A simple model of the input of wild and reared smolts and the total catch showed that the liming efforts on the Swedish west coast during the 1980s have led to a considerable increase in the catch of Atlantic salmon. It is suggested that continuous liming until the acidifying emissions of sulphur and nitrogen have been substantially reduced is a prerequisite if the wild Atlantic salmon stock in Sweden is to be maintained and increased.

Introduction

Due to the construction of hydro-electric power dams only a small fraction of the former available river stretches in Sweden produce Atlantic salmon (*Salmo salar*) at present (Hannerz and Degerman 1984). The majority of the streams and rivers available for the Atlantic salmon are either small streams, mainly dominated by brown trout (*Salmo trutta*) habitats, or streams not suitable for salmonids. On the Swedish west coast, stocking of reared salmon smolts in order to compensate for lost production due to the hydro-electric power plants is carried out continuously, and the number of smolts stocked has increased from an average of 67,000 smolt/year in the 1970s to 123,000 in 1987. In 1987, salmon smolts were stocked mainly in the River Lagan (64,500), the River Göta älv (20,600) and in the River Nissan (18,000).

In addition to the reduction of available salmon habitats, the acidification of western Scandinavia has been a threat to the Atlantic salmon since the early 1920s (Huitfeldt-Kaas 1922). According to recent estimates, about one fourth of the area of Sweden is so affected by acidification that the run-off water is harmful to aquatic life (Dickson 1988). The western part of the country is the most threatened region and several studies have shown the negative effects of acidification on salmon production since the 1960s, as have been reported from the Rivers Högvadsån (Edman and Fleischer 1980, Edman et al. 1988), Kungsbackaån (Hasselrot and Alenäs 1988), Suseån and Fylleån (Degerman et al. 1985). The number of young salmon parr in the spawning streams has been severely reduced and in some instances populations have disappeared. Degerman et al. (1986) showed that acidified streams had a low abundance of salmonids whereas

streams with a pH above 6 had slowly increasing salmonid populations, the latter probably due to fishing regulations and improved water quality as sewage treatment plants have been built.

By 1988, liming had been carried out in 5,000 Swedish lakes and in several thousand km of acidified watercourses in order to counteract the negative effects of acid precipitation, at a total cost of 670 million SEK (about 100 million US$) (Nyberg and Thörnelöf 1988). Liming has been conducted in all but four of the rivers inhabited by Atlantic salmon on the west coast. However, in some of the rivers only the smaller tributaries have been seriously affected by acidification. Liming operations in the acidified streams have been proven to reduce the negative effects of the acid rain and resilience has been reported for the salmon populations (Nyberg 1984, Nyberg et al. 1986, Edman et al. 1988).

Due to the improved water quality after liming salmon have spontaneously returned to rivers where only brown trout remained before liming; the Rivers Löftaån, Kungsbackaån, Solbergsån, and Tvååkerkanal. After liming, restocking, and elimination of dams, salmon have also returned to the River Sennan and to a lesser degree the River Enningdalsälven.

In the present paper the potential production of Atlantic salmon in Sweden has been estimated on the basis of available data on spawning habitats, potential salmon smolt production, and water quality and then compared with the catch statistics for salmon from the Swedish west coast.

Material and methods
Water quality demands

Most of the water chemical data was obtained from the County Administrative Boards in the counties of Halland, Älvsborg and Kristianstad, and from monitoring programs after liming (Edman et al. 1988, Andersson and Henriksson 1988, Hasselrot and Alenäs 1988).

ICES (the International Council for the Exploration of the Sea) proposed 150 μeq/l of summer alkalinity as the lowest acceptable criterion for salmon habitats (Anon. 1988). If the alkalinity falls below this value during the summer, the alkalinity may be too low at some times of the year to protect salmon against low pH and metals due to acidification. This summer value was considered to correspond to an average alkalinity over the year of 75 μeq/l (op. cit.).

Available habitat

On the west coast of Sweden there are approximately 120 streams inhabited by anadromous brown trout which flow into the Skagerrak and Kategatt. Self-sustaining populations of Atlantic salmon are found in 34 of these streams, and another 10 streams contain occasional or negligible populations (Fig. 1).

Data on the area of salmon rearing habitats was estimated from electrofishing and habitat field surveys conducted by the National Board of Fisheries in the counties of Halland, Göteborg and Bohuslän, and from the Regional Fisheries Offices in Jönköping and Göteborg. Only habitats which were classified with certainty as rearing habitats during field surveys were included. These areas generally had a water velocity of 0.25–1.5 m/s and the bottom substratum consisted of gravel, stones and boulders (Karlström 1977a). The young-of-the-year (0+) occupy areas with lower water velocity and finer substratum within these ranges (op.cit.).

The density of large salmon parr found when electrofishing in the Swedish west coast rivers was 10–20 times higher compared with rivers in northern Sweden (Karlström 1977b). It was also high when compared with many rivers in southern Norway (Rosseland 1967) and Scotland (Mills 1964). This large difference can be explained by the high food density in southern Swedish rivers (Karlström 1977b). Similar density levels occur for instance in some rivers in south Norway, which are fertilized by agricultural activities (Hesthagen et al. 1986). It has been shown that undisturbed river stretches on the Swedish west coast may have salmonid parr populations above 1.0/m² (Degerman et al. 1985).
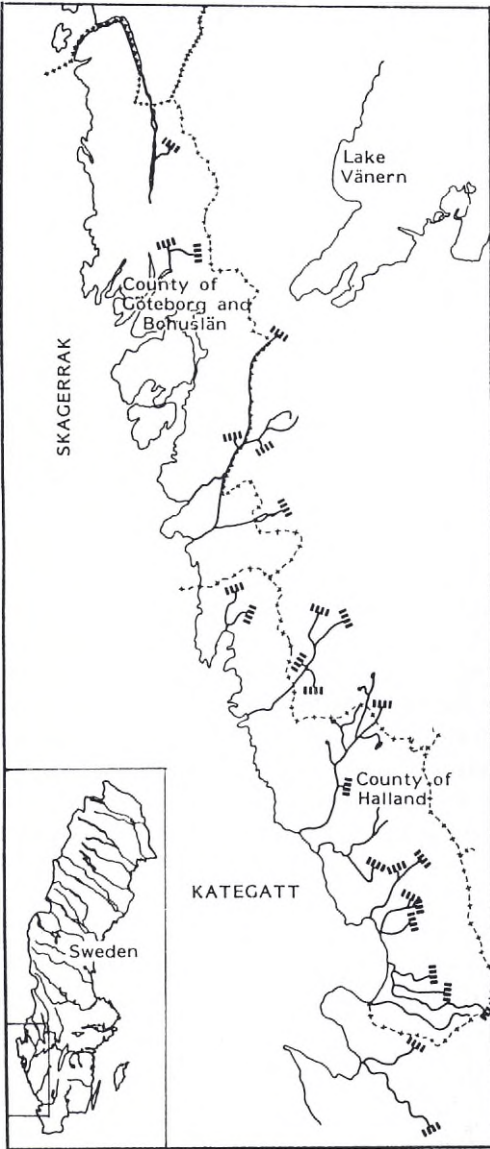
Fig. 1. Location of the available Atlantic salmon habitats on the west coast of Sweden. Crossed bars indicates obstructions for upstream migrating fish.

Salmon smolt production

The number of smolts produced in a river is generally given for the whole watercourse surface area. Rasmussen (1986) and Bohlin et al. (1987) estimated that the average annual production of brown trout smolt in rivers in Denmark and on the Swedish west coast respectively, was between $0.1–0.15/m^2$ for the entire river area. Egglishaw (1970) found the annual salmon smolt production to range between 0.1 and 0.22 smolts/m^2 in the lower reaches of a small Scottish stream. The estimated potential salmon smolt production in the present study was calculated on the basis of the empirical model used by the Swedish fishery authorities (e.g. Karlström 1966), where 0.2 (0.1–0.4) smolts is the estimated annual smolt production per m^2 rearing area on the Swedish west coast. These values for smolt production, given as numbers per m^2 rearing area, will therefore be higher in comparison with values estimated for the smolt production per m^2 whole watercourse surface area.

For several rivers, more precise estimates of the potential salmon smolt production were derived by the local fishery authorities by also taking into account the number of salmon parr found during electrofishing surveys. For the Rivers Örekilsälven and Stensån this estimate resulted in a higher smolt output (0.4 and 0.3 per m^2 rearing habitat, respectively) than would have been estimated by the simple model above. For the Rivers Göta älv, Kungsbackaån, Viskan, Ätran, Nissan, Fylleån and Rönneå the estimated smolt output was lower than 0.2 per m^2, and averaged 0.12 smolts per m^2 rearing habitat.

A comparison between the estimated area of rearing habitat and the total area available for salmon of the River Örekilsälven revealed that the rearing habitat comprised 23 % of the total area. The potential smolt production, given as number per m^2 total stream area, would then be 0.09.

In addition to the above estimates, which were based to a large extent on field surveys, a more conservative estimate of salmon smolt production was calculated by maximizing the highest smolt output to 0.1 smolt/m^2 rearing habitat in all rivers. As an example, this lower estimate would estimate the smolt output for the whole area of the highly productive River Örekilsälven at $0.023/m^2$.

Table 1. Estimated abundance of Brown trout and Atlantic salmon parr at 41 stations in 12 rivers at the west coast of Sweden at water with different summer alkalinity values (after Degerman et al. 1985). Mean and SE given.

Alkalinity class μeq/l	Number of age 0+	Number of age 1+	Total number of salmonid parr
<100	1.5± 0.6	1.6±0.7	3.1± 1.4
100–250	16.7±12	12.8±9.0	29.5± 8
>250	80.0±22	26.1±6.3	106.1±19

Results

Alkalinity criterion

In a study of the occurrence of brown trout and Atlantic salmon in 12 small acidified watercourses on the Swedish west coast Degerman et al. (1985) noted that the abundance of the youngest age groups of salmonids was significantly higher at stations with a summer water alkalinity above 250 μeq/l (Table 1).

Due to large increases in the water flow during the spring flood and sometimes during the autumn rains the alkalinity was reduced and sometimes reached zero. Several studies have shown that Swedish rivers with high alkalinity in summer (between 500 and 1,000 μeq/l) may drop to alkalinity values below 50 during high flow (Nagell and Lettesjö 1976, Bjärnborg 1983, Degerman et al. 1985, Jacks et al. 1986). The variation in the water flow and water quality was to a great extent determined by the size of the drainage area.

The ratio between mean high flow and mean low flow may be used to describe the variation in water flow during a normal year. This ratio was below 10 in large rivers (the Rivers Göta älv, Lagan and Mörrumsån, all with drainage areas larger than 3,000 km²), whereas the ratio was much higher in streams with small drainage areas (<1,000 km²). A linear regression on 34 Swedish rivers using the flow-ratio as dependent variable and the drainage area as independent, revealed that 59 % of the variation of the ratio could be explained by the drainage area size (data from SMHI, the Swedish Meterological and Hydrological Institute, Fig. 2);

$$LOG_{10} \text{ (Flow-ratio)} = 2.51 - 0.41 \times LOG_{10} \text{ (Area)}$$
$$r^2 = 0.59$$
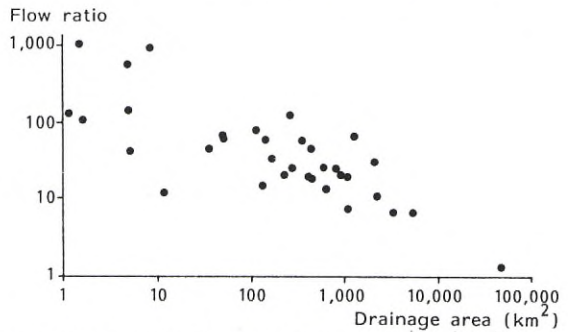
Fig. 2. Flow ratio (the ratio between mean high-flow and mean low-flow) of 34 Swedish rivers in relation to the size of the drainage area (km²) of the river.

The regression found implies that the flow-ratio in small streams with drainage areas of less than 10 km² and without lakes may be as high as 260. With a summer alkalinity below 250 μeq/l no alkalinity would be left during high flow and pH could drop below 5.5. This shows the ICES criterion for summer alkalinity to be somewhat low for Swedish situations. Thus, it was considered appropriate to use the ICES criterion of an annual mean alkalinity of 75 μeq/l in rivers with catchment areas larger than 1,000 km² and an alkalinity of 100 μeq/l for rivers with smaller catchments.

Potential areas of Atlantic salmon rearing habitats

The drainage areas of the Atlantic salmon rivers on the Swedish west coast are generally small. Estimates of available rearing habitats in these systems, water quality before and after liming, and estimates of the potential smolt production are given in Table 2.

About 62 % of the rearing habitats were located in streams with drainage areas of less than 1,000 km². These rivers are considered to be the most productive ones and the potential smolt production in them comprised about 78 % of the total Atlantic salmon smolt production on the Swedish west coast (Table 3).

In total, 15 main rivers comprising at least 20 smaller tributaries, had habitats larger than 0.01 km² available for Atlantic salmon parr. In

Table 2. Area of the rearing habitats and potential smolt production of Atlantic salmon on the west coast of Sweden in relation to mean annual water alkalinity before and after lime treatment and size of drainage areas.

Main river	Tributary	Potential smolt production (numbers)	Area of rearing habitat (ha)	Mean before liming (μeq/l)	alkalinity after liming (μeq/l)	Liming	Drain. area class[1]
R. Enningdals-älven	Kynneälv	(1000)	(4)	< 50	>100	Yes	C
R. Örekils-älven	Main stream & tributaries	30000	9.7	<100	<100	Yes	B
R. Göta älv	Brattorpsån	600	0.3	< 50	>100	Yes	D
	Västerlandaån	160	0.08	< 50	>100	Yes	D
	Grönån	480	0.24	>100	>100	Yes	D
	Forsån	1000	0.6	<100	>100	Yes	D
	Sörån	200	0.1	< 50	>100	Yes	D
	Solbergaån	580	0.29	< 50	<100	Yes	D
	Säveån	10000	6.2	>100	>100	Yes	D
R. Kungs-backaån	Main stream	3000	3.4	<100	>100	Yes	C
R. Rolfsån	Main stream	6200	3.1	<100	>100	Yes	C
R. Viskan	Main stream	4000	4	>100	>100	Yes	B
	Surtan	2200	1.2	< 50	>100	Yes	C
	Lillån	400	0.25	>100	>100	Yes	C
	Hornån	350	0.17	< 50	>100	Yes	D
R. Löftaån	Main stream	1400	0.7	>100	>100	No	C
R. Tvååkersån	Main stream	1200	0.6	>100	>100	No	D
R. Ätran	Main stream	10000	29	>100	>100	Yes	B
	Högvadsån	40000	15.2	< 50	>100	Yes	C
	Tributaries	8600	4.3	< 50	>100	Yes	C
R. Suseån	Main stream	1400	0.7	>100	>100	Yes	C
	Slisseån	4600	2.3	< 50	>100	Yes	D
	Mostorpsån	7200	3.6	< 50	>100	Yes	D
R. Nissan	Main stream	1200	6	>100	>100	Yes	B
	Sennan	9000	4.5	< 50	>100	Yes	D
R. Fylleån	Main stream	19000	12.5	< 75	>100	Yes	C
R. Lagan	Tributaries	11000	5.5	>100	>100	Yes	C
R. Stensån	Main stream & tributaries	25000	8.5	>100	>100	Yes	C
R. Rönneån	Main stream		1	—	>100	Yes	B
	Bäljaneå	1000	1	—	>100	No	C
	Rössjöholmsån		2.4	—	>100	Yes	C
	Kägleån		0.5	—	>100	No	C

[1] B = 10,000–1,000 km², C = 1,000–100 km², D < 100 km².

Table 3. Area of Atlantic salmon habitats (km²) and estimated potential smolt production (numbers) in relation to the river drainage areas.

Drainage area (km²)	Area of habitat (km²)	Potential smolt production (numbers)
10,000–1,000	0.497 (37.6 %)	45,200 (22.5 %)
1,000– 100	0.632 (47.9 %)	120,200 (59.9 %)
<100	0.190 (14.5 %)	35,370 (17.6 %)
TOTAL	1.319	200,770

production in the Norwegian part was estimated to be about 10,000–15,000 smolt/year.

Nearly all rivers inhabited by salmon were limed at least once during the period 1977–88 (Table 2). Most of the liming efforts were upstream of the salmon habitat, but the goal was to improve the water quality downstream in the salmon spawning areas. In several cases lime dosers were used, often in combination with lake liming further upstream. In four of the rivers, the area accessible for salmon production was near the coast and for that reason not influenced by the acidification before liming (the Rivers Stensån, Örekilsälven, Lagan and Rönneån). In six others, (the Rivers Göta älv, Viskan, Ätran, Fylleån, Nissan and Suseån) salmon productive areas were to a greater or lesser extent dependent on lime treatment (Table 4).

the case of one river, the River Enningdalsälven, which is near the Norwegian border, reliable data on salmon habitats was not available. However, the contribution of salmon smolts from the Swedish part of this river was estimated to be small, less than 1,000 smolt/year, whereas the

Using annual mean alkalinity values of 75 and

Table 4. Estimated available area (in km²) of Atlantic salmon rearing habitat on the west coast of Sweden before and after liming. Potential number of smolts produced which should have been lost if liming had not been undertaken are also given. The acidified area is estimated according to annual mean values of alkalinity below 75 μeq/l and 100 μeq/l (see text for explanation).

River	Total available area	Acidified area[1]	Estimated potential no. of smolts[2]		No. of smolts which should be lost without liming[2]	
Enningdalsälv	0.040	0.040	1,000		1,000	
Örekilsälven	0.097	0.0	30,000	(9,700)	0	
Göta älv	0.078	0.008	13,020	(7,800)	1,500	(800)
Kungsbackaån	0.034	0.034	3,000		3,000	
Rolfsån	0.031	0.0	6,200	(3,100)	0	
Viskan	0.056	0.016	6,950	(5,600)	1,990	(1,600)
Löftaån	0.007	0.0	1,400	(700)	0	
Tvååkerssån	0.006	0.0	1,200	(600)	0	
Ätran	0.485	0.195	58,600	(48,500)	45,000	(19,500)
Suseån	0.066	0.059	13,200	(6,600)	11,800	(5,900)
Nissan	0.105	0.045	10,200		9,000	(4,500)
Fylleån	0.125	0.125	19,000	(12,500)	19,000	(12,500)
Lagan	0.055	0.0	11,000	(5,500)	0	
Stensån	0.085	0.0	25,000	(8,500)	0	
Rönneå	0.049	0.0	1,000		0	
Total	1.319	0.773	200,770	(124,300)	92,290	(48,800)

[1] The acidified area is estimated according to annual mean values of alkalinity below 75 μeq/l and 100 μeq/l in rivers with drainage areas above and below 1,000 km², respectively.

[2] If the conservative estimate was lower than the field estimate, it is given within brackets.

Table 5. Potential production and estimated loss of Atlantic salmon due to acidification. Smolt loss was estimated according to Table 4 and text. Two levels of survival from smolt to adult salmon, 15 % and 25 %, were utilized to give the range of salmon lost.

	Potential production	Estimated loss
Smolt number	124,300–200,700	48,800–92,290
Adult salmon (number)	18,645–50,175	7,320–23,072
Adult salmon (tonnes)	61.5–165	24.2–76.1
Total salmon catch (tonnes)	49.2–132	19.3–60.9
Swedish salmon catch (tonnes)	31.5–92.7	13.5–42.6

100 μeq/l as the criterion for water deleterious to Atlantic salmon in rivers with drainage areas above and below 1,000 km², respectively, 0.773 km² (59 %) out of the total area of 1.319 km² of rearing habitat was estimated to be acidified before lime treatment (Table 4). The total potential production of Atlantic salmon smolts on the west coast of Sweden in 1988 was estimated to be within the range 124,300 to 200,770. Applying the annual mean alkalinity criterion, potentially some 48,800–92,290 (39–46 %) smolts would have been harmed or lost due to acidification if liming had not been performed (Table 4).

Data on survival of wild smolts to adult salmon is scarce for the Swedish west coast. In the south of Norway, however, Jensen (1981) esti-mated the survival of wild smolts from the River Imsa to be at least 20 %. Hesthagen and Hansen (1990), when estimating the total loss of salmon due to acidification in Norway used the two levels 15 and 25 % survival from smolt to adult. The same figures were applied in the present study. The average weight of salmon caught at the Swedish west coast is 3.3 kg and exploitation rate of adult fish is almost 90 %, according to Carlin taggings of reared smolt in the River Lagan, a harnessed river. Fishery regulation rules concerning wild stocks are in most cases much stricter and we assumed 80 % exploitation rate of wild stocks. According to Carlin taggings of River Lagan smolts, about 75 % of the total catch is taken in Swedish waters. If the coastal exploitation for wild stocks is lower compared to the River Lagan stock, the Swedish share of the catch may decrease to about 70 %. The resulting production of fish and Swedish catch using these figures ranged between 33.8 and 92.7 tonnes/year, whereas the potential loss due to acidification would have ranged between 13.5 and 42.6 tonnes/year if liming had not been carried out (Table 5).
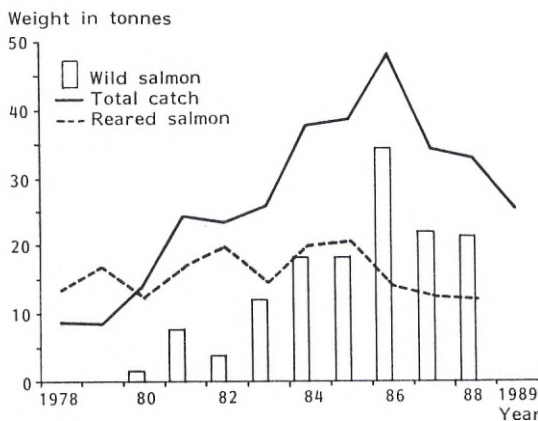
Fig. 3. Swedish catch of Atlantic salmon in the county of Halland during the years 1978–1989. Lines indicates total catch and catch of reared salmon. Bars indicates estimated catch of wild salmon (see text for calculations). The discrepancies in the years 1978 and 1979 are due to fallacies in data.

Comparison between estimated production and catch of Atlantic salmon

As catch statistics for the county of Göteborg and Bohuslän were not available for the end of the 1970s and the beginning of the 1980s, the catch statistics from 1978 to 1989 for the county

of Halland were used to describe the development of the Swedish Atlantic salmon catch (Fig. 3). The catch increased steadily from 1978 which was described as "the worst year ever" (B. Almer, pers. comm.) and the estimated catch of wild salmon was at most 34.2 tonnes in 1986. The total catch of Atlantic salmon at the west coast was about 53 tonnes in 1987 (National Board of Fisheries, B. Almer and I. Lundh, pers. comm.). In 1988 and 1989 the catch decreased, probably partly due to a poisonous algal bloom in the Skagerack in May and June 1988. The algal bloom may have caused some mortality among homing adult salmon and probably caused heavy mortality among emigrating smolts (Skjoldal and Dundas 1989).

The number of hatchery-reared Atlantic salmon released in rivers on the west coast of Sweden increased from an average of 67,000 smolts in the 1970s to 123,000 smolts in 1987. The main production of reared smolts in the county of Halland takes place in the River Lagan. Carlin taggings of salmon smolts in the River Lagan were used to calculate the catch of reared salmon in the county of Halland. In these calculations a 75 % tag reporting rate was assumed and the catch in kg per smolt in Swedish water was multiplied by the number of reared smolts released each year in Halland. When the catch of reared salmon was subtracted from total catch, the remainder consisted primarily of production from wild salmon stocks (Fig. 3). In the late 1970s and early 1980s the subtraction resulted in negative numbers, clearly indicating the roughness of the estimate. However, in later years the situation indicates a positive development of the wild stocks.

Discussion

According to the estimated production of wild Atlantic salmon, the annual Swedish catch should range between 34.5–92.7 tonnes/year (5.1–20.3 tonnes/year in the county of Göteborg and Bohuslän and 29.4–72.4 tonnes/year in the county of Halland). A comparison of these figures with the total Swedish catch in 1987,

which was 53 tonnes, and the highest estimated Swedish catch of wild salmon in the county of Halland, which was 34 tonnes in 1986, supports the view that the calculations used are within plausible ranges.

The catch statistics from the county of Halland clearly illustrate that the wild stocks of salmon have increased considerably during the 1980s. Due to the negative estimates of the wild stock in the early 1980s, which indicate fallacies in the data and also a probable decrease in the exploitation rate of the wild salmon stocks during the 1980s, the catch statistics can not be used to estimate the actual population size of the wild stocks with any certainty.

Besides the uncertainty in the catch statistics, there are several factors which may influence a discrepancy between the estimate of produced salmon smolt and the actual estimate based on catch statistics. Firstly, it must be taken into account that much of the liming has been carried out during the 1980s, and the new habitats available to salmon are not yet fully occupied. It sometimes takes 5–10 years before a normal population abundance can be expected to be resumed (Edman et al. 1988). It may therefore be suggested that the natural production of salmon in the limed rivers will successively contribute more to the actual salmon catch, which may continue to increase during the next decade.

A second reason for a discrepancy between the estimated production and the catch figure may be that the criterion for water alkalinity negatively affecting salmon has been set too low. Perhaps it would be more appropriate to use a higher value, i.e. we may have underestimated the deleterious effects of acidification and there may not be full smolt production. Hultberg (1988), in a review, suggests pH 5.5 and an alkalinity of 10 μeq/l as the lowest, minimum values during the year, acceptable for Atlantic salmon production. However, it is unlikely that there is full production above these values and zero below them. It is possible that a successive decrease in the salmon parr production could be expected as the pH drops. It has been shown that damage to the biota starts as the pH drops below 6 (e.g. Mills and Schindler, 1986). Hence,

a more refined model of the deleterious effects of pH would improve the model. Moreover, it is likely that the presence of labile aluminium is at least as deleterious as low pH. Aluminium content and speciation has not been included in the present evaluation.

As a third reason, other causes than acidification may affect the salmon smolt production. An important factor is the negative influence of water regulation, which sometimes may reduce the available rearing habitats by drainage in some of the regulated streams. Also discharge of industrial waste water may restrict the smolt production in some streams.

It is possible that the estimates of the potential smolt outputs for certain rivers may be too high. Unfortunately, no reliable verification of the figures is available. Edman et al. (1988) using data from a smolt trap in the River Högvadsån, estimated the smolt production of Atlantic salmon to be 10,500, which is considerably lower than the values given here (19,500–40,000), based on field surveys of the spawning area combined with electrofishing. However, the reliability of the smolt trap may be questioned, as it is probable that the majority of the smolts passes the trap during a short period of high water-flow.

Undoubtedly, acidification is one of the major causes of the loss of Atlantic salmon in Scandinavia. The estimated potential of the Swedish catch of wild salmon was shown to be highly dependent on liming. If liming had not been carried out the potential loss of wild salmon would be within 13.5–42.6 tonnes/year. In other words, 39–46 % of the total Swedish catch of wild salmon would be eradicated. These figures may be compared with the disastrous situation in Norway, where the Atlantic salmon was reported to be nearly extinct, due to acidification in 25 rivers in southern Norway (Hesthagen and Hansen, 1990). The same authors estimated the annual loss of Atlantic salmon smolts to be between 623,400 and 1,245,000 individuals.

Distinct increases in salmon populations and catch in specific rivers have been shown; the Rivers Ätran (Edman et al. 1988), Fylleån (Sjöstrand 1988), Kungsbackaån (Hasselrot and Alenäs, 1988) and the small tributaries of the River

Göta älv (Key Höglind, pers. comm.). It may be argued that the figures given for the potential smolt production and catch indicate that there will be a further increase in the actual salmon catch. However, as 60 % of the rearing habitats for Atlantic salmon are located within river stretches which must be limed to avoid low pH, the future salmon catch will to a large degree be dependent on continuous liming until there has been a substantial reduction in the acidifying emissions of sulphur and nitrogen.

Acknowledgment

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Natural Hybridization between Arctic Char (*Salvelinus alpinus*) and Lake Char (*S. namaycush*): Evidence from Northern Labrador

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Abstract

Though suspected to occur, natural hybridization between Arctic char (*Salvelinus alpinus* (L.)) and lake char (*S. namaycush* (Walbaum)) has not as yet been documented. Observations reported here on *Salvelinus* specimens collected in a biological survey of Tasialuk Lake in northern Labrador confirm their occurrence. Two individuals were identified as F_1 hybrids between these species based on electrophoretic analyses of variation at the *AAT-1,2**, *PGM-1**, and *SOD** enzyme loci and on intermediate numbers of pyloric caeca. In support of this morphometry, visual appearance, and growth combined typical characteristics of the two parental species. As the hybrids came from two different year classes, the observations seem unlikely to represent an isolated incident. A number of potential mechanisms which might give rise to such hybridization in areas where the two species coexist are considered, along with the systematic significance and management implications of the findings.

Keywords: Natural hybridization, Arctic char × lake char, *Salvelinus alpinus* × *Salvelinus namaycush*, Systematics, Electrophoresis, Morphology, Meristics, Labrador.

Introduction

The systematic status and phylogenetic relationship of chars, salmonids within the genus *Salvelinus*, is a topic of international research and controversial debate (e.g. Behnke 1972, 1980, 1984, Nyman 1972, Savvaitova 1980, 1983, 1989). The theories involve Linnaean and biological species concepts, erratic lack of intra- as well as intergeneric sexual barriers and the fact that char populations must have evolved unique genetic and ecological characteristics during long term isolation before and during, as well as after recent glacial periods (Hammar 1989).

The Arctic char (*Salvelinus alpinus* (L.)) and the lake char (*S. namaycush* (Walbaum)) are widely distributed in recently glaciated lakes of northern North America. The two species coexist in southern Alaska, along the northern coast of the mainland of the Northwest Territories, in Banks, Victoria, and King William Islands, in northern Quebec, northern Labrador and a region along the St. Lawrence River (Scott and Crossman 1973) (Fig. 1). Various ecological interactions have been recorded, and the two species are reported to interact with respect to competition and predation (Grimås and Nilsson 1962, Nilsson and Svärdson 1962, Filipsson and Svärdson 1976, Fraser 1981, Fraser and Power 1984, 1989, Gönczi and Nilsson 1984, Kircheis 1985).

Although both species are restricted by narrow northern environmental thresholds, they represent two divergent evolutionary paths within the genus *Salvelinus* (Morton and Miller 1954, Savvaitova 1969, 1983, Behnke 1972, 1980). The Arctic char is a "polymorphic" species complex with a well documented ecological plastici-
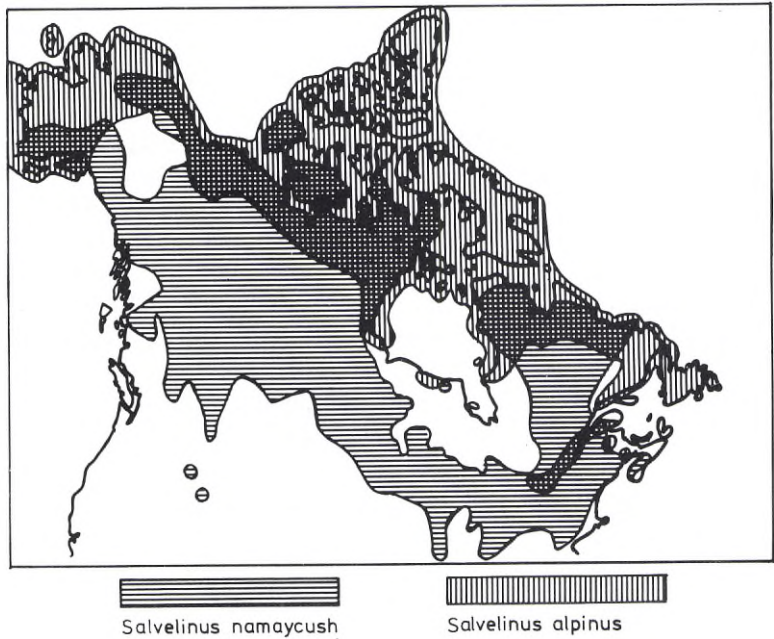
Fig. 1. The geographical distribution of lake char (*Salvelinus namaycush*) and Arctic char (*S. alpinus*) in North America. (Modified from Scott and Crossman 1973.)

Salvelinus namaycush   Salvelinus alpinus

ty. Arctic char populations exist throughout the circumpolar region in a variety of different habitats as anadromous, stream resident and/or true landlocked forms (Johnson 1980, Savvaitova 1989). In allopatry, the landlocked Arctic char demonstrate intraspecific segregation between alternative and/or combined life history strategies, modal size groups, and choice of habitats (e.g. Nilsson 1955, Skreslet 1973, Johnson 1976, 1983, Jonsson and Hindar 1982, Nordeng 1983, Balon 1984, Barbour 1984, Hammar 1984, 1989, Klemetsen et al. 1985, 1989, Sparholt 1985, Riget et al. 1986). In some lakes genetically discrete populations of Arctic char occur sympatrically (e.g. Frost 1951, Nilsson and Filipsson 1971, Nyman 1972, 1984, Klemetsen and Grotnes 1975, 1980, Henricson and Nyman 1976, Nyman et al. 1981, Child 1984, Hammar 1984, Sahonero-Irahola 1985, Hammar and Filipsson 1988, Partington and Mills 1988).

Lake char on the other hand is considered an "evolutionarily stable" species (Behnke 1972), and is endemic to North America (Lindsey 1964). It is typically restricted to fresh water and considered extremely piscivorous (Dryer et al.

1965, Martin and Olver 1980). The lake char is serologically, ontogenetically, and morphologically divergent from other *Salvelinus* species (e.g. Vladykov 1954, Rounsefell 1962, Tsuyuki et al. 1966, Balon 1980, Cavender 1980, Clayton and Ihssen 1980, Johnson 1984). Although originally treated as a member of the genus *Salvelinus*, the lake char was considered part of a separate genus, *Cristivomer*, between 1883 and 1950 (Morton and Miller 1954). Behnke (1980), however, still distinguishes the taxonomic unit, *Cristivomer*, as a valid subgenus, whereas the Arctic char is placed within the subgenus *Salvelinus*.

In comparative genetic analyses by Johnson (1984), both species expressed small numbers of electrophoretic variants, with several alleles demonstrating identical mobility. These studies suggested, that Arctic char and lake char are evolutionary closer than, for example, Arctic char and brook char (*S. fontinalis*). This is in contrast with the more common opinion based on morphology, meristics and ecology. However, more recent electrophoretic analyses, representing a larger number of populations, have revealed the lake char to be highly variable

(Ihssen et al. 1988). This may in fact be valid also for the Arctic char, when anadromous populations are included in such comparisons (J. Hammar and E. Verspoor unpublished data).

The rate and success of interspecific hybridization provides further information about the systematic status of these two species. Artificial hybrids between Arctic char, lake char and brook char are frequently produced in hatcheries. Although splake (lake×brook) (Berst et al. 1980) and sparctic char (Arctic×brook) (Alm 1955) are successfully produced (often with fertile outcome), the hybrid between lake char and Arctic char are less successful (e.g. Sutterlin et al. 1977, Chevassus 1979). In fact Behnke (1980) indicated that natural hybridization between lake char and Arctic char has never been documented. Additional extensive literature reviews have failed to identify any such incidence (Slastenenko 1957, Schwartz 1972, 1981, Dangel et al. 1973, Marshall 1977, 1981, Chevassus 1979, Marshall and Layton 1985). Kircheis (1985), however, mentioned that natural hybridization between Arctic char and introduced lake char was suspected in lakes in Maine, New Hampshire and Vermont (USA). Some additional fish from Lake Minto, Northern Quebec, were also tentatively identified as Arctic×lake char hybrids based on intermediate appearance and pyloric caeca counts (G. Power, Waterloo, pers. comm.).

In this paper we provide electrophoretic and meristic evidence of natural hybridization between Arctic char and lake char in Tasialuk Lake. The systematic significance of this is discussed and mechanisms suggested why this rare crossing has occured.

Material and methods

Study area

Tasialuk Lake (56°44'N, 62°42'W) forms a spectacular canyon in the lower part of the Kamanatsuk Brook, which drains into Tikkoatokak Bay, west of Nain, northern Labrador (Fig. 2). The lake is 10 km long, approximately 1 km wide and is located 42 meters above sea level. A waterfall close to the outlet into Tikkoatokak Bay provides a complete obstruction to upstream migrating fish. The fish fauna is dominated by landlocked Arctic char and lake char. Brook char, threespine stickleback (*Gasterosteus aculeatus*), and slimy sculpin (*Cottus cognatus*) however, are also found within the system (J. Hammar and E. Sköld unpublished data).

Collection and preparation of samples

Lundgren experimental gillnets of multiple mesh size, 10–75 mm knot to knot, were set during the period of July 26–30, 1984, following the methods of Hammar and Filipsson (1985). In this survey only benthic gillnets were used. Gillnets were set in different depths, 0.5–32 m, along the shore close to the outlet and in a shallow pool 500 meters further downstream from the lake's outlet (Fig. 2).

A total of 58 Arctic char, 33 lake char, 2 specimens intermediate to Arctic char and lake char, and 2 brook char were caught. Length, weight, sex and stage of maturity was recorded for all specimens. Otoliths were removed for ageing according to criteria given by Nordeng (1961). The stomachs were preserved for laboratory analyses of food habits and intestinal parasites. The Arctic char were also sampled for electrophoretic studies of muscle, liver and eyes. Results of these ecological and genetic studies will be presented elsewhere. However, 19 whole specimens of Arctic char and one specimen showing intermediate characters to Arctic char and lake char were frozen and later brought back to the Northwest Atlantic Fisheries Centre in St. John's for further meristic and morphological analyses, as well as sampling for analyses on heavy metals.

Biochemical analyses

The analyses were carried out using horizontal starch-gel electrophoresis of isozymes of at least 23 loci coding for AAT, ADH, EST, GPD, GPI, IDH, LDH, MDH, PGM, SDH, and SOD. The tissues examined and buffers used for different

Table 1. Enzymes, sample tissue, buffer systems and identified loci in a electrophoretic study of Arctic char and two hybrids with lake char in Tasialuk Lake, August 1984.

Enzyme	Abbreviation	E.C.No.	Tissue	Buffer system[1]	Locus/loci
Alcohol dehydrogenase	ADH	1.1.1.1	Liver	A	1
Aspartate aminotransferase	AAT	2.6.1.1	Muscle	B	1,2
Esterase	EST	3.1.1.–	Liver	A	1
			Muscle	A	2
Glucose-6-phosphate isomerase	GPI	5.3.1.9	Muscle	A	1,2,3
Glycerol-3-phosphate dehydrogenase	GPD	1.1.1.8	Muscle	A	1
Isocitrate dehydrogenase	IDH	1.1.1.42	Liver	B	3,4
Lactate dehydrogenase	LDH	1.1.1.27	Muscle	A	1,2
			Liver	A	3
Malate dehydrogenase	MDH	1.1.1.37	Liver	B	1,2
			Muscle	B	3,4
Phosphoglucomutase	PGM	5.4.2.2	Muscle	A	1,2
Sorbitol dehydrogenase	SDH	1.1.1.14	Liver	A	1,2
Superoxidase dismutase	SOD	1.15.1.1	Liver	A	1
Total number of loci:					23

[1] A: pH 8.5 (modified Ridgway et al. 1970)
  B: pH 6.1 (Clayton and Tretiak 1972)

enzymes and their abbreviations are summarized in Table 1. All tissue samples were homogenized in 0.025 M mercaptoethanol. A potential of 300 volts was applied for approximately 3 hours. The staining procedures follows Nyman (1967), Harris and Hopkinson (1976) and Allendorf et al. (1977). Genetic interpretation of banding patterns and designation of the various loci were based on a combination of papers reviewing the electrophoretic variation within Arctic char (Ferguson 1981, Kornfield et al. 1981, Andersson et al. 1983, Johnson 1984) and on a more extensive study on Arctic char populations throughout Labrador and Newfoundland (J. Hammar and E. Verspoor unpublished data). The common allele in Arctic char was designated *100 and the various other alleles were numbered by their anodal mobility. In other respects the nomenclature follows the AFS-standard proposed by Shaklee et al. (1989).

Morphometric analyses

The morphological and meristic study examined parameters listed in Table 2 and were made fol-

lowing the criteria proposed by Hubbs and Lagler (1970) and used in previous studies on Labrador Arctic char (Dempson 1984, 1985, Dempson and Misra 1984). The first gill arch on the left side of the fish was removed and stained with Alizarin red. All rakers on both limbs, including rudiments, were counted under binocular microscope. Vertebrae and fin ray counts were taken from radiographs. All vertebrae centra were counted including those articulating with the fourth and fifth hypurals but excluding the urostyle, as illustrated by Vladykov (1954). Fin ray counts also included rudimentary rays. Pyloric caeca were counted as they were detached from the intestine during the food and parasite study.

Interspecific comparisons

Genetic, morphologic and meristic comparisons of individual fish from the given lake were restricted to Arctic char and the intermediate specimens. Additional information on the electrophoretic variation in lake char is given by Dehring et al. (1981), Johnson (1984) and Ihssen
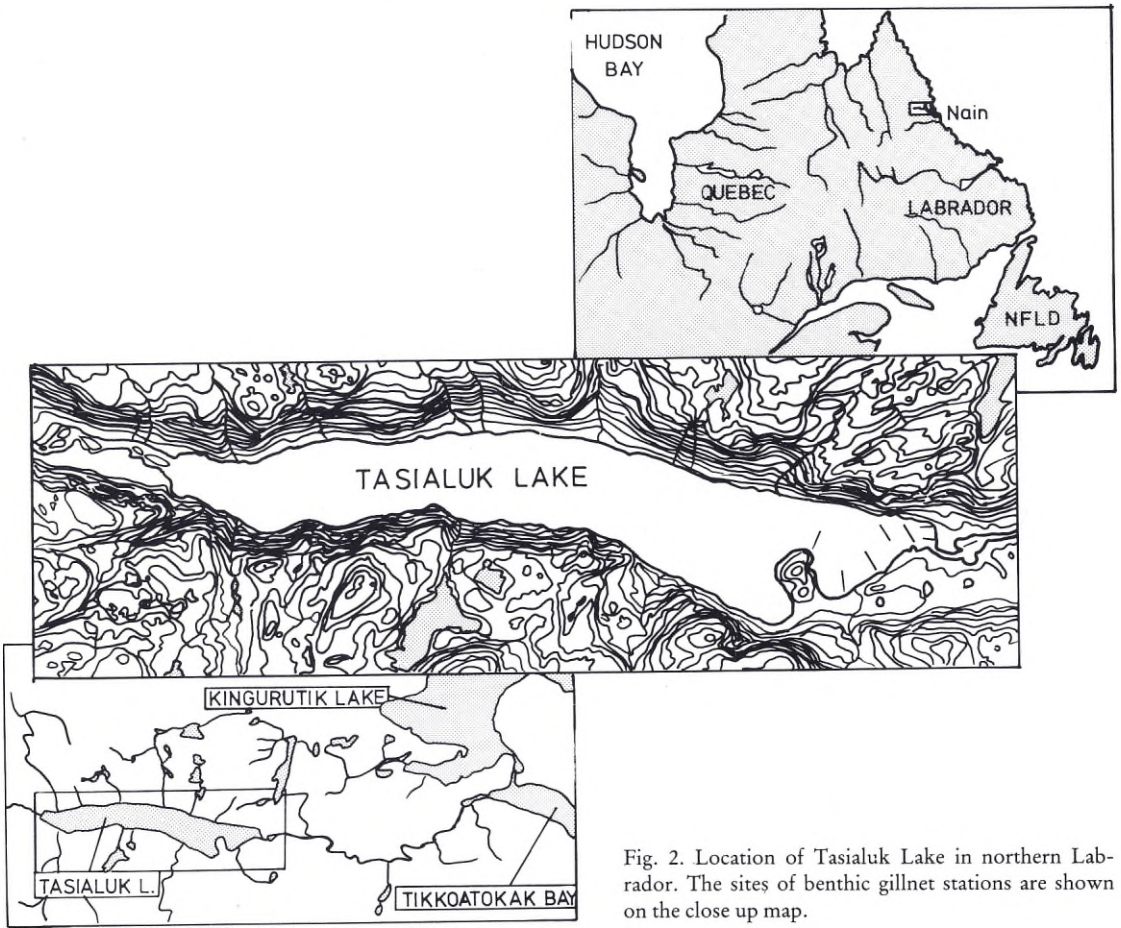
Fig. 2. Location of Tasialuk Lake in northern Labrador. The sites of benthic gillnet stations are shown on the close up map.

et al. (1988). The meristic variation within this species is given by Khan and Qadri (1971).

Results

Specimens of landlocked Arctic char analysed from Tasialuk Lake were large in size with sea-run characteristics. This was assumed to be an effect of food habits and the predation by the sympatric lake char population (J. Hammar and E. Sköld unpublished data). Two specimens with intermediate characters were identified. Only one was recognized in the field. Both intermediate specimens were, however, documented on photographs (Fig. 3, 4).

Electrophoretic characteristics

The Arctic char population demonstrated electrophoretic variation in the *EST-2**, *IDH-3,4** and *MDH-3,4** loci whereas *ADH**, *AAT-1,2**, *EST-1**, *GPD**, *GPI-1**, *GPI-2**, *GPI-3**, *LDH-1**, *LDH-2**, *LDH-3**, *MDH-1,2**, *PGM-1**, *PGM-2**, *SDH-1,2** and *SOD** were considered monomorphic. Two specimens, generally identified as intermediate to Arctic char and lake char, showed deviant phenotypes for *AAT-1,2**, *PGM-1** and *SOD** (Fig. 5). Allelic variation at the other loci was confined to individuals identified as Arctic char.

All specimens of Arctic char were fixed for the common allele (1111) at the duplicated loci *AAT-1,2** expressed in muscle. An intermediate

Fig. 3. Lake char and Arctic char caught in a shallow pool 500 m downstream from Tasialuk Lake, July 27, 1984. Specimen number 6 from the top is a hybrid between Arctic char and lake char.
(Photo: J. Hammar)
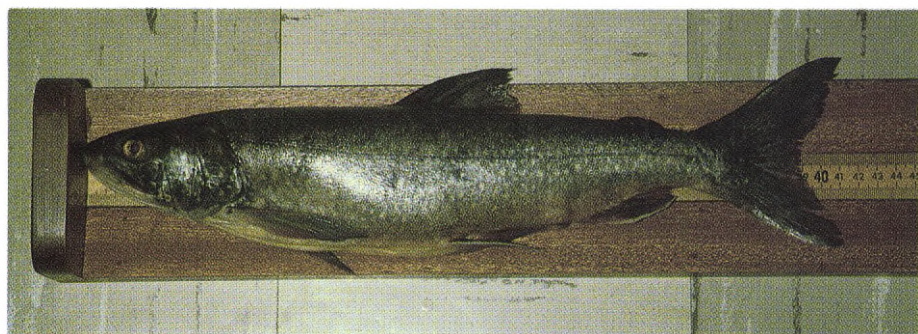
Fig. 4. The natural hybrid between Arctic char and lake char sampled for morphological and meristic characters.
(Photo: J. Hammar)

Table 2. Comparison of mean meristic characteristics and morphometric measurements of Arctic char with hybrid specimens between lake and Arctic char. Morphometric measurements are expressed as a percentage of fork length.

Meristics	Arctic char n=16		Hybrid n=1	Hybrid n=1	Lake char n=20	
	Mean	Range			Mean	Range
Dorsal fin	15.1	14–16	16	—	—	—
Anal fin	13.3	12–14	14	—	—	—
Pectoral fin	14.3	13–15	14	—	—	—
Pelvic fin	9.3	8–10	9	—	—	—
Vertebrae	63.4	63–64	63	—	—	—
Upper gill rakers	10.4	9–12	10	—	—	—
Lower gill rakers	15.8	15–17	17	—	—	—
Total gill rakers	26.2	24–29	27	—	—	—
Pyloric caeca	39.0	31–54	72	69	137.8	118–164
Morphometrics						
Total length (cm)	41.2	31.3–50.5	42.5	46.0	48.6	27.6–73.2
Fork length (cm)	37.9	28.7–46.5	38.9	42.4	44.4	25.2–68.5
Head length	20.7	19.2–22.9	24.6	—	—	—
Snout length	5.7	4.6– 7.2	7.0	—	—	—
Orbit length	3.0	2.4– 3.8	3.2	—	—	—
Postorbital length	11.5	10.8–12.7	14.7	—	—	—
Upper jaw length	9.9	8.5–12.2	13.0	—	—	—
Pectoral fin length	17.3	14.1–22.7	19.4	—	—	—
Predorsal length	40.9	38.5–43.2	42.3	—	—	—
Dorsal length to adipose fin	22.7	19.7–25.4	16.1	—	—	—
Caudal peduncle depth	6.9	6.3– 7.7	7.1	—	—	—
Whole weight (grams)	667	278–1121	730	551	997	139–3500

specimen expressed the 1223 allele combination. This phenotype was reported for eastern North American lake char by Johnson (1984), although Johnson designated this phenotype 1224. The other intermediate specimen expressed the 1122 allele combination, which has been recorded within the Arctic char variation in eastern USA

Fig. 5. Zymograms for the electrophoretic products of *AAT-1,2*, *PGM-1*, *PGM-2* and *SOD* loci expressed by Arctic char and its hybrids (↑), with lake char, Tasialuk Lake.

and Canada by Kornfield and others (1981), Johnson (1984), and J. Hammar and E. Verspoor (unpublished data) (Fig. 5).

The zymogram for PGM comprised two zones of anodal activity. In both zones strong additional bands of likely non-genetic post-translational modifications of the primary proteins (Harris and Hopkinson 1976) were noted. However, the less anodal *PGM-1*, which only showed homozygotes for the fast allele (22) in the Arctic char population examined here, was heterozygous (12) for the two intermediate specimens (Fig. 5). Although not recorded in Arctic char in Tasialuk Lake this phenotype has been recorded in other Arctic char populations in northern Labrador (J. Hammar and E. Verspoor unpublished data). Dehring et al. (1981) and Johnson (1984) reported *PGM-1* to be monomorphic (11) in lake char, whereas Ihssen et al. (1988) reported a null allele for *PGM-1* as well.
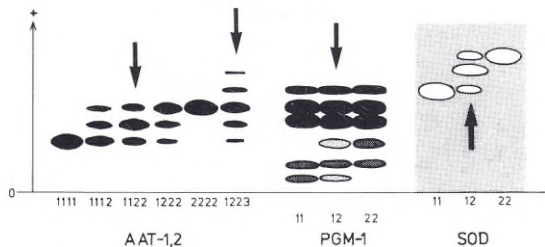
Johnson (1984) described the monomorphic product of the *SOD** locus to be coded for by three different alleles in *Salvelinus*: brook char (**100*), Arctic char (**190*) and lake char (**240*). The two intermediate specimens in the present study were heterozygous (**190/240*) for the genotypes demonstrated in Arctic char and lake char according to Johnson's study.

AAT-1,2* and *PGM-1** may thus be treated as discrete population markers, whereas *SOD** may be used as a species marker, and the recorded zymograms clearly demonstrate hybrid pattern between Arctic char and lake char. Except for *SOD**, Johnson (1984) also reported diagnostic allele differences in the products of the *AK-2**, *FDP**, *G3P-3**, *LDH-1**, *MDH-3,4**, *ME-2**, *PEPB-2** and *PEPD-2** loci in lake char and Arctic char. These loci were either not analysed or not identified as divergent in the present study.

The comprehensive study by Johnson (1984) also presented descriptions of the electrophoretic variation among various artificial hybrids within Salmonidae, but did not unfortunately include hybrids between Arctic char and lake char. However, splake and sparctic char were reported to be electrophoretically intermediate to the parental species. Nyman (1967) studied serum proteins, liver and kidney esterases from an artificial hybrid between Arctic char and lake char ("kröding"), and found the pattern to be a very incomplete summation of the parental phenotypes. Also Tsuyuki and Roberts (1965) recorded variation in parental similarity in electrophoretic analyses of muscle myogen, hemoglobins and serum proteins in artificial hybrids of Arctic char and lake char.

Morphological characteristics

With the exception of pyloric caeca counts, meristic characteristics of lake char and Arctic char are not discrete and overlapping makes identification of hybrids difficult. Meristic values for Arctic char specimens from Tasialuk Lake (Table 2) were consistent with values reported for other Arctic char populations in insu-

lar Newfoundland and Labrador (Dempson and Misra 1984, Dempson 1985). However, the number of vertebrae was significantly lower ($P < 0.001$), and the total number of gill rakers significantly higher ($P < 0.001$) in comparison with an anadromous population of char from the same area in northern Labrador (Tikkoatokak Bay) (Dempson and Misra 1984). Only the number of pyloric caeca clearly identified the intermediate specimens as hybrids since values were intermediate between the two parental types (Table 2), a feature often, but not exclusively, characteristic of hybrids (Hubbs 1955, Leary et al. 1983).

Morphometric characters also indicated differences between the measured intermediate specimen and the Arctic char. Lake char generally have larger heads relative to body size than Arctic char (Vladykov 1954). In addition, the dorsal fin is usually placed further away from the head such that the predorsal length in lake char would be greater than in Arctic char while the dorsal to adipose length would be smaller.

The fork length of the intermediate specimen was not significantly different from the mean value for the measured Arctic char specimens ($P = 0.84$). Thus, measurements of relative morphometric characters are comparable. Head length, predorsal length and dorsal to adipose length in Arctic char specimens were consistent with mean values calculated from anadromous Arctic char from Tikkoatokak Bay, Labrador (Dempson 1984), and expressed as a percentage of fork length, were 21 %, 41 %, and 23 % respectively (Table 2). Head length in the one intermediate specimen available for analysis was 25 % of the fork length and similar to values reported for head size in lake char (Vladykov 1954, Qadri 1967). The predorsal length was greater than in the Arctic char specimens, but was intermediate between values reported for the two parental types (Vladykov 1954, Qadri 1967). As expected, the dorsal to adipose length in the intermediate specimen was substantially less than in the Arctic char (Table 2).

Both intermediate specimens showed external characters typical of both Arctic char and lake char (Fig. 3, 4). The general shape of the body

Table 3. Size, age and maturity data on Arctic char, lake char and brook char collected in Tasialuk Lake, July 26–30, 1984.

	Arctic char	Lake char	Brook char
Number	58	33	2
Fork length, mm			
Range:	93–465	200–685	250–258
Mean:	275	423	254
Stand.dev:	132	98	
Whole weight, g			
Range:	7.5–1190	69–3500	155–155
Mean:	380	865	155
Stand.dev:	356	664	
Age, years			
Range:	2+–15+	5+–34+	5+–6+
Mean:	7.6	17.4	5.5
Stand.dev:	4.2	6.4	
Youngest recorded mature fish			
Females:	6+	18+	
Males:	4+	14+	(5+)

was intermediate to Arctic char and lake char. Besides being comparably longer, the head showed yellow spots on the operculum. Also the body coloration was typical for lake char with numerous yellow spots. The ventral fins were colored as typical for Arctic char, whereas the caudal and dorsal fin were spotted as in lake char.

Based on the intermediate morphology, the discrete meristics and the presence of three diagnostic electrophoretic variants, the two intermediate specimens are considered hybrids between Arctic char and lake char. Owing to the fact that no tradition of transplantations of fish is known from Labrador, neither by the government nor by the Inuits, the hybrids recorded in Tasialuk Lake should be treated as natural. No results indicate the hybrids to be older than of F_1 generation.

Ecological characteristics

Arctic char generally dominated the catches in the littoral zone at 0–5 m (mean 2.2 m), although they were caught down to 15 meters depth. Lake char, however, were caught in all depths in equal amounts from the shore down to 32 m (mean 5.9 m). The length distribution of the two collected species greatly overlapped, whereas both age distribution and age and size at maturity revealed major differences (Table 3, Fig. 6, 7).

The two hybrid specimens which were caught in different locations, between 1.2 and 3 meters depth, measured 42.4 cm/551 grams and 38.9 cm/730 grams. One specimen was a female with approximately two thirds of the body cavity filled with ova of approximately 1 mm size. The size and shape of her gonads suggested that the fish had spawned previously, but would probably not spawn that fall. The second specimen was a mature male. No macroscopic signs of gonadal anomalies were detected. The hybrid otoliths revealed one year's difference in age, 16+ and 17+. The size of the hybrid otoliths were also slightly larger than the otoliths from the parental species, although still within the range of variation observed (Fig. 8). The weight and banding pattern were, however, more comparable to lake char otoliths. Length at age of the hybrids was similar to both parental species, although their high age approximate the lake char (Fig. 6, 7).
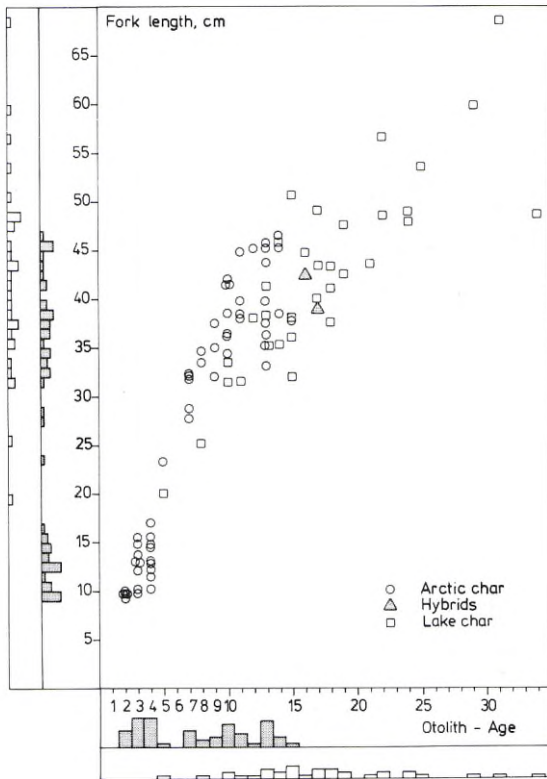
Fig. 6. Relationship between fork length and otolith age in individual Arctic char, lake char and their hybrids caught with experimental gillnets in Tasialuk Lake. The age and length distributions of both species (Arctic char shaded) are also shown along the axes.
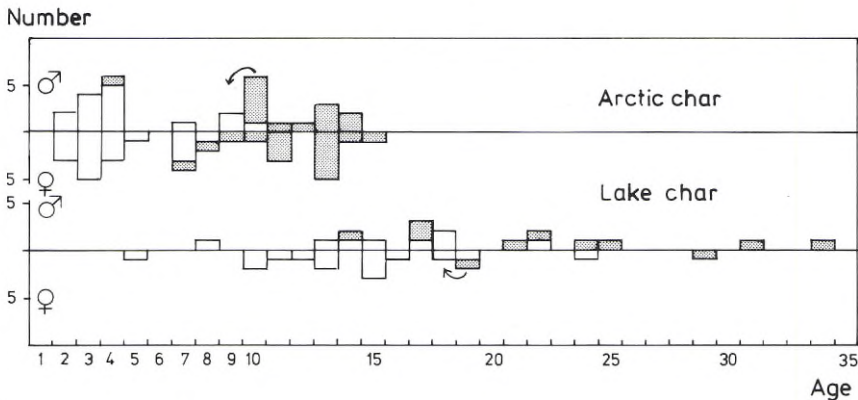
General discussion
Artificial and natural hybrids

As previously mentioned, natural hybrids involving Arctic char and lake char are not known to have been documented before, although artificial hybrids have infrequently been produced in hatcheries with varying success since 1948 (Seguin 1957, Sormunen and Kajosaari 1963, Nilsson and Svärdson 1962). Usually this hybrid is associated with low survival rate (Sutterlin et al. 1977) and a reduced fertility (Chevassus 1979). These observations suggest genetic barriers between Arctic char and lake char or postmating limitations in their hybrids. The low survival rate of the hybrids emphasize the importance of these limiting processes. However, since the reproductive barrier between the two species obviously is not complete, it may also include various premating isolation factors. In order to understand how these two species can coexist in nature, without any extensive hybridization it is important to know the ecological mechanisms that keep them isolated reproductively.

Ecological reasons for hybridization

Arctic char and lake char are assumed to have invaded the lakes in Labrador in two fundamentally different ways. Anadromous Arctic char

Fig. 7. Age distribution and frequency of mature specimens (shaded) among Arctic char and lake char collected in Tasialuk Lake, July 1984. Age groups with individuals showing gonadal signs of spawning activity the previous year have been indicated with arrows.
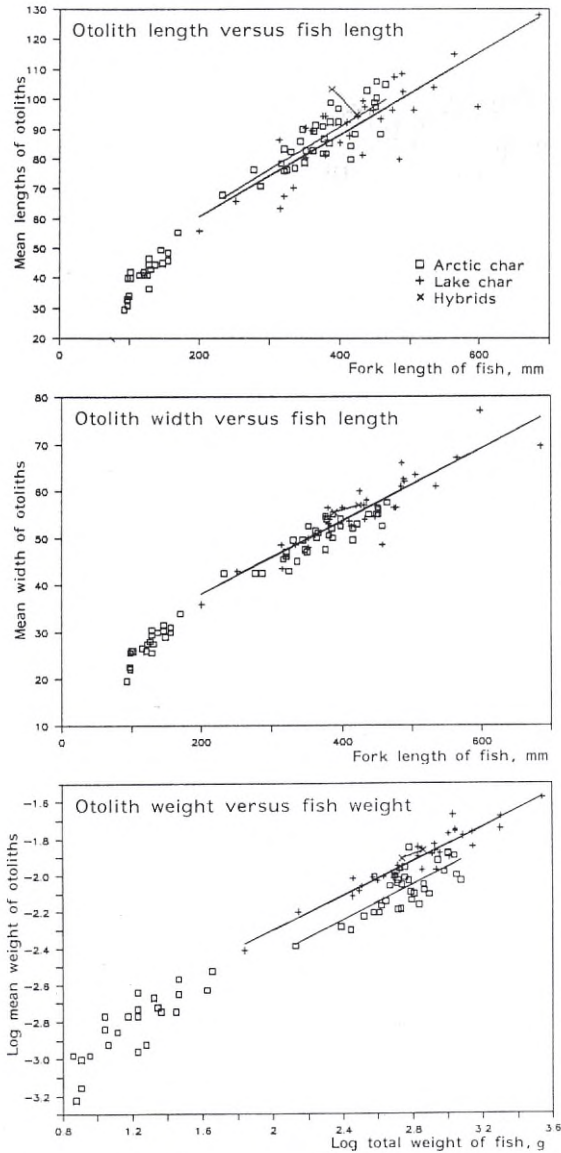
Fig. 8. Relationships between length (ocular units), width (o.u.) and weight (g) of otoliths, and forklength (mm) and whole weight (g) of Arctic char, lake char and two hybrids.

dispersed from the coast into freshwater systems where it now also forms numerous isolated landlocked populations. The postglacial lake char invasion, however, was overland from Quebec (Black et al. 1986). The lake char is considered to have low tolerance to saltwater, although some coastal dispersion of lake char of

later origin may have played a minor roll in the rivers close to Nain (Black et al. 1986). The presence of Arctic char and lake char in sympatry could thus be expected to have existed for many thousands of years, and mechanisms of reproductive isolation between the species are well established. Spawning may be periodically, spatially or ethologically different.

If one discriminating character becomes overlapping, the other isolating mechanisms should become more important. If the sexual barriers are incomplete a very low frequency of natural hybrids may always be present, which is very likely based on the frequency of natural interspecific and intergeneric hybridization among other salmonids (e.g. Brown 1966, Suzuki and Kato 1966, Payne et al. 1972, Honma 1974, Kato 1977, Campton and Utter 1985, Verspoor 1988, De Leaniz and Verspoor 1989). As the two hybrids came from two different year classes, the observations seem unlikely to represent an isolated incident. However, if natural hybridization between Arctic char and lake char is purely coincidental at least four reasons may be proposed:

1. Total random mixing of sexual products from two different species, due to other reasons than those under control by the parental specimens. For example, water currents may transport milt from one spawning ground to another, if spawning occurs simultaneously but spatially different. However, this seems an unlikely explanation in light of the exponential rate of incapacitation of sperm once in the water.

2. Incomplete reproductive isolation due to overlap in spawning time, and spawning habitat and/or spawning behaviour. Since sexual maturation seems to occur very late in the life history of lake trout, combined with the interrupted reproductive pattern, the total number of spawners in a given year may actually be a very small proportion in comparison with the number of spawning Arctic char, and thus further increasing the risk of hybridization.

General information on spawning times and the preferred spawning temperatures available in the literature, however, suggests that lake char

would spawn earlier than Arctic char (Johnson 1980, Martin and Olver 1980). In general, northern stocks of lake char spawn earlier than those in more temperate regions. Lake char may also spawn earlier in smaller and shallower lakes (Martin and Olver 1980). Owing to the fact that Tasialuk Lake may be looked upon as an extreme locality – a deep canyon with steep slopes, thus a possible lack of diverse spawning facilities and generally low water temperature – the reproductive segregation may be very subtle in terms of time and space, and easily disturbed by climatic changes.

The population of Arctic char in Tasialuk Lake displayed some characteristics usually associated with anadromous fish; large body size, silver coloration, few parasites (J. Hammar and E. Sköld unpublished data). The length distribution of the catch of Arctic char and lake char (Fig. 6.) thus show large proportions of fish of similar size, which may be of importance for mixed mating on a spawning ground used by both species. The spawning behaviour of lake char and Arctic char are on the other hand very different. Although they are reported to spawn both on shallow and deep bottoms, the Arctic char is territorial and spawns in pairs (Fabricius 1953), whereas the lake char is a nonaggressive multiple spawner, with males generally in excess of females (Martin and Olver 1980, Berst et al. 1981). Although exhibiting some sexual dimorphism, this is not as marked in lake char as in other chars. Both species are reported to spawn at night time, and in stagnant as well as in running water, although the Arctic char would be more commonly seen in the latter habitat in Labrador.

Eggpredation is a common character in char, and such feeding behaviour may in fact be another primary explanation for the occurrence of other char species on a spawning ground (G. Svärdson, Drottningholm, pers. comm.).

3. "Gene-vector", bridging the gap between spawning periods. If Arctic char and lake char segregate in terms of spawning time, a mature specimen from one of the species may ripen early or late and thus act as a gene-vector. Preco-

cious males of the Arctic char may ripen at an earlier date and then act as the gene carrier. An Arctic char is also more likely to be accepted on the spawning ground of nonterritorial lake char. The other alternative would be unusually late maturing females of lake char occurring among spawning Arctic char.

4. "School-trapping". A fourth way of transferring genes would be if specimens of one species would change its niche or its ecological characteristics and behave more as an other sympatric species, i.e. copy the biology of the other species. Svärdson (1970) and Hammar and Svärdson (1987) suggest "school-trapping" as an important mechanism for introgression between different sibling species within the *Coregonus* complex. Specimens of one species have been caught in schools of another species with dissimilar ecological characters, and more or less converted to the life history strategy of the second species. With this mechanism, the limiting premating processes are obliterated and this may explain some of the cases of natural hybridization between nonterritorial lake dwelling species.

Systematic implications

Johnson (1984) reports the electrophoretic variation in Arctic char and lake char to be very similar and thus suggests that lake char and Arctic char are genetically closer than Arctic char and brook char. Tsuyuki et al. (1966) also found muscle and plasma proteins of Arctic char and lake char to be more similar to each other than with those of brook char. Measures of Nei's genetic distance showed 0.26 between Arctic char and lake char while the distance between brook char and Arctic char was 0.36 (Johnson 1984). These findings may in fact already demonstrate a certain rate of introgression, and comparisons of populations collected in other regions of North America may be genetically more divergent. However, Hutchings and Morris (1985) compared the covariation of female life history traits within the family Salmonidae, and found lake char and Arctic char to cluster in a group separate from brook char. These studies

contradict the common opinion of the phylogenetic relationship within *Salvelinus* based on morphological differences, where lake char has been considered to have diverged from Arctic char and brook char at an earlier state (Vladykov 1954, Rounsefell 1962, Behnke 1972, Cavender 1980).

Hybridization success is correlated with phylogenetic relationships (Hubbs and Drewry 1959, Hubbs 1967) and provides a practical test of the degree of genetic isolation between species. The diploid chromosome numbers of Arctic char and lake char have been estimated to be 80 and 84 respectively (Svärdson 1945, Buss and Wright 1956). However, as evident from other intra- as well as intergeneric crossings, within salmonids at least, differences in karyotypes do not possess a genetic barrier (Naevdal and Dalpadado 1986). In fact natural hybridization between Arctic char and brook char is suggested to be more common than previously thought and is reported to be rather extensive in another Labrador river (Hammar, Dempson and Verspoor in prep., Hammar 1989). This supports the traditional opinion of a closer relationship between Arctic char and brook char. The Arctic char and brook char are ecologically very similar but genetically more different than Arctic char and lake char. The latter species, on the other hand, are more ecologically different. The rarer occurrence of natural hybridization between the latter two species emphasizes the importance of both genetical and ecological barriers between coexisting species within the genus *Salvelinus*.

Implications for introductions into systems with Arctic char

Lake char has commonly been used in management programs of northern Europe and North America, and has been introduced to lake reservoirs as a new target for sport fisheries as well as to provide a new predator on small pelagic whitefish or stunted Arctic char populations (Nilsson and Svärdson 1962, 1968, Kircheis 1985). The significance of such predation on

Arctic char in natural coexistence was recently presented by Fraser and Power (1989). Experiences from Swiss reservoirs (Grimås and Nilsson 1962) also indicated possible competition for food resources between small-sized lake char and Arctic char.

In at least one Swedish reservoir natural reproduction of introduced lake char has been documented (E. Fisk, Umeå, pers. comm.). In 1989 two suspected hybrid specimens, identified by intermediate appearance between Arctic char and lake char, from another lake in northern Sweden were recorded (O. Filipsson and J. Hammar, Drottningholm, unpublished data). The fish were not of the same age and no indication of hatchery origin could be detected in the otoliths. Possible hybridization between introduced lake char and native Arctic char may be more common than previously expected, and stocking of lake char may in fact jeopardize original char gene pools. This seems, however, to be in disagreement with the low rate of natural hybridization recorded between native sympatric populations of Arctic char and lake char in North America, and the assumed reduced fertility. Whether reproductive isolation is sustained in regions where one of the species is introduced, or exists on the border of its distribution, is, however, unknown.

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The Effect of Osmotic Stress on The Anti-Predatory Behaviour of Atlantic Salmon Smolts: A Test of The 'Maladaptive Anti-Predator Behaviour' Hypothesis

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Abstract

The smolts of Atlantic salmon, *Salmo salar*, are liable to a high mortality rate on their way from the rivers to the open sea. A cumulative effect of osmotic stress and the physiological stress caused by the fright-reaction of the predator-naive smolts to predators in the estuaries, is considered to inhibit the normal adaptive response of the smolt to predation to such an extent that their chance of escaping an attack by a predator are significantly reduced (i.e. the 'MAD' hypothesis). The MAD hypothesis was tested by comparing the anti-predatory behaviour and the stress symptoms of five groups of six seawater-adapted smolts (SWA smolts) with those of five groups of six non-adapted smolts (NA smolts) when transferred to seawater. The behavioural studies, made in a circular observation tank (72m²), revealed that the reaction distance of the NA smolts was shorter than that of the SWA smolts when approaching the predator. There was no major difference in the reaction distance between the two categories of smolts when the predator approached the prey. The SWA fish showed shoaling behaviour more frequently than the NA fish and, when attacked, the NA smolts escaped when at a closer distance to the predator than the SWA smolts. The SWA smolts showed stress symptoms less frequently and, furthermore, their risk of predation was less than for the NA smolts. Because many of the results obtained were in line with those predicted, the MAD hypothesis is considered not to have been disproven.

Introduction

Seaward migrating Atlantic salmon, *Salmo salar*, smolts are subjected to a heavy mortality rate from predation (e.g. Larsson 1985, Hvidsten and Møkkelgjerd 1987). In Norway, for example, less then 3 % of the smolts migrating seawards are likely to return to spawn (e.g. Hansen 1987), the rest having died. The highest mortality is thought to occure during the seaward migration and during the first few days there after. A cumulative effect of two main factors is thought to be the cause of this high rate of predation, viz. osmotic stress and the physiological stress caused by the fright-reaction of the predator-naive smolts to the predators (Järvi 1989). Such a cumulative, acute, physiological stress response, is considered to inhibit the normal adaptive response of the smolt to predation to such an extent that their chances of escaping an attack from

a predator are significantly reduced (Järvi 1989). In fact, Atlantic salmon smolts were found to show such a cumulative physiological stress response, in terms of increased levels of glucose and lactate in the blood, together with chloride ionic changes, when exposed to osmotic stress and the presence of predators (Järvi 1990). The stress response to these two stress-stimuli can be so severe that the smolt dies (Järvi 1989). That environmental stressors can inflict behavioural changes has long been known from experience with hatchery fish. These include behavioural changes such as the inhibition of feeding or of migratory activity (Wedemeyer and McLeay 1981). From this knowledge, therefore, it seems reasonable to assume that a whole-animal response is made to osmotic stress and fright, in terms of maladaptive anti-predatory behaviour.

The aim of the present study was to test the predictions arising from the 'maladaptive anti-

predator behaviour' (MAD) hypothesis. This was done by exposing either seawater acclimatised (SWA) or freshwater acclimatised (NA), predator-naive, smolts to six cod (*Gadus morhua*) in an experimental arena. Such an experimental design only subjects the SWA smolts to the stress due to the presence of predators, but will subject the NA smolts to a cumulative stress both from osmosis and the presence of predators. One would deduce from the MAD hypothesis that the SWA smolts should react more appropriately towards the presence of the cod than the NA smolts.

Methods
General

The experiments were carried out during the normal smolt-migration period in May, 1987, at the Research Station for Freshwater Fish at Ims, near Stavanger, in south-western Norway. The fish used were two years-old, tank reared, Atlantic salmon smolts originating from the Imsa River. A large number of smolts were divided into two groups (>>1,000 individuals). One group was kept in seawater (25 ‰ salinity) for three weeks before the start of the experiments (the SWA group) and the other group was kept in freshwater for the same length of time (the NA group). Both groups were naive, as regard the presence of predators, prior to the experiments. 24 hrs before each trial, the smolts were individually marked with a colour tag behind the dorsal fin, which made them easy to identify. Six cod (weighing between 1.0 and 2.5 kg), bought live from the local fishermens' association, were used as the predators in the experiments.

The behaviour of the fish were observed while they were in a circular tank (72 m²), on the bottom of which a square grid (0.2×0.2 m) had been painted, so as to enable the distance between a predator and its prey to be estimated. The water-level in the tank was approx. 0.6 m and the water velocity was negligible. The tank-water salinity was 32 ‰. An observation tower

(3 m high), from which the observations were made, was constructed close to the tank.

Experimental design

The validity of the MAD hypothesis was tested by designing an experiment in which both anti-predator behaviour and stress symptoms could be studied, and the results were considered in relation to the aforementioned predictions.

Before the first trial started, the six cod were placed in the observation tank. Six smolts, taken either from the freshwater tank (5 trials), or from the seawater tank (5 trials), were used in each trial. They were placed in the study tank for an observation period of one hour. Each smolt was only used once in each trial. The reaction-distances, escape-distances, and type of escape behaviour (freezing, escape swimming, non-reaction) of the smolts were recorded by scan-sampling (Lehner 1979). In addition, the numbers of smolts seen shoaling and of those seen wobbling at the surface (stress symptom) were noted on six occasions during each trial (after 5, 10, 20, 30, 40, 60 mins).

Because each individual smolt might react several times in the same way, i.e. intra-individual ties, the median value for each individual was used in the statistical analyses of the data for escape distance, and stress symptoms. In the analyses of the numbers of smolts observed shoaling, or displaying stress symptoms, both the median and the maximum values for each trial were used.

Predictions

1) Normally, when a predator is in the vicinity of a smolt, the smolt tries to keep a certain distance away from the predator. This is valid both when the predator approaches the smolt, or when the smolt approaches the predator (reaction distance) (Jakobsson and Järvi 1977). Thus, if the MAD hypothesis is a valid one, then the reaction distances of the NA smolt, in both cases, should be shorter than that of the SWA smolt.

2) If several smolts are present within a limited area, the smolts should form a shoal, in order to increase vigilance (Milinski 1977) or to achieve a dilution effect (Hamilton 1971) when a predator is present. Thus, according to the MAD hypothesis, one would expect that the SWA smolts should shoal more readily than the NA smolts. The magnitude of the benefit derived by the individual shoal members tends to be greater for fish in larger than in smaller shoals when attacked by a predator (Morgan and Colgan 1987). Thus, the maximum number of smolts observed shoaling, should be greater for the SWA than for the NA smolts.

3) If a predator attacks a smolt, then the smolt possesses the ability to exhibit one of three different kinds of escape behaviour (Jakobsson and Järvi 1977): a) It may suddenly swim away, panic-like; b) such a panic-like swimming may change into 'surfing', which is a panic-like swimming at the surface; c) the smolt may quickly swim down to the bottom and stay there absolutely immobile (freezing). The distance from the predator at which a smolt reacts, showing escape behaviour, is defined as escape-distance (Jakobsson and Järvi 1977). From the MAD hypothesis one would expect to find that the NA smolts show escape behaviour, i.e. react, only when closer to the predator, and that they should react by either surfing or freezing less frequently than the SWA smolts.

4) Acute exposure of fish to sublethal concentrations of stressors is known to impair their swimming performance (Waiwood and Beamish 1975). When Atlantic salmon smolts are subjected to physiological stress, they appear to change their swimming behaviour and remain at the surface, showing 'wobbling' (a tertiary behavioural stress response) (Järvi, in prep.). Thus, for the MAD hypothesis to be valid, the NA smolts should display this stress response more frequently than the SWA smolts.

5) The ultimate postulate of the MAD hypothesis is that the NA smolts should be subject to predation more frequently than the SWA smolts, due to the cumulative stress response inhibiting the normal, adaptive, anti-predator behaviour. Thus, the risk of being killed by a predator should be less for the SWA smolts than for the NA smolts.

Results

Reaction distance

The median distance that an approaching NA smolt kept away from the predator was significantly shorter than that for the SWA ones (Fig. 1 A–B). There was no difference in the reaction distance between the first and the second half-hours of the trials (Mann-Whitney test; NA H_o: $md_1 = md_2$, N=16/14, Z=1.2, $P > 0.05$; SWA H_o: $md_1 = md_2$, N=30/24, Z=-0.7, $P >> 0.05$).

When the predator approached from behind, no difference was noted in the median reaction distances of the two groups of smolts (Fig. 1 C–D). However, the NA smolts increased their reaction distances during the second half-hours of the trials (Mann-Whitney test; H_o: $md_1 = md_2$, N=25/24, Z=2.6, $P < 0.01$), but the SWA smolts did not (Mann-Whitney test; H_o: $md_1 = md_2$, N=30/30, Z=-0.5, $P >> 0.05$).

When the predator frontally approached the prey, there was no statistically significant difference in the median reaction distance values for the two groups (Fig. 1 E–F). Nevertheless, the median reaction distance of the SWA group did increase during the second half-hours of the trials (Mann-Whitney test; H_o: $md_1 = md_2$, N=30/27, Z=3.0, $P < 0.01$), but not that of the NA group (Mann-Whitney test; H_o: $md_1 = md_2$, N=19/20, Z=1.0, $P >> 0.05$).

During the trials, the NA smolts did not show any difference in their reaction distances either when the predator approached the prey, or when the prey approached the predator. An exception was during the second half-hours of the trials, when the NA smolts reacted when a greater distance away when the predator approached from behind, but not frontally (Table 1). During the first half-hours of the trials, the reac-
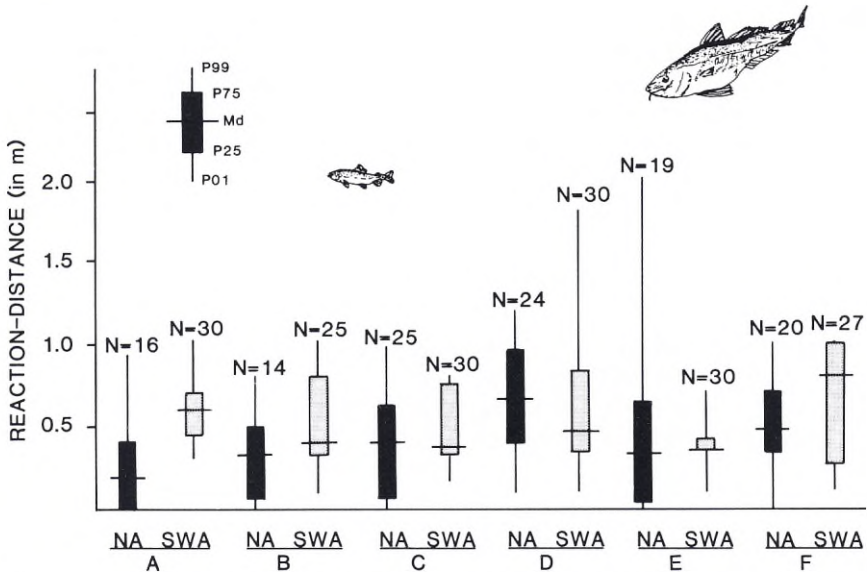
Fig. 1. A–B; Median reaction-distances for NA and SWA smolts when approached by a cod. The differences in the distances were tested using a Kruskal-Wallis test. A) The results during the first half-hour of each trial: H_o: $md_1 = md_2$, H=15.2, $P < 0.0001$. B) The results during the last half-hour of each trial: H_o: $md_1 = md_2$, H=4.8, $P < 0.05$. The black boxes indicate the median values for the NA smolts and the grey boxes those for the SWA smolts.

C–D; Median reaction-distances for NA and SWA smolts when the predators approached from behind. The differences were tested using a Kruskal-Wallis test. C) The results from the first half-hour of each trial: H_o: $md_1 = md_2$, H=0.7, $P \gg 0.5$. D) The results from the second-half hour of each trial: H_o: $md_1 = md_2$, H=3.8, $P > 0.05$.

E–F; Median reaction-distances of NA and SWA smolts when the predators approached from the front. The differences were tested using a Kruskal-Wallis test. E) The results from the first half-hour of each trial: H_o: $md_1 = md_2$, H=0.0, $P \gg 0.88$. F) The results from the second half-hour of each trial: H_o: $md_1 = md_2$, H=2.7, $P > 0.05$.

Table 1. The reaction distances for the SWA smolts and the NA smolts. SWA1 alt. NA1 are the smolts during the first half of the trials and SWA2 alt. NA2 during the second half of the trials. Factors 1 and 2 are the median values tested: (1) when the smolt approaches the predator, (2) when the the predator approaches the smolt from front, and (3) from behind. A non-parametric pair-test was used to analyse the data. H_o: Factor 1 = Factor 2.

Category	Factor 1	Md	Factor 2	Md	N	Z	P
NA1	1	2.0	2	3.5	16/19	1.51	0.13
	1	2.0	3	4.0	16/25	1.47	0.14
	2	3.5	3	4.0	19/25	0.11	0.91
NA2	1	3.4	2	4.2	14/20	1.41	0.16
	1	3.4	3	6.8	14/24	2.64	0.008
	2	4.2	3	6.8	20/24	1.74	0.08
SWA1	1	6.0	2	3.7	30/30	4.31	0.001
	1	6.0	3	3.6	30/30	2.56	0.011
	2	3.7	3	3.6	30/30	1.52	0.12
SWA2	1	4.0	2	8.0	25/27	1.04	0.30
	1	4.0	3	4.5	25/30	1.32	0.19
	2	8.0	3	4.5	27/30	2.06	0.039

Table 2. The number of smolts in the two groups that allowed the predator to approach within 0.1 m.

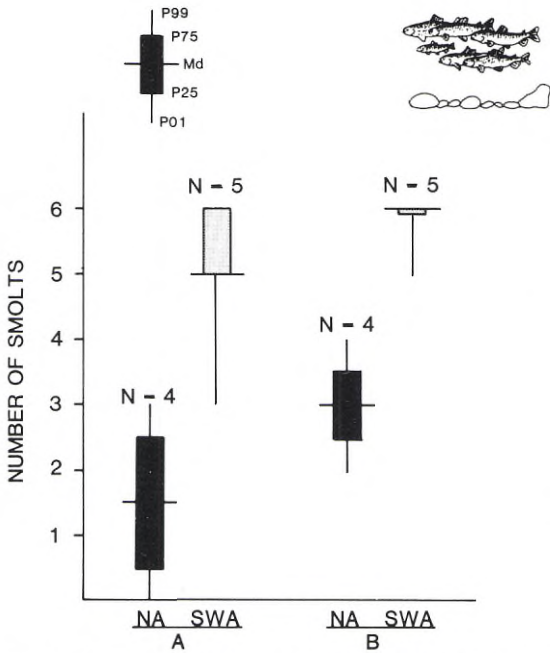|	Reaction-distance		
	<1 dm	>1 dm	Total
NA	22	8	30
SWA	13	17	30

Fig. 2. Shoaling tendencies for NA and SWA smolts in regard to A) the median numbers and B) the maximum numbers of smolts shoaling in each trial. The differences were analysed using a Kruskal-Wallis test: A) median number: H_o: $md_1 = md_2$, H = 5.6, $P < 0.05$, B) maximum number: H_o: $md_1 = md_2$, H = 6.6, $P < 0.01$. N is the number of trials. The black boxes indicate the median values for the NA smolts and the grey boxes those for the SWA smolts.
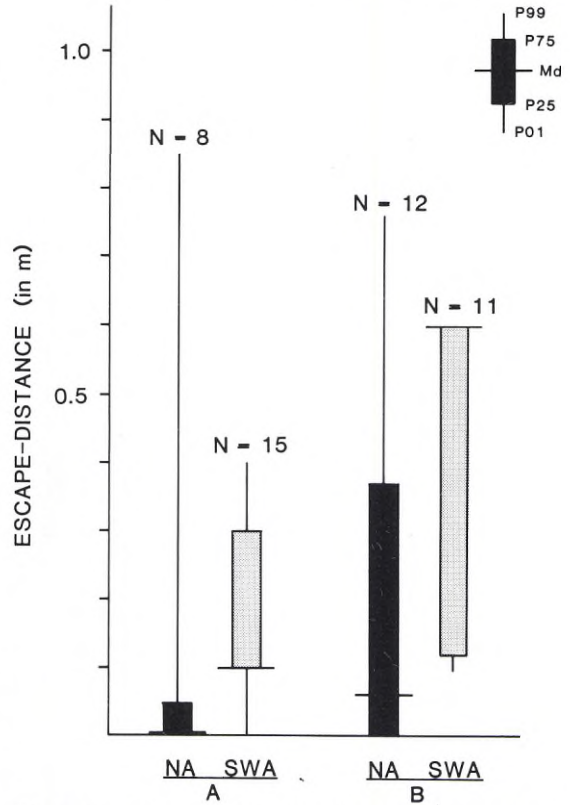

Fig. 3. Comparison of the escape-distances of the NA and SWA smolts. The differences were tested using a Kruskal-Wallis test. A) Test of differences during the first half-hour of each trial: H_o: $md_1 = md_2$, H = 4.0, $P < 0.05$. B) Test of differences during the second half-hour of each trial: H_o: $md_1 = md_2$, H = 6.6, $P < 0.01$. The black boxes indicate the median values for the NA smolts and the grey boxes those for the SWA smolts.

tion distances of the SWA smolts were shorter when the predator approached the prey, either frontally or from behind, than when the prey approached the predator (Table 1). Such differences were not noted during the second half-hours of the trials (Table 1).

A chi-square test showed that the SWA smolts did not allow the predator to approach closer than 0.1 m as frequently as the NA smolts did (Table 2; H_o: reaction-distance was independent of the previous seawater adaptation, $\chi^2 = 4.4$, df = 1, $P < 0.05$).

Shoaling behaviour

A Kruskal-Wallis test of the data revealed that the median number of NA smolts that shoaled was significantly lower than that of the SWA

smolts (Fig. 2A). Furthermore, the maximum number of SWA smolts shoaling was significantly higher than that of the NA ones (Fig. 2B).

Escape distance and response

When attacked by a predator, the escape-distances of the SWA smolts were shorter than those of the NA smolts (Fig. 3).

Different behaviour patterns were shown by both groups of smolts when attacked by a predator. A high percentage reacted by making an escape-response (NA = 55 %, SWA = 89 %), a

Table 3. The number of smolts in the two groups that responded with adequate anti-predator behaviour when attacked by a predator.

	No response*	Freezing	Escape	N
NA	8	2	12	22
SWA	2	0	16	18

* 'No response' is when the smolt did not react at all when the predator approached.

somewhat lower percentage did not react at all when the predator attacked (NA=36 %, SWA=11 %) and an even lower percentage froze (NA=2 %, SWA=0 %). There was no statistical difference in adequate anti-predator behaviour between the SWA smolts and the NA smolts when
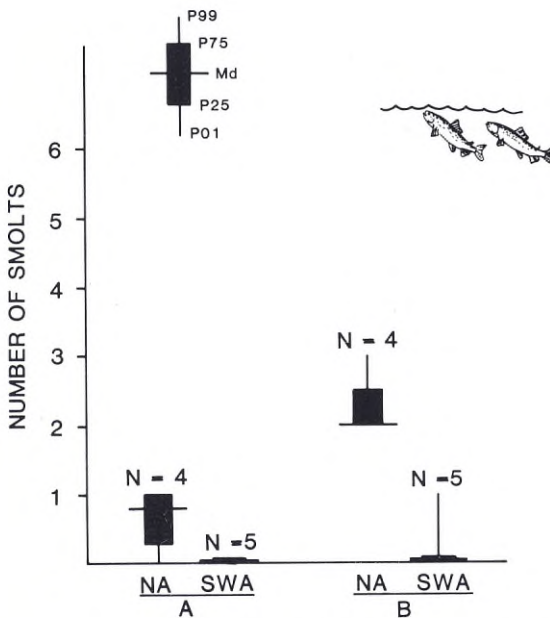

Fig. 4. Stress tendencies for NA and SWA smolts in regard to A) the median numbers and B) the maximum numbers of smolts that wobbled at the surface. The differences between the groups were tested using a Kruskal-Wallis test. A) The median numbers seen wobbling each trial: H_o: $md_1 = md_2$, $H = 4.8$, $P < 0.05$. B) The maximum numbers seen wobbling each trial: H_o: $md_1 = md_2$, $H = 6.8$, $P < 0.01$. The black boxes indicate the median values for the NA smolts and the grey boxes those for the SWA smolts.

Table 4. The number of smolts in the two groups that reacted when a predator was in the vicinity (<0.1 m).

	Not reacting	Reacting	Total
NA	16	14	30
SWA	6	20	26

a predator attacked (Table 3; H_o: the anti-predator response was independent of previous seawater adaptation, $\chi^2 = 5.8$, df = 2, $P = 0.054$). However, did the SWA fish escape more frequently than the NA fish did (Table 3; H_o: escape-response was independent of the previous seawater adaptation, $\chi^2 = 4.5$, df = 1, $P < 0.05$).

Stress behaviour

Both the median and the maximum numbers of the NA smolts that remained at the surface, wobbling, were significantly greater than those of the SWA ones (Fig. 4). Furthermore, the NA smolts stayed put and did not react more often when a predator was in the close vicinity (<0.1 m) (Table 4; H_o: adequate behaviour was independent of the previous seawater adaptation, $\chi^2 = 4.2$, df = 1, $P < 0.05$).

Predation risks

In this study I have considered four different ways of estimating the risks of smolts being predated: 1) the number of smolts actually killed by the predator, 2) the number of smolts that did not react when the predator approached and 'butted' its prey, but did not kill it, 3) the number of smolts that stayed put and did not react at all when the predator approached its prey but made no attempt to catch it, 4) the number of smolts that stayed put and did not react at all when the predator was close-by (<0.1 m). A statistical analysis of the pooled data for all four categories of risk of predation showed that the NA smolts were more liable to be exposed to

Table 5. The number of smolts in the two groups that A) were actually killed by the predator; B) were 'butted' or buzzed by the predator; C) stayed put when the predator attacked; D) stayed put when the predator approached to within 0.1 m but did not make an actual attack; E) were not in any of the categories A–D.

	A	B	C	D	E	Total
NA	3	3	3	7	14	30
SWA	0	1	1	4	24	30

'predation' than the SWA smolts were (Table 5; H_o: predation was independent of previous seawater adaptation, $\chi^2 = 5.8$, df = 1, $P < 0.05$).

Discussion

The general impression gained from the results of these experiments is that both groups of smolts showed a great variety of anti-predator behaviour. As a rule, there were no great differences in the reaction distances between the two categories of smolts when a predator approached its prey. However, when the smolts approached the predator, the NA smolts approached closer than the SWA smolts. The prediction from MAD hypothesis was that the NA smolts should show a shorter reaction distance than the SWA ones. This was only confirmed when the prey approached the predator and not vice versa.

The MAD hypothesis also predicts that the SWA smolts should shoal more frequently and form larger shoals than the NA smolts. The results of the present study support this prediction. The MAD hypothesis also predicts that the SWA smolts should 'freeze' and thereby escape detection or alternatively flee when the predator attacked them. No statistically significant difference was found between the two groups in regard to the frequency of 'freezing', but the SWA smolts showed escape-behaviour more frequently than the NA smolts. Thus, the prediction was fullfilled and the MAD hypothesis cannot be rejected. Moreover, the median escape-distance of the NA smolts was shorter than that of the SWA

smolts. The SWA smolts, furthermore, did not allow the predator to approach close to them as frequently as the NA smolts. These two results provide further support for the MAD hypothesis.

The data analyses have revealed that both groups of smolts showed the previously-defined stress symptoms. However, the NA smolts showed a greater tendency to adopt a stress behaviour pattern than the SWA ones did. They showed a greater tendency to remain at the surface, wobbling, or not to react at all, when a predator attacked or approached close to them. Such difference between the two groups agrees with the prediction made.

Although the estimated predation rate was only 10 % for the NA group and nil for the SWA group, a number of the smolts from both experimental groups that survived were nonetheless exposed to a risk of predation. In some cases the predator attacked but only butted the prey with its nose, or stopped when very close to the prey. In some other cases the predator swam very close to the prey without actually trying to catch it. In all of these cases it would have been quite a simple matter for the predator to have caught the smolt. All these smolts were therefore regarded as having been exposed to a high risk of predation. The results of this study therefore indicate that the NA smolts were exposed to a greater risk of predation than the SWA ones, and hence, that the prediction from the hypothesis can be considered to have been fulfilled. A similar lack of response towards a predator has also been reported for Baltic salmon smolts when attacked by burbot (*Lota lota*) (Jakobsson and Järvi 1977). However, when these same smolts were attacked by pike (*Esox lucius*) their behavioural response was prompt. The fact that the smolts reacted in an adequate way towards the pike suggests that the lack of reaction towards the burbot was due to a difference in the predatory behaviour of the burbot, which enabled the smolts to react adequately. Because the burbot is also a gadoid fish, the reason why the Atlantic salmon smolts did not always respond to the cod as a predator could also be due to the predation behaviour of the latter. However, if gadoid predatory behaviour

was the sole reason why the smolts did not react adequately, then such a great difference, as that found between the two experimental groups of smolts, would not be expected. It thus seems reasonable to suggest that at least two reasons exist as to why the smolts did not react adequately when the predator approached, viz. the behaviour of the predator and the physiological stress response to the osmotic change and the fright.

Although the seawater adapted smolts behaved in a significantly different way to the non-adapted smolts, there was a great variation in the responses made by the individual smolts in the two groups. This intra-group variability is probably due to individual differences in their ability to resist the stress, induced by the fright due to the presence of a predator. The psychological fright responses to stress appears to be important in terms of the physiological responses induced by stressful situations (Schreck 1981). In fact, the fright associated with the presence of predators does indeed stress the smolt physiological, shown as an increase in the glucose and lactate levels in its blood for Atlantic salmon (Järvi 1990) and an increase in the glucose and cortisol levels in its blood for Coho salmon (*Oncorhynchus kisutch*) (Rehnberg and Schreck 1987). The stress response of teleostean fishes is considered to be similar in nature to the General Adaptation Syndrome (GAS) proposed for mammalian vertebrates (Schreck 1981). GAS can be subdivided, on a temporal basis, into the separate stages of alarm, resistance and exhaustion (Pickering 1981). Rapid change in the ambient salinity may produce a physiological stress response in its own right (e.g. Schreck 1981, Järvi 1989, 1990). Normally, during the alarm phase of stress response, a loss of water occurs in parallel with the osmotic gradient from freshwater to seawater. This entails that some of the stored energy will have to be mobilized to restore the osmotic equilibrium. If stress reduces the ability of a fish to maintain homeostasis, then physiological exhaustion may result. The psychological aspects of stress appear to be important in terms of the physiological responses involved. Järvi (1990) has shown that psychological stress and osmotic stress together have a

cumulative, physiological, stress effect on smolts. This increased stressful situation may greatly reduce the ability of the fish to defeat exhaustion and it may eventually die (Järvi 1989). If stress reduces the ability to maintain homeostasis, then the normal, adaptive behavioural response to a further stress factor may be inhibited. In the present study, osmotic stress apparently inhibited the normal, adaptive anti-predator behaviour of the smolts so as when they were confronted with a predator their chance to escape an attack were significantly reduced.

Acknowledgments

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Delayed Release of Salmon Smolts (*Salmo salar* L.) of Different Ages at the Coast of Gotland, Baltic Main Basin

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Abstract

Young salmon of three different ages were released in brackish water at the coast of the Isle of Gotland in the Baltic Main Basin. In late May, hatchery reared and tagged three-year-old smolt were released in the sea, directly after transport from the hatchery. On the same occasion, two-year-old and one-year-old salmon were transferred to a net-pen in brackish water for prolonged rearing during the summer and release, after tagging, in late August. Recapture data reveal a very high survival rate (reported recaptures range from 43.5 to 51.6 %) in all groups.

A size dependent increase in recapture rate was found within the three-year-old group. This increase may be due to the high proportion (41 %) of mature males in the group. These mature males were of smaller size than the immature fish, thus the size-dependent lower survival rate could also be explained by a lower survival of mature males in general. No size-dependent increase in survival rate could be found within the groups released in the autumn. This fact is discussed and proposed to be dependent on the very high rate of reported recaptures.

No difference in mean weight at catch during the second autumn in the sea (i.e. the season with highest fishing pressure) could be found between normal river-released young salmon and those kept in a net-pen throughout the summer prior to release. The distribution of recaptures within fishing seasons reveals the high efficiency in the off-shore fishery in the Baltic Main Basin. This high efficiency is an obstacle to the full benefit of rearing and release of big, three-year-old smolt in the spring.

Introduction

In the salmon compensatory programme in Sweden, the normal rearing time for Baltic salmon smolt is two years, but in the southernmost part of Sweden one year is common (Ackefors et al. 1989). Stocking results are highly dependent on smolt size, i.e. the bigger the smolt the better the survival after release. The main reason for this is supposed to depend on a relatively higher predatory pressure on the smaller smolt (Larsson 1977b).

This size-dependency on the stocking results can be found both within stocking groups (e.g. Carlin 1969, Larsson 1977a, Johansson 1981, Lundquist et al. 1988, Karlsson et al. 1989) and between different rivers and year-classes (unpublished material, Salmon Research Institute). Thus a prolonged rearing in fresh water normally results in a totally higher return rate due to the bigger smolt (Carlin 1955, Eriksson and Johansson 1989).

It was also found that absolute size was not the only factor influencing the results. Experiments with releases in the same river on different occasions during the same year, indicate that also a correlation to time, i.e. water temperature, has a major influence on the total stocking results within rivers and years (Peterson 1973b, Larsson 1977a, Larsson and Eriksson 1979).

When comparing results with smolt of different ages released in the same river and year, the relatively larger size of the younger smolt give equal or better results than the relatively smaller size of the older smolt, even if the latter group are bigger on the average (Petersson 1973a, Eriksson and Johansson 1989). These results indicate that also factors such as a presumed higher general vitality of the relatively bigger smolt within each group of smolt are of importance to the stocking results. This presumption of a higher general vitality is underlined by results obtained with young salmon reared in high water velocity. When released, these young salmon gave higher recap-

tures compared to young salmon reared under normal conditions, even if the later group were bigger on the average (Petersson 1973 b).

Delayed release of salmon (Novotny 1980) has been tested in the northern part of the Baltic area. In combination with conventional rearing for two years in fresh water, an extended rearing period of different length in net-pens in brackish water in the Bothnian Sea during the third summer has given a size-dependent increased survival after release, both between and within different groups (Eriksson and Eriksson 1985, Eriksson et al. 1987, Eriksson 1988, 1989).

In the Baltic Main Basin the first experiment with delayed release took place in 1983 (unpublished). The present work was initially a continuation of that work and a pilot test to investigate the possibility of keeping one-year-old salmon in brackish water during their second summer.

The report evaluates the results obtained with salmon of three different ages, three-year-olds released in the spring, three-summer-olds and two-summer-olds released in the autumn after rearing in a net-pen in brackish water during three months.

Material and methods

All salmon in this experiment were of River Lule origin and reared in the hatchery of the Salmon Research Institute (SRI) in Älvkarleby. The eggs were transferred from River Lule in the eyed stage and mixed before rearing, thus all salmon originate from a number of parents.

In late May 1984, salmon of different ages were transferred in the same transport from the hatchery (Lat 60° 34′) to Ar, Gotland (Lat 57° 55′). The transport included 6–7 hours on a ferry, during which time brackish water (salinity 8 to 10 ppt) was pumped through the fish tanks. It was estimated that the water in the tanks was fully exchanged when the transport left the ferry.

At the release site, 494 tagged three-year-old salmon were released directly from the tank into the sea, without further temperation. These young salmon were randomly taken as two-year-olds

6

from those released in 1983 and kept during the third year in the hatchery for other purposes.

The two other groups consisting of 4,000 two-year-old and 4,000 one-year-old salmon were transferred into a net-pen of 100 m^3 at the same site, the later group adipose fin-cut. The two-year-olds were taken at random from those intended to be released in rivers in the spring. The one-year-olds were taken at random from the group with the highest mean weight after grading in sizes in the hatchery.

In late August, after 100 days of rearing in the net-pen, 508 three-summer-olds and 488 two-summer-olds were randomly selected, tagged and released together with the remaining untagged lot.

Tagging data and reported recaptures have been recorded according to normal routines at SRI (Carlin 1971). The material includes recaptures reported and processed before the end of December 1988. In the Baltic area some of the tags are reported with incomplete or no information. In order to obtain total biomass (kg/1,000 released) of salmon caught, necessary weight estimates have been made according to time of report and reported weights from the different experimental groups. These reports with estimated data are excluded in classifications of weight at catch and proportion of catches within seasons.

Tagging data from these experiments are compared with data from the total taggings in 1984 of salmon released into rivers during the spring within the Swedish compensatory programme. In the text, these data are referred to as controls.

Salmon weighing less than 1 kg when caught are regarded as post-smolt and are not included in any data discussed.

No corrections for unreported recaptures have been made.

Statistical analyses are made with principles and formulas given by Bonnier and Tedin (1940).

When testing for any correlations between length at release and recapture rate, the material was summarised so that each point on the curve represented at least 10 observations. This can be regarded as incorrect in some aspects but, on the other hand, the number of reported recaptures

Table 1. Tagging and recapture data from experiments with delayed release in the Baltic Main Basin and the compensatory programme in Swedish rivers 1984. The table includes level of significance between percentages of recaptures.

Age at release (years)	Release time	Number tagged	Mean length in mm	Recaptures		kg/1,000 released	Significance level			
				number	%		3	2+	1+	2
3	May (21)	494	318	215	43.52	1854	—			
2+	Aug (28)	508	293	236	46.46	2146	NS	—		
1+	Aug (28)	488	263	252	51.64	2258	*	NS	—	
2 (controls)	May–Jun	46987	179	4862	10.35	427	***	***	***	—

was so scarce in some length-groups that it was impossible to use the material in any other way. Where the material was summarized, the mean-length for the whole group was calculated and used as a base in the analysis.

Results

Net-pen period

In the net-pen during the summer, a mortality of around 10 % was observed for the two groups together. Besides the mortality, it was observed that some of the smallest one-year-old salmon managed to pass through the net in the net-pen during the first two days.

No data on individual length at transport or mean weight at release were available. The mean weight of the two-year-olds at transport was 69 grams which corresponds to a mean length of around 185 mm. Mean length of the tagged three-summer-olds at release was 293 mm. Corresponding data for the one-year-olds were 20 grams at transport or a mean length of around 135 mm and a mean length at tagging as two-summer-olds of 263 mm.

Survival after release

The recaptures from all experimental groups were very high compared with young salmon released in the rivers (Table 1). On the other hand, the differences between the experimental groups were tiny and only significant at the lowest level in one case, two-summer-olds versus three-year-olds.

In the group of three-year-old salmon, sexual maturation, i.e. running milt, of a large proportion (41 %) of the group was noticed during tagging in the early April. This group of mature males gave a lower recapture rate than the group of immature salmon (Table 2).

A positive correlation between length at release and recapture rate can only be found among three-year-olds (Fig. 1). The mean value for this increase in recapture rate was 4.5 % per 10 mm increase in length.

The number of recaptures of immature and mature males respectively was too low to establish a definite correlation between length at release and recapture rate. Attempts to analyse the material indicated that the correlation was not linear in any of the two subgroups.

Table 2. Tagging and recapture data of sexually immature and mature males together with level of significance between the two groups.

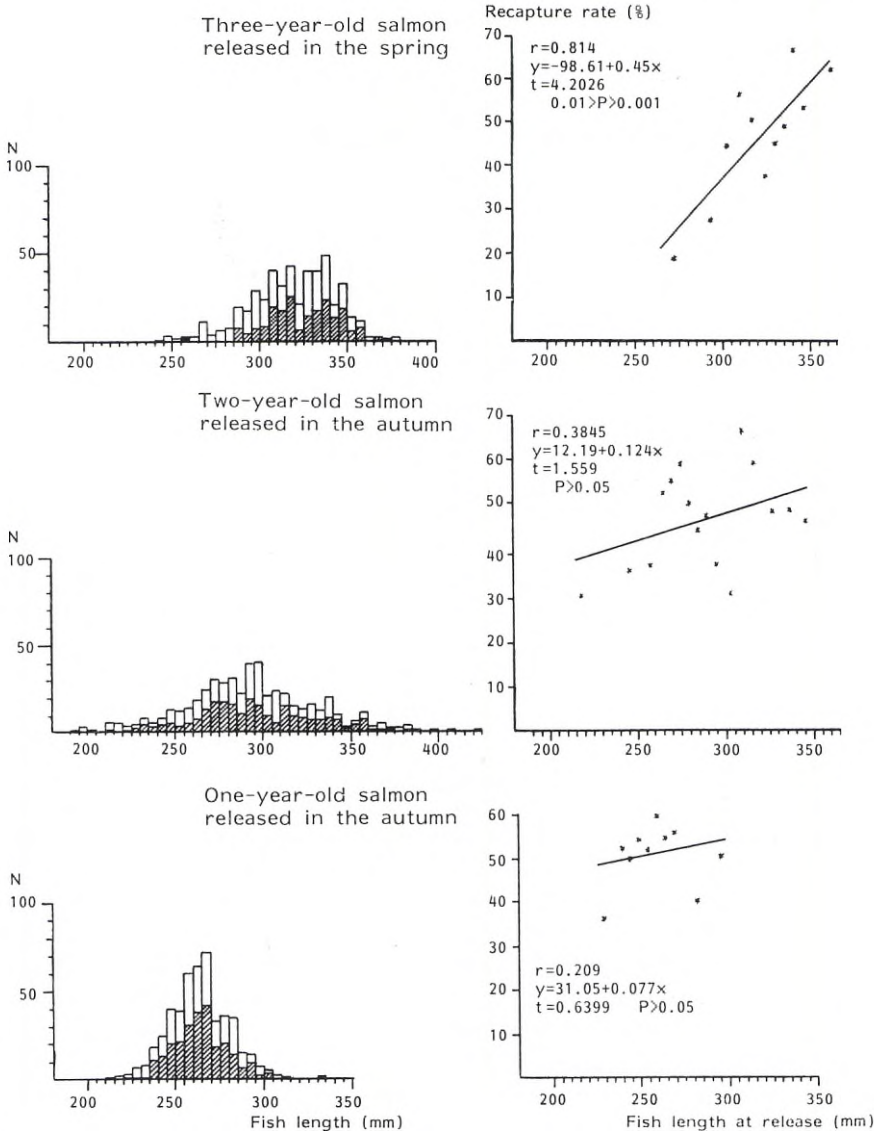| Fish-group	Number tagged	Mean length in mm	Recaptures		kg/1,000 released	Significance level	
			number	%		immature	mature
Immature	291	330	150	51.55	2196	—	
Mature	203	300	66	32.51	1385	***	—

Fig. 1. Size distribution (left) and regression between size at release and recapture rate (right) for salmon released at different age.
□ Number released salmon
■ Number recaptured salmon

Growth after release

Of the reported recaptures from the tagged salmon released in 1984 in the Baltic area, almost 75 % were reported from the off-shore fishing during their second winter in the sea (Anon. 1988). Within this winter more than 70 % were reported from the first part of the winter (September–December, unpublished SRI data). Therefore, in order to estimate growth after release, data from this period were used. Mean weights and numbers recaptured, month by month, are given in Table 3a and levels of significance of the differences in mean weights in Table 3b.

The mean weights during the second autumn in the sea were significantly higher for the three-

Table 3 a. Reported mean weights from the off-shore fishing during the second autumn after release. Figures in brackets indicate number of recaptures with complete data.

Age at release (years)	Release time	Mean weights in kilogram $\pm$ SE		
		September	October	November–December
3	May (21)	5.4$\pm$0.50 (12)	5.4$\pm$0.32 (19)	6.7$\pm$0.64 (4)
2+	Aug (28)	3.9$\pm$0.18 (33)	4.1$\pm$0.15 (37)	4.7$\pm$0.35 (13)
1+	Aug (28)	3.3$\pm$0.10 (38)	3.6$\pm$0.14 (59)	3.8$\pm$0.29 (16)
2 (controls)	May–Jun	3.7 (614)	3.9 (708)	4.1 (443)

Table 3 b. Level of significance in a paired comparison of the mean weights given in Table 3 a.

Age at release (Years)	Level of significance			
	3	2+	1+	2
3	—			
2+	*	—		
1+	**	NS	—	
2	*	NS	NS	—

year-old salmon. The favour of size at release in the spring resulted in a different exploitation pattern for the three-year-olds in the sea. They reached catchable size already during their first winter in the sea; the reported mean weight for salmon from this group during that period was 2.65 kg. The proportion of catches within seasons is given in Table 4.

Thus the three-year-olds reached catchable size faster than the other groups and the control, they also had a higher mean weight at catch during the second autumn in the sea.

Discussion

The recapture rates reported for the salmon released in the autumn were the highest ever recorded from Swedish taggings of young salmon. For the three-year-olds released in the spring the result was similar to some releases of very big two-year-old smolts from River Mörrumsån. No equally good results have been reported from other countries in the Baltic area. There was no difference in survival after release between big one-year-old fish or two-year-old fish of ordinary size when released from a net-pen.

These extremely good results probably depend on a combination of several factors. The growth of the salmon in the net-pen was very good and at the place of release it was observed, both in the spring and the autumn, that there were large numbers of small herrings present. The 1984 smolt-year-class has shown an unusually good survival, 10.35 % reported recaptures, and growth; reported mean weights of the controls from the second autumn in the sea were

Table 4. Proportion of catches within seasons (winters) in the off-shore fishing in the Baltic Main Basin. Level of significance calculated for the proportions caught during the second winter in the sea.

Age at release (years)	First winter		Second winter		Third winter		Significance level			
	number	%	number	%	number	%	3	2+	1+	2
3	89	51.5	76	43.9	8	4.6	—			
2+	6	2.9	181	86.6	22	10.5	***	—		
1+	6	3.1	173	90.1	13	6.8	***	NS	—	
2	123	3.9	2485	78.1	575	18.1	***	***	***	—

about 0.6 kg higher than from normal years in the Baltic area (Larsson, 1984).

In experiments with delayed release in 1980 at the coast of the Bothnian sea, Eriksson and Eriksson (1985) obtained reported recaptures of 27 % and 30 % respectively from two groups released in the autumn, while the total recaptures in the Baltic for river-based releases in 1980 were 7 %. Eriksson (1989) reports increased survival of delayed releases in 1980–82 with net-pen reared salmon, which is three to five times higher than river-based releases in the spring. Recaptures of the delayed released in 1984 are around five times higher than from the controls; the high proportion in the present experiments can be explained by the favourable release site in the middle of the Baltic proper. Finally, it must be observed that the one-year-olds used in the experiment were taken from the biggest in the hatchery of that year-class, and from them some of the smallest escaped in the net-pen. Thus the generally higher vitality of the relatively bigger fish within each year-class could have had an effect on the result.

Eriksson (1988) reports a correlation between length at release and recapture rate for delayed released young salmon that persists to a length at release of 390 mm. In the present experiments, no correlation between length at release and recapture rate could be found in the groups released in the autumn. The rich supply of food at the release site could be one factor giving high survival of the relatively smaller fish. The extremely high rate of reported recaptures could be another explanation of the missing correlation. Anon. (1988) uses a correction factor of 1.65 to compensate for lost and unreported tags. With that factor applied to these results, 77 and 85 %, respectively, of the salmon have been recaptured. It is hard to believe in a higher survival from release until catch than around 90 %, thus a recapture of 85 % is so near the absolute limit of recaptures that almost all of the possible catch is taken and no increase correlated to length at catch can be expected. This is in line with the tiny, although not significant, difference in angle of inclination in the regression lines between the two groups released in the autumn.

On the other hand, the same factor used on the result of the three-year-olds gives a recapture of almost 72 %. A positive correlation between recapture and length at release, cf. Eriksson (1988), is found in this group. The difference between this estimated recapture rate and that for the three-summer-olds (77 %) is small.

Within the group of three-year-olds, however, slightly more than 40 % were mature males, giving lower recaptures than the immature group. This proportion of relatively smaller mature males has a major influence on the length curve of the whole group and the lower recapture rate for the males is well in line with the size when released.

It has been discussed that mature males ought to give better results when released directly in the Baltic proper. Lundqvist et al. (1988), suggest that the lower recapture rates of precocious males, released in rivers, is dependent on the predation in the river. Eriksson et al. (1987) found a lower recapture rate of mature males than of immature young salmon of the same size when they were simultaneously released in a river in the spring. On the other hand, with salmon kept in a net-pen during the summer and released in the autumn in the sea, this difference could not be found. They could also state that males with early sexual maturity had a higher preference for staying in the river after release from the hatchery than the immature fish, which is in accordance with Hansen et al. (1989) who showed a lower degree of seaward migration for sexually mature males.

The three-year-olds in the experiment were released in the sea in the spring and the lower recapture rate for the smaller of the group could be explained both by size and sexual maturation as the major part of the relatively smaller ones were males at tagging.

Growth rate of salmon in the Baltic sea is difficult to estimate. The high selectivity in the drift-net fishery, together with an extremely high fishing pressure on growing salmon, results in catches more at a certain size than in different periods of fishing. In order to estimate growth

after release, both weight at catch during a chosen period and variance in catch within seasons have to be considered.

In the present experiments, no significant difference in weight at catch during the second autumn in the sea was found between the salmon released in the autumn and the controls. The proportion of catches within seasons shows that the two groups released in the autumn were caught to a higher extent during their second autumn in the sea. Together, these two facts indicate that net-pen reared young salmon obtain at least the same development in size as those released in the rivers in the salmon compensatory programme.

The group of three-year-old salmon released in the spring shows an even more complicated pattern. During their second autumn in the sea the mean weight at catch was definitely higher than for both those released in the autumn and the controls released in the spring. A rough comparison between reported weight at catch during the second autumn and estimated weight at release, however, gives a factor of around 15 times higher weight at catch. This can be compared with the same rough comparison of the gain in weight by the controls which gives a factor of around 60. On the other hand, the proportion of catches within seasons shows that the three-year-olds to a very high extent were caught already during their first winter in the sea. A true comparison of growth is prevented by this pattern of catch. Those captured during the first winter ought to have reached a considerably higher weight during the second winter in the sea than those caught during that period if they had survived to the second winter.

The fishing pressure, which takes salmon at a certain size more than within seasons, is thus an obstacle to the full benefit of rearing big three-year-old smolt for release in the spring.

Acknowledgments

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Delayed Release of Young Baltic Salmon (*Salmo salar* L.) in the Baltic Area. Comparative Releases of Salmon from Different Salmon River Stocks

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Abstract

In the Baltic area, releases of young tagged salmon from the southern stocks in their home rivers give a higher yield in survival and growth in the sea than young salmon of the northern stocks released in home rivers. In the present study, young salmon of five different stocks, ranging from the most southern to the most northern ones, were reared in the same locality and released simultaneously into the Baltic Main Basin. The main factor influencing survival after release and mean weight at catch was found to be individual length at release.

No evidence could be found for an assumption that delayed release of salmon from the southernmost stock should give better results than salmon of the northern stocks. On the contrary, the results, when related to mean length at release, were poorest with salmon of the southernmost stock. It is thus proposed that the differences obtained with releases in home rivers are dependent on climatic factors.

It was also found that young Baltic salmon, kept in net-pens during the summer and released in the autumn, ought to reach a length of at least 22 cm when released in order to obtain a reasonable rate of survival.

Introduction

In the Baltic area it has been shown that the yield of reared salmon (*Salmo salar* L.) released as smolt in their home rivers, is correlated to latitude. The more southern the stocks the better the results, both in growth and survival (Larsson 1984, Anon. 1989).

Experiments with delayed release of Baltic salmon have given a considerably increased survival compared to releases of salmon in rivers in the Swedish salmon compensatory programme (Ackefors et al. 1989, Eriksson and Eriksson 1985, Eriksson et al. 1987, Eriksson, T. 1988, 1989, Eriksson, C. 1989).

It has been suggested (Hannerz and Degerman 1984) that the yield of such delayed releases of Baltic salmon would increase even more, to at least a 2-fold improvement in the results presented so far if stocks from the southernmost Swedish rivers were used. The reason for this assumption would be expected stock differences in fitness during the sea phase.

This assumption is tested in the present study, where results are presented of survival and growth in the sea after release, from comparative experiments with young salmon originating from five Swedish Baltic salmon rivers, ranging from the northernmost to the southernmost river.

The experiments were parts of a major national project to investigate the possibilities of delayed release of salmon in the Baltic Area.

Material and methods

The juvenile salmon used in the experiments originated from Rivers Torne, Lule, Indalsälven, Dalälven and Mörrumsån (Fig. 1). They were reared in the same river under equal climatic conditions and partly released with the use of the delayed release technique.

The most characteristic data of these five salmon stocks are (partly from Nyman and Norman, 1987):
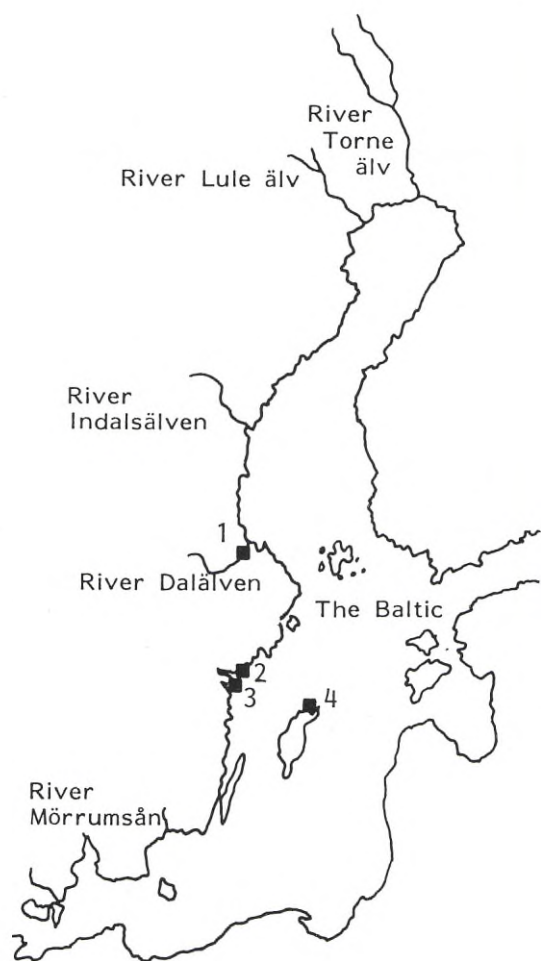
Fig. 1. Map of the Baltic area. Home rivers of used salmon stocks, rearing stations (1 Swedish Salmon Research Institute and National Fish Research Station, Älvkarleby) and release sites (2 Örsbaken, 3 Lilla Rimmö, 4 Ar) are indicated.

River Torne: Wild stock, no releases of other stocks, some enhancement with parr has been done during the last decade.

River Lule: Reared stock since around 1960, mixed with foreign stocks to a large extent.

River Indalsälven: Reared stock since around 1955, only occasionally mixed with foreign stock.

River Dalälven: Reared stock since around 1920, in addition a minor production of wild salmon. Only occasionally mixed with foreign stock.

River Mörrumsån: Mixed wild and reared stock, efforts are made to keep a fifty/fifty level of wild/reared migrating smolts, no releases of foreign stocks reported.

Eggs of salmon of the River Dalälven stock were collected in the autumn of 1982 and the salmon were reared at the hatchery of the National Fish Research Station, Älvkarleby (Fig. 1) as a part of the salmon compensatory programme.

In the spring of 1983, eggs in the eyed stage of the four other salmon stocks were transported to the hatchery of the Salmon Research Institute, situated at River Dalälven (SRI, Fig. 1). Salmon of River Lule stock are normally reared at our hatchery and eggs originating from a large number of parents are mixed. From the salmon stocks of Rivers Torne, Indalsälven and Mörrumsån a sample of about 3,500 eggs was randomly taken from several batches, thus ensuring a sufficient number of parents to get access to a representative sample of each stock.

In both hatcheries, each stock was kept separately and reared until two-year-olds with normal rearing routines, without grading.

In March 1985, as two-year-olds, 1,000 salmon of each of the Torne, Lule, Indalsälven and Mörrumsån stocks were tagged with Carlin tags, and kept in groups of 500 in the hatchery. They were all transported in late May to the release site at Ar, in the northern part of Gotland (Fig. 1). The transport was partly made on a ferry, during which time sea water was pumped through the tanks to give a complete exchange of water. Immediately after arrival at the release site, 500 tagged salmon of each stock were released in the sea. 500 tagged salmon of each stock, together with around 1,000 untagged, were kept and fed for 22 days in brackish water (8–10 ppt) in a net-pen of 100 m^3. Before release, a few individuals were randomly sampled, anaesthetized, tag number read and length measured. The number checked had to be kept low because of the very delicate status of the fish.

In early June, 3,000 two-year-old salmon of River Dalälven stock together with 3,000 adipose fin cut two-year-olds of River Lule stock, were transported to each of two commercial fish-

farms at the Swedish coast, Örsbaken and Lilla Rimmö (Fig. 1). At each place they were reared in brackish water (6–8 ppt) in a net-pen of 100 m³ for around 3 months (91 and 89 days). Just prior to release, 1,000 salmon of each stock were tagged at both places.

Tagging and recapture data were processed according to normal routines at our institute (Carlin 1971). The material includes reported recaptures processed before the end of December 1988. Salmon with reported weight of less than 1 kg were excluded in analysis of data. In the Baltic area some of the recaptures are reported with no or incomplete information. For assessment of total biomass (kg/1,000 released) of salmon caught, necessary estimates of weight have been made according to time of report and reported weights from the different experimental groups. Recaptures with estimated data were excluded in classifications of weight at catch and proportions of catches within seasons. No corrections for lost or unreported tags have been made.

Statistical analysis of the results was performed by analysis of variance and covariance using the GLM (General Linear Model procedure) in SAS (Statistical Analysis System), version 6.

These analysis were followed by a paired t-test of differences in recapture rates and regression between length at release and recapture rates according to principles and formulas given by Bonnier and Tedin (1940).

Tests for correlation between length at tagging/release and recapture rate was performed with the material pooled so that each point on the curve represented at least 10 observations. From a statistical point of view it may be discussed whether this is entirely correct, but the number of reported recaptures within certain length-groups were so scarce that there was no any other way to use the material. When the reports were summarized, mean length for released fish within this group was calculated and used as a base in the analysis.

In order to indicate the level of recaptures from normal spring-time releases within the Swedish salmon compensatory programme in 1985, data on taggings in the home rivers of the salmon stocks used in the experiments are given. No taggings were performed in River Torne in 1985. Due to the diversity of the background in rearing and release history, these data were not used in any statistical analyses.

Results

Net-pen periods

No mortality was observed in the net-pen at Ar and the measured fish showed an overall mean growth of just below 15 mm. The low number examined (57) gave no possibility to estimate differences in growth rate between the different salmon stocks. In further analyses of data from these groups, tagging length was used.

Observed mortality in the net-pens at Örsbaken and Lilla Rimmö was less than 5 % during the rearing period. Due to the necessary handling of the fish when the cutting of the adipose fin of the salmon from the River Lule stock was performed late in the spring, an outbreak of wart disease (Wirén 1971) just prior to transport, resulted in an observed reduced feeding activity during the first weeks in the net-pens for the salmon of this stock.

No data on length distribution at transport or weight at release are available. In comparing an estimated mean length at transport and mean length at tagging, no significant difference in gain of length could be found, either between stocks or places (range of gain in length was 0.45–0.50 % day⁻¹).

Recaptures after release

Recapture rates for the tagged salmon of the different stocks in the experiments were high, compared with data of tagged salmon in home rivers (Table 1).

The major factor influencing the survival of the releases at Ar in the sea was length at release. The period in the net-pen had a positive effect on the general survival after release. The salmon of River Mörrumsån stock, when taking into

Table 1. Tagging and recapture data on salmon released in the experiments and salmon of the same stocks released in their home rivers. Given mean length refers to length at tagging.

Stock/ origin	Release method/ site	date	Number released	Mean length	Recaptures in number	%	kg/1,000
Torne	Direct	850528	497	208 mm	126	25.35	1299
Torne	Net-pen	850618	488	218 »	160	32.79	1656
Torne	Total		985	213 »	286	29.04	1476
Lule	Direct	850528	498	191 mm	121	24.30	1120
Lule	Net-pen	850618	492	187 »	141	28.66	1482
Lule	Total		990	189 »	262	26.46	1300
Indal	Direct	850528	496	229 mm	148	29.84	1383
Indal	Net-pen	850618	485	233 »	166	34.23	1813
Indal	Total		981	231 »	314	32.01	1596
Mörrum	Direct	850528	499	235 mm	102	20.44	979
Mörrum	Net-pen	850618	492	239 »	125	25.41	1188
Mörrum	Total		991	237 »	227	22.91	1083
Mixed	Direct	850528	1990	216 mm	497	24.97	1195
Mixed	Net-pen	850618	1957	219 »	592	30.25	1533
Dalälven	Örsbaken	850905	998	247 mm	329	32.97	1410
Lule	Örsbaken	850905	996	226 »	192	19.28	765
Dalälven	L:a Rimmö	850903	998	241 mm	265	26.55	1139
Lule	L:a Rimmö	850903	999	226 »	192	19.22	781
Dalälven	Total	Mixed	1996	244 mm	594	29.76	1275
Lule	Total	Mixed	1995	226 »	384	19.25	773
Mixed	Örsbaken	850905	1994	237 mm	521	26.12	1088
Mixed	L:a Rimmö	850903	1997	233 »	457	22.88	960

Stock/ origin	Release date	Number released	Mean length	Recaptures in number	%	kg/1,000
Lule	850528–0613	8794	178 mm	568	6.46	259
Indalsälven	850520	4940	168 mm	515	10.43	398
Dalälven	850604	478	208 mm	46	9.62	410
Mörrumsån	850531	496	215 mm	40	8.06	337

consideration their length at release, gave poorer results than the other three stocks in the experiments. In no case had a combined factor significant influence on the results (Table 2 and 3).

The major factor influencing the survival after release at Örsbaken and Lilla Rimmö was length at release. Place of release was of greater importance to the results than stocks, especially when combined with length at release. The high degrees of significance in per cent recaptured between salmon of the two stocks were not fully explained by length and place (Table 2 and 3).

Number released and recaptured within length groups together with correlations between length and recapture rates from the releases at Ar are given in Fig. 2. As salmon of all

Table 2. Data on statistical analyses of survival after release. The upper part of the table has the results of the multiple analysis Anon. (GLM), with releases at Ar at the top. The lower part of the table gives levels of significance from a paired t-test of recapture rates, with releases at Ar at the top. In this part of the table the river names are coded as follows: River Torne=001; River Lule=009; River Indalsälven=040; River Dalälven=053 and River Mörrumsån=086.

Factor tested	Df	SS	F	
Length (at tagging)	1	1721.0651	37.33	***
Stock	3	1115.3576	8.06	***
Date (of release)	1	513.2030	11.13	**
Stock × Time	3	21.7289	0.16	
Length × Stock	3	114.0751	0.82	
Length × Time	1	130.8809	2.84	
Length × Stock × Time	3	88.6854	0.64	
Length (at tagging)	1	7092.4164	155.25	***
Stock	1	248.0117	5.43	*
Site (of release)	1	456.0873	9.98	**
Stock × Place	1	9.5011	0.21	
Length × Stock	1	0.0014	0.00	
Length × Place	1	603.4522	13.21	***
Length × Stock × Place	1	3.4207	0.07	

	Direct released				Net-pen reared				Stock total			
Stock	001	009	040	086	001	009	040	086	001	009	040	086
001	—				—				—			
009	NS	—			NS	—			NS	—		
040	NS	NS	—		NS	NS	—		NS	**	—	
086	NS	NS	***	—	*	NS	**	—	**	NS	***	—

	Örsbaken		Lilla Rimmö		Stock total		Release site			
Stock	009	053	009	053	009	053	site	Örsbaken	Rimmö	
009	—		—		—		Örsbaken	—		
053	***	—	***	—	***	—	L:a Rimmö	*	—	

Table 3. Temporal distribution of recaptures within fishing seasons (winters). Data on the different stocks released at Ar are summarized. The figures on per cent within season are based on total numbers of recaptures with date reported, i.e. catches out of the periods in the table are included.

Stock/ Origin	Release time/site	First winter		Second winter		Third winter	
		number	%	number	%	number	%
Torne	Mixed	22	14.7	111	74.0	9	6.0
Lule	Mixed	12	7.9	114	75.0	11	7.2
Indal	Mixed	23	10.5	161	73.5	21	9.6
Mörrum	Mixed	18	11.1	115	71.0	14	8.6
Direct	850528	37	12.3	223	73.8	24	7.9
Net-pen	850618	38	10.0	278	73.3	29	7.7
Dalälven	Örsbaken	2	1.0	170	81.0	27	12.9
Lule	Örsbaken	1	1.0	85	84.2	13	12.9
Mixed	Örsbaken	3	1.0	255	82.0	40	12.9

Table 3. Cont.

Stock/ Origin	Release time/site	First winter		Second winter		Third winter	
		number	%	number	%	number	%
Dalälven	L:a Rimmö	3	1.9	125	80.6	21	13.5
Lule	L:a Rimmö	2	1.8	91	79.8	21	18.4
Mixed	L:a Rimmö	5	1.9	216	80.3	42	15.6
Dalälven	Mixed	5	1.4	295	80.8	48	13.2
Lule	Mixed	3	1.4	176	81.9	34	15.8
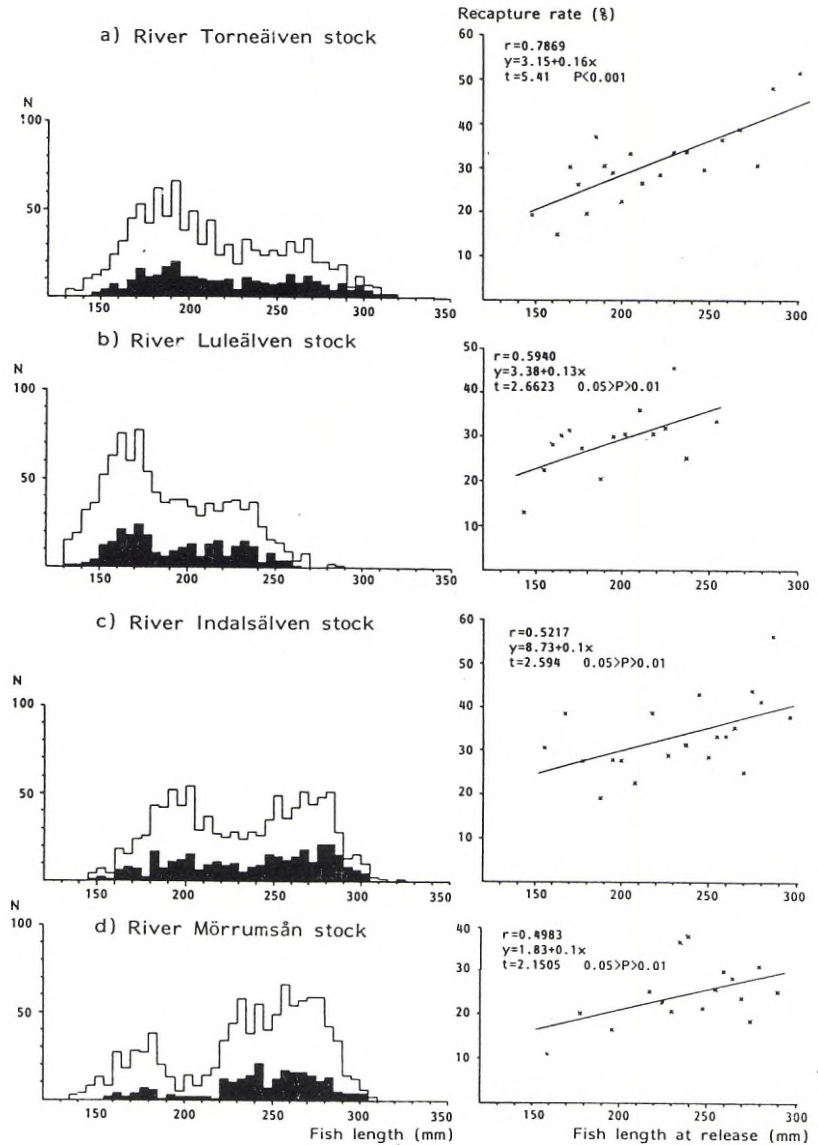
Fig. 2. Size distribution (left) and regression between size at release and recapture rate (right) for fish of different stock origin released at Ar 1985.

☐ Number released salmon
■ Number recaptured salmon
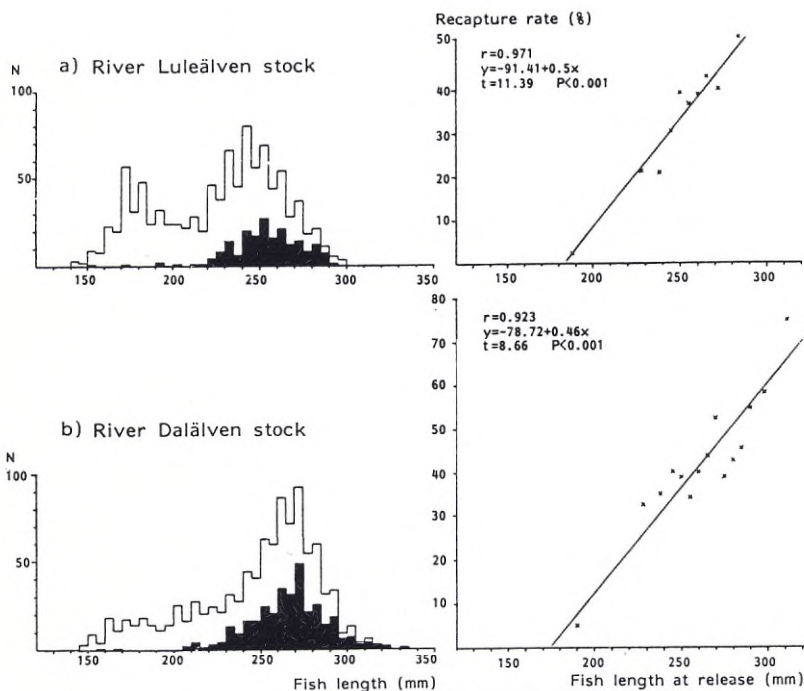
Fig. 4. Size distribution (left) and regression between size at release and recapture rate (right) for fish of different stock origin released at Lilla Rimmö in the autumn 1985.

☐ Number released salmon
■ Number recaptured salmon
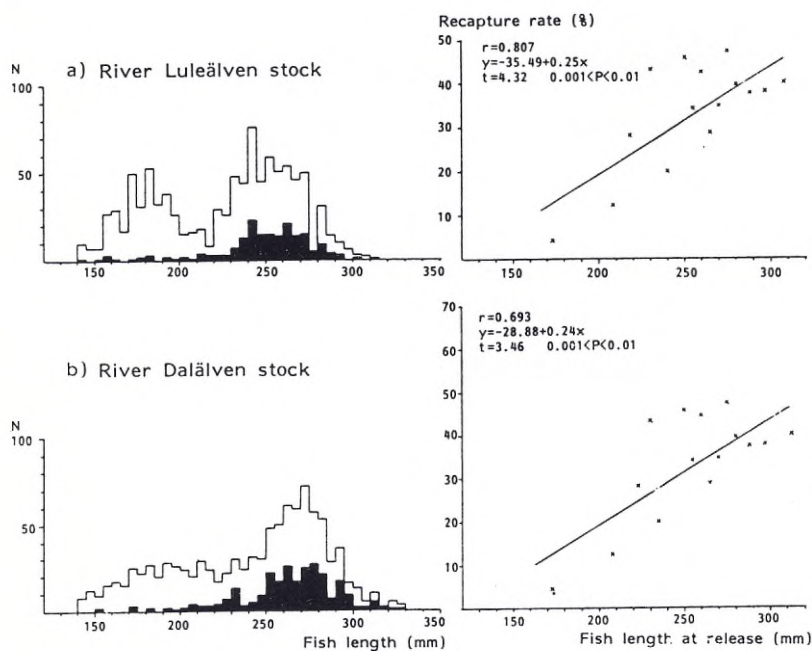
Fig. 3. Size distribution (left) and regression between size at release and recapture rate (right) for fish of different stock origin at Örsbaken in the autumn 1985.

☐ Number released salmon
■ Number recaptured salmon

stocks reacted equally to release methods, the summarised results were used.

Number released and recaptured within length groups and correlation between length at release and recapture rates from the groups at Örsbaken and Lilla Rimmö are given in Figs. 3 and 4. Because of the combined difference found in response to length and place, results from the two salmon stocks were not summarised.

A distinct difference was found in the angle of inclination between the releases at Ar and those at Örsbaken and Lilla Rimmö (Figs. 2, 3 and 4). The major factor creating that difference seemed to be the recapture rates of the relatively smaller fish within the different groups.

Temporal distribution of catches and growth in the sea

No significant differences in per cent recaptured within seasons were found, either between sal-

Table 4. Mean weights (kg) in the off-shore fishing during the second autumn after release. In the lower part of the table, data on releases in home rivers. Figures in brackets indicate number of observations.

Stock/ Group	Release time/site	Reported mean weights			
		September	October	November	December
Torne	850528	4.6 (17)	5.1 (16)	— —	7.0 (1)
Torne	850618	4.4 (17)	4.1 (13)	— —	8.0 (1)
Torne	Mixed	4.5 (34)	4.7 (29)		7.5 (2)
Lule	850528	4.2 (21)	4.7 (16)	3.8 (6)	3.7 (2)
Lule	850618	4.5 (22)	3.9 (15)	4.8 (5)	5.2 (5)
Lule	Mixed	4.4 (43)	4.3 (31)	4.3 (11)	4.8 (7)
Indal	850528	4.7 (26)	4.9 (12)	5.6 (9)	3.9 (5)
Indal	850618	4.7 (19)	4.7 (21)	5.0 (10)	4.7 (5)
Indal	Mixed	4.7 (45)	4.8 (33)	5.3 (19)	4.3 (10)
Mörrum	850528	3.6 (17)	4.3 (13)	— —	8.0 (1)
Mörrum	850618	4.4 (30)	3.7 (14)	4.7 (4)	6.1 (1)
Mörrum	Mixed	4.1 (47)	4.0 (27)	4.7 (4)	7.1 (2)
Direct	850528	4.3 (81)	4.8 (57)	4.9 (15)	4.7 (9)
Net-pen	850618	4.5 (88)	4.2 (63)	4.9 (19)	5.3 (12)
Dalälven	Örsbaken	3.1 (49)	3.3 (31)	4.0 (17)	4.0 (10)
Lule	Örsbaken	3.4 (15)	3.1 (21)	3.0 (10)	2.8 (6)
Mixed	Örsbaken	3.2 (64)	3.3 (52)	3.6 (27)	3.5 (16)
Dalälven	L:a Rimmö	3.0 (55)	3.2 (25)	3.6 (15)	4.2 (6)
Lule	L:a Rimmö	3.0 (17)	3.1 (24)	3.2 (11)	3.4 (9)
Mixed	L:a Rimmö	3.0 (55)	3.1 (49)	3.5 (26)	3.7 (15)
Dalälven	Mixed	3.0 (87)	3.3 (56)	3.8 (32)	4.0 (16)
Lule	Mixed	3.2 (32)	3.1 (45)	3.1 (21)	3.2 (15)

Stock/ origin	Release date	Reported mean weights			
		September	October	November	December
Lule	850528–0613	3.0 (59)	3.2 (51)	3.3 (27)	3.8 (13)
Indalsälven	850520	2.8 (61)	3.3 (51)	3.6 (31)	3.6 (14)
Dalälven	850406	3.4 (7)	4.9 (5)	3.9 (1)	—
Mörrumsån	850531	4.2 (2)	5.2 (4)	4.3 (3)	4.2 (2)

Table 5. Data on statistical analyses Anon. (GLM) on mean weights (growth after release) during the second autumn in the sea. The upper part of the table gives the experiments at Ar and the lower part those at Örsbaken and Lilla Rimmö.

Factor tested	Df	SS	F	
Length (at tagging)	1	9538.4420	55.83	***
Stock	3	3192.9330	6.23	***
Date (of release)	1	54.9255	0.32	
Month (of recapture)	3	914.1950	1.78	
Stock × Time	3	356.6669	0.70	
Length × Stock	3	956.9621	1.88	
Length × Time	1	20.6218	0.12	
Length (at tagging)	1	1773.5704	29.52	***
Stock	1	0.1158	0.00	
Place (of release)	1	37.7108	0.63	
Month (of recapture)	3	1761.3719	9.77	***
Stock × Place	1	81.5395	1.36	
Length × Stock	1	14.1495	0.24	
Length × Place	1	137.1705	2.28	

mon stocks or between release method from any of the release sites. The majority of recaptures were made during the second winter in the sea (Table 3). Within that period, 65–70 % were reported from the second autumn (September–December). With this background, estimates of weight at catch were based on reported weights from the second autumn in the sea.

Though not fully comparable, it is evident that monthly mean weights from the second autumn of salmon released in the experiments at Ar, the salmon of the River Mörrumsån stock excluded, were higher than mean weights of salmon released in home rivers in the spring. The salmon released in the autumn from Örsbaken and Lilla Rimmö seemed to obtain almost equal mean weights as salmon released in home rivers (Table 4).

A chi-square test on the mean weights of the salmon released at Ar and of those released in the autumn gave a significant difference ($P < 0.001$).

Length at release was the most important factor on growth in the sea for all salmon released within the experiments (Table 5). The releases at Ar also revealed a difference in mean weight between salmon stock, i.e. salmon of the River Mörrumsån stock seemed to have a lower weight at recapture than salmon of the other stocks. The

salmon released at Örsbaken and Lilla Rimmö had an increase in weight during the investigated period, which seems to depend on a positive development in weight of the salmon of the River Dalälven stock.

Discussion

In the Baltic area, a length-correlated increase in survival after release of reared young salmon in rivers has been demonstrated repeatedly, e.g. Carlin (1969), Larsson (1977b), Johansson (1981), Lundqvist et al. (1988), Eriksson and Johansson 1989, and Karlsson et al. (1989). Eriksson et al. (1987) and Eriksson, T. (1988, 1989) have shown that this length-correlated increase in survival also occurs with delayed releases of salmon in the Baltic area. Lundqvist et al. (1988) and Karlsson et al. (1989) found a similar increase in mean weight at recapture. Well in line with these earlier reports, it is evident, from the results obtained in this comparative release of salmon of different river stocks, that the most important factor for survival and growth after release is the length of the tagged fish.

Larsson (1977a) showed an increased survival with releases outside the river compared with releases in the river and Eriksson et al. (1981) report an increased survival of salmon from River Ljusnan which was 1.2 times higher if the releases were made in the river mouth, or in the open sea, instead of the river. The present results with direct releases of young salmon of different stocks into the sea in the spring gave at least a doubling of recapture rates compared with releases of tagged salmon of the same stocks in their home rivers.

As mentioned in the introduction, the technique with prolonged rearing in net-pens in sea water prior to release described by Novotny (1980) has been shown to improve survival after release also in the Baltic area. Eriksson (1988) found that only a short period of rearing in net-pens gave a higher survival after release. A similar increase is obvious in the experiments at Ar and seems to be independent of which salmon

stock is used. Compared with those released directly in the sea at Ar, the increase is about 1.2-fold, while compared with releases of salmon in their home rivers it is slightly over 3-fold. Eriksson, T. (1989) has estimated the general gain in survival with delayed release of young salmon in the Baltic area to be between 3-fold to 5-fold that of releases in rivers in the spring, while Eriksson, C. (1989) reports an increase of around 5-fold with delayed release at Ar. The salmon released in the autumn in this study gave an increase of a little over 3-fold compared to releases of tagged salmon in spring in their home rivers, but no increase in weight, cf. with Eriksson, C. (1989).

All these results of increased survival and growth appear, with a couple of exceptions, to be more or less independent of salmon stock used.

The small difference in survival that can be found in the results between salmon of the two stocks released in the autumn, depends most probably on the wart disease that hit the salmon of the River Lule stock just prior to transport and that was still visible at tagging and release.

However, no support for the gain in survival and growth after release by using the southern-most salmon stocks for delayed release, as proposed by Hannerz and Degerman (1984), can be found in the material. On the contrary, the results indicate that the only salmon which differ are those of the stock from River Mörrumsån which, when taking into account their relatively big size at tagging, showed both lower survival and growth after release than the salmon of the three other stocks released simultaneously. The gain, correlated to latitude, in salmon meat with releases of reared salmon that has been demonstrated by the Baltic Salmon and Trout Assessment Working Group, Anon. 1989) and Larsson (1984) is most probably an effect of climatic factors.

Normally, the young salmon of River Mörrumsån stock are released in late April or early May in the southern part of the Baltic which, according to Christensen and Larsson (1979), is the main feeding area of the Baltic salmon. On the other hand, the young salmon of, for example, the River Lule stock are released in late May or early June into an area with a sparse food supply and have to migrate a distance of at least 1,000 kilometres to reach the same feeding areas.

When compared with the tagged salmon released in their home rivers the salmon of the stocks from River Lule and River Indalsälven reach a considerable increase in mean weights when released at Ar in the Baltic Main Basin. On the other hand, the salmon of the River Mörrumsån stock show almost equal, or even less, mean weights, when released at Ar compared with salmon in their home river.

Although not fully comparable, the difference in increased survival with releases in the sea that can be found between Ar and those of River Ljusnan underlines the presumed effect of a favourable release site.

In the present material, differences are found both in reached weight at catch during the second autumn after release and in recaptures within seasons between those released at Ar in early summer and those released in the autumn at Örsbaken and Lilla Rimmö. It is close at hand to assume that salmon, when reared in a net-pen, have a slower growth than those feeding on natural food items in the sea, especially when the latter are released in the main feeding areas. Together with the fact that salmon released in River Lule obtained almost equal mean weight as those released in the autumn, these data underline the importance of a favourable release site.

The correlation between length at release and recapture rates of salmon released in the autumn (Figs. 3 and 4), show an extremely low recapture rate for salmon of both stocks with release length under 22–23 cm. Carlin (1969) suggests that the correlation between length at release and recapture rate is relative, i.e. the smaller individuals in each population, independent of absolute size, give poorer results. This theory cannot fully explain the drastic change in recapture rate that occurred with salmon over 22–23 cm. Lindroth (1961) found that the main food for post-smolt in the first stages in the sea was flying insects, of which very few can be expected in the sea in the autumn. It is therefore tempting to assume that

the extremely low survival of individuals under 22–23 cm depends of a lack of suitable food in the sea, i.e. only those who have reached a size where they can start feeding on small fishes will find enough food. This is underlined by the large difference in angle of inclination that can be found when comparing with the correlation lines of those released at Ar in the spring. Thus, in the Baltic area, in order to obtain a reasonable rate of recaptures with delayed release of salmon in the autumn, the size of the released fishes ought to be at least 23–24 cm.

Acknowledgments

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Zoobenthos and Food of Atlantic Salmon (*Salmo salar* L.) Fry in Alta River, North Norway – and Notes on the Measurement of Faunal Resemblance

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Abstract

Since 1980, 17 species of Ephemeroptera, 17 species of Plecoptera and 13 species of Trichoptera have been recorded at five localities in Alta River and its tributary Eiby River. The presences and absences of these species formed the basis of a comparison between the localities, employing the UPGMA clustering method and six different qualitative resemblance coefficients. All dendrograms showed the same pattern, which apparently reflected the different living conditions at the stations. An attempt was also made to compare the bottom fauna between the localities through five years, employing two quantitative resemblance coefficients. The year-to-year changes did not follow any particular trend, and it is presumed that repeated sampling for at least 20 years is necessary to include natural changes in the fauna composition. The properties and uses of the resemblance coefficients are discussed.

At any given time, 2–4 prey species usually dominate the stomach contents. These very often were insect larvae in their rapid growth period, and were eaten 1–2 months before emerging or during the emerge. After the emerge and disappearance of an important prey species, the salmon fry year-classes respond differently to the new situation. The similarities between stations and between years which were found from the bottom samples were poorly reflected in the stomach content, presumably due to this food selection. Hence an overall correlation between bottom samples and stomach contents was difficult to find. Schoener diet overlap indices were calculated between year-classes of salmon fry. From these it is concluded that the salmon fry switch their prey to a progressively smaller extent as they grow older.

At the end, the general development of the insect fauna in Alta River through the season is discussed.

Introduction

The Alta River, North Norway, was regulated for hydroelectric purposes in 1987, giving an electricity production of about 625 gwh per year. This regulation was quite controversial at the time; taking place in a relatively undisturbed area it was in conflict with the interests of the reindeer herding Sami and the traditional salmon fishery. The Alta River was (and still is) by many people regarded as the life nerve in West Finnmark.

Freshwater investigations have been conducted since 1980, under the aegis of the Directorate of Nature Management, Trondheim. The main purpose is to analyse the effects of the regulation on the salmon population and the salmon fishery, and to advise on how to run the power station with as small damaging effects as possible. A number of reports and articles have been published (Heggberget 1985, 1987, 1988, Heggberget and Wallace 1984, Heggberget et al. 1986a, 1986b, 1988a, 1988b, Huru 1986, 1987, Mork and Heggberget 1984, Wallace and Heggberget 1988).

The sampling program in the Alta River is intended to continue until at least 1992. As a side effect, bottom samples of macroinvertebrate fauna and the contents of salmon fry stomachs have also been analysed. This paper presents some preliminary results from these analyses, along with a discussion of some methods for the measurement of faunal resemblance.
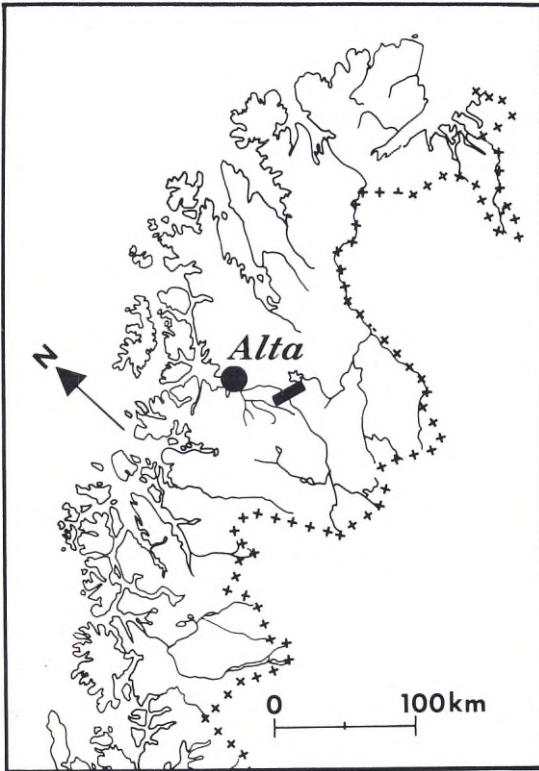
Fig. 1. Map of Finnmark County, North Norway.
■■ marks the dam construction in Alta River, below which the samples were taken.

Study area

The Alta River, located in the subarctic, is about 160 km long. The catchment area is 7,400 km², and the annual rainfall is 300–400 mm. The river freezes in November. Primo May there are some open leads, and ultimo May/primo June the ice breaks up and there is a short, moderate spring flood. Maximum summer water temperature is 13–15°C, falling to less than 1°C at the end of October.

The river is regarded as the best salmon producing system in Norway. The sport fishery catches are about 12–16 tonnes per year. This fishery often takes place from long and narrow, specially designed river boats, most of them coming from the small town Alta at the river outlet.

In general, more than 95 % of the fish fry in the river is salmon fry. Other fish species below the reservoir are anadromous and resident trout (*Salmo trutta*), anadromous and resident Arctic charr (*Salvelinus alpinus*), grayling (*Thymallus thymallus*), European minnow (*Phoxinus phoxinus*), whitefish (*Coregonus* sp.), pike (*Esox lucius*), burbot (*Lota lota*), perch (*Perca fluviatilis*), eel (*Anguilla anguilla*), flounder (*Platichtys flesus*) and three-spined stickleback (*Gasterosteus aculeatus*).

About 46 km from the sea, in the famous Šavčo canyon, a waterfall prevents further upstream salmon migration. One km above this waterfall a dam of 110 m height was constructed, and the upstream reservoir was filled during the spring of 1987.

The 4 sampled stations are all located downstream the reservoir (Fig. 1): 45 km from the sea (A16), 39 km (A12), 28 km (A8) and 12 km from the sea (A4). The two upper stations (A12 and A16) are located in the Šavčo canyon. A8 is located 13 km upstream of the confluence with the tributary Eiby River, and A4 3 km downstream. The bottom substrate at A4 is sandy and unstable due to erosion from the river bank; at A8 the substrate is stony but still unstable, heavily overgrown with algae. At A12, and especially at A16, the water current is stronger and the substrate more settled. In addition one station in the tributary Eiby River was sampled (E1). A detailed description of the Alta River and the sampling stations is found in Bergersen (1987).

Materials and methods

Bottom samples were collected by the kicking method of Hynes (1961). About 4 m × 0.25 m of the river bottom was stirred up, and the downstream material was collected in a plankton net with a square opening (29 × 29 cm) and a mesh size of 250 μm. The whole sample was then conserved in 96 % ethanol. At depths of 0.3–0.5 m, 3–5 replicate samples were taken. Clearly this method gives inadequate density measures, but it is a quick and fairly good way to estimate the faunal composition. A disadvantage is some un-

derestimation of attached forms such as snails and simuliid larvae.

Salmon fry were collected employing electric fishing gear. The fry were directly conserved in 96 % ethanol. This proved sufficient to fixate the stomach content.

In May, samples from A4, A8 and A16 were collected. The two other stations were then ice-covered. Samples from all 5 stations were collected in August and September. The discussion in this paper is based on Huru (1984) and on data from May 1984–88 and August/September 1984–87. Owing to lack of space, almost all results presented here are based on data from May 1984–88. Additional data from May, and from August/September is found in Bergersen (1987).

At each station, bottom samples were pooled and the proportion of each taxon calculated (see Table 4). Each taxon in the fry stomachs was counted and also given a fullness index, ranging from 0 (not present) to 100 (extended stomach). This is essentially the points method of Hynes (1950), slightly modified. The advantage of this method is that it becomes possible to compare fishes of different size or different year-classes, since the V % (see below) is independent of fish size (Hyslop 1980). Stonefly larvae (Plecoptera), mayfly larvae (Ephemeroptera) and caddis fly larvae (Trichoptera) were as far as possible identified to species. The identification level of the remaining taxa varies from family to order. The identification literature was Lepneva (1970, 1971), Lillehammer (1974a), Merrit and Cummins (1978), Solem (1983, 1985) and Svensson (1986).

Salmon fry stomachs were only treated when they exceeded a number of 20 within each year-class (Table 1). Percentage contribution by volume of a taxon i in a sample of salmon fry (V %$_i$) was calculated as in Hyslop (1980):

$$V \%_i = \frac{\text{mean stomach fullness of } i \times 100}{\text{mean stomach fullness of all food taxa}}$$

Nine different resemblance coefficients have been used to detect the faunal similarity between stations and between fry samples (Table 2). The procedure of making raw data matrices, compute the resemblance index and finally execute

Table 1. Number of examined salmon fry stomachs (5 year-classes, May only), from which the Schoener diet overlap indices were calculated.

		1984	1985	1986	1987	1988
A4	1+	30	—	48	—	25
	2+	30	—	26	—	—
	3+	—	—	37	—	—
	4+	—	—	—	—	—
	5+	—	—	—	—	—
A8	1+	30	—	38	30	26
	2+	30	—	—	22	40
	3+	30	—	21	32	28
	4+	—	—	21	37	40
	5+	—	—	—	—	21
A16	1+	—	24	27	66	—
	2+	—	25	31	33	28
	3+	—	30	30	34	33
	4+	—	—	21	—	43
	5+	—	—	—	—	—

the clustering follows Legendre and Legendre (1983) and Romesburg (1984). The raw data matrices in this paper could in some sense be called standardized (Romesburg 1984), since the original raw data are transformed into proportions (equation 7.8, p. 85 in Romesburg 1984).

For the qualitative data set of Table 3, where 0 means absence and 1 means presence of a taxon, six resemblance coefficients for qualitative data were used. These are the Sokal's binary (Cheetham and Hazel 1969), simple matching (Sokal and Michener 1958), Tanimoto and Phi (Sokal and Sneath 1963), Jaccard (Jaccard 1908) and Sørensen (Sørensen 1948) coefficients (Table 3). By convention, **a** means the number of cases when two stations share a taxon in common, that is, **a** = the number of 1–1 matches. **b** means the number of presences in first station along with absences in the second (1–0 matches); **c** means the number of 0–1 matches and **d** means the number of 0–0 matches. The equations of **Sb**, **Si**, **T** and **Phi** takes **d** into account, that is, absence of a species at both stations contributes to the similarity between them. The equations of **J** and **Sø** excludes **d**, and reckons only **a** (the presence of a taxon at both stations) to contribute to similarity. All coefficients except Sokal's bi-

Table 2. Resemblance coefficients used in this study. Arrows indicate monotonic relationships (see text). X_{ij} = the measured value in the raw data matrix for the ith taxon at the jth locality. X_{ik} = the value for the ith taxon at the kth locality. $n = a+b+c+d$ = the number of taxa considered. For definitions of a, b, c and d: see text.

Range

$$\text{Euclid's average (E)} = \left[\sum_{i=1}^{n} (X_{ij} - X_{ik})^2 / n \right]^{0.5} \qquad 0 - \sqrt{\frac{2}{n}}\,^*$$

$\updownarrow$

$$\text{Sokal binary (Sb)} = \left[\frac{b+c}{a+b+c+d} \right]^{0.5} \qquad 0 - 1$$

$\updownarrow$

$$\text{Simple matching (Si)} = \frac{a+d}{a+b+c+d} \qquad 0 - 1$$

$\updownarrow$

$$\text{Tanimoto (T)} = \frac{a+d}{a+2(b+c)+d} \qquad 0 - 1$$

$$\text{Phi} = \frac{ad - bc}{\left[(a+b)(a+c)(b+d)(c+d) \right]^{0.5}} \qquad -1 - 1$$

$$\text{Jaccard (J)} = \frac{a}{a+b+c} \qquad 0 - 1$$

$\updownarrow$

$$\text{Sørensen (Sø)} = \frac{2a}{2a+b+c} \qquad 0 - 1$$

$\updownarrow$

$$\text{Schoener (Sc)} = 1 - 0.5 \sum_{i=1}^{n} |X_{ij} - X_{ik}| \qquad 0 - 1\,^*$$

$\updownarrow$

$$\text{Bray-Curtis (B)} = \frac{\sum_{i=1}^{n} |X_{ij} - X_{ik}|}{\sum_{i=1}^{n} (X_{ij} + X_{ik})} \qquad 0 - 1\,^*$$

* For the quantitative resemblance coefficients, the range of values only applies when the objects are described by the proportion of each attribute, or when the data matrix is standardized so that each object sums to 1 (that is, when $\Sigma (X_{ij}+X_{ik})=2$).

nary are similarity coefficients, with a range of 0 to 1, where 0 indicates maximum dissimilarity and 1 indicates identical fauna. Sokal's binary is a dissimilarity coefficient with 0 indicating perfect similarity and 1 indicating perfect dissimi-larity. Presence-absence resemblance coefficients are discussed in Simpson 1960, Cheetham and Hazel 1969, Baroni-Urbani and Buser 1976 and Romesburg 1984.

Faunal similarity between stations (bottom

Table 3. Since 1980, 46 species of Ephemeroptera (1–16), Plecoptera (17–33) and Trichoptera (34–46) are recorded at 5 localities in Alta River and Eiby River (locality numbers: see text).

1 means presence and 0 means absence of the species. From this raw data matrix, similarity between the localities were calculated using the qualitative resemblance coefficients in Table 2. The resulting dendrograms are shown in Fig. 2.

		Stations			
	A4	A8	A12	A16	E1
1 *Ameletus inopinatus*	1	1	1	1	1
2 *Parameletus chelifer*	1	0	0	0	0
3 *Metretopus sp.*	1	0	1	1	0
4 *Baetis fuscatus/scambus*	1	1	1	1	1
5 *B. lapponicus*	1	0	1	1	1
6 *B. muticus*	1	1	1	1	1
7 *B. rhodani*	1	1	1	1	1
8 *B. subalpinus*	0	1	1	1	0
9 *B. vernus*	0	0	1	1	0
10 *Centroptilum luteolum*	1	0	0	1	0
11 *Heptagenia dalecarlica*	1	1	1	1	1
12 *H. joernensis*	1	1	1	1	1
13 *H. sulphurea*	0	0	0	1	0
14 *Ephemerella aurivillii*	1	1	1	1	1
15 *E. mucronata*	1	1	1	1	0
16 *Caenis sp.*	0	0	0	1	0
17 *Taeniopteryx nebulosa*	1	1	1	1	1
18 *Amphinemura borealis*	1	0	1	0	1
19 *A. sulcicollis*	1	1	1	1	1
20 *Nemoura avicularis*	1	0	0	0	0
21 *Protonemura meyeri*	0	1	0	1	0
22 *Leuctra digitata*	1	1	0	1	1
23 *L. fusca*	1	1	1	1	1
24 *L. hippopus*	1	1	0	1	1
25 *L. nigra*	1	0	0	0	0
26 *Capnia atra*	0	0	1	1	1
27 *C. pygmaea*	1	1	1	1	0
28 *Capnopsis scilleri*	0	0	0	0	1
29 *Arcynopteryx compacta*	1	1	1	1	1
30 *Diura nanseni*	1	1	1	1	1
31 *Isoperla obscura*	0	0	1	1	1
32 *Dinocras cephalotes*	1	1	1	1	1
33 *Siphonoperla burmeisteri*	1	1	0	1	1
34 *Rhyacophila nubila*	1	1	1	1	1
35 *Mystrophora intermedium*	1	1	1	1	1
36 *Hydroptila pulcricornis*	0	0	1	0	0
37 *H. tineoides*	1	1	0	0	0
38 *Philopotamus montanus*	0	0	0	0	1
39 *Arctopsyche ladogensis*	1	1	1	1	1
40 *Hydropsyche nevae*	1	1	1	1	0
41 *Polycentropus flavomaculatus*	0	1	1	1	1
42 *Apatania stigmatella*	1	1	1	1	1
43 *Potamophylax latipennis*	0	0	0	0	1
44 *Chaetopteryx spp.*	1	1	1	0	1
45 *Lepidostoma hirtum*	0	1	0	0	0
46 *Ceraclea nigronervosa*	0	1	1	0	0

Table 4. The standard set-up for the calculation of faunal resemblance between localities (bottom samples, May only), using the quantitative resemblance coefficients in Table 2. The resulting resemblance matrices are shown in Table 5.

The example below is from A8 (May), and shows the proportional contribution of each taxa by numbers.

	Year			
	84	86	87	88
Nematoda	0	0	0	0
Lymnaea peregra	0	.02	.02	0
Oligochaeta	.01	.10	.01	.02
Hydrachnidae	0	.04	0	0
Ameletus inopinatus	.16	.01	.01	.01
Parameletus sp.	0	0	0	0
Baetis spp.	.20	.30	.39	.31
Heptagenia dalecarlica	.21	0	0	0
Ephemerella aurivillii	.17	.02	.03	.05
E. mucronata	0	0	0	0
Taeniopteryx nebulosa	0	0	0	0
Amphinemura borealis	0	0	.02	0
Leuctra hippopus	.01	0	.02	.01
Arcynopteryx compacta	.01	0	0	0
Diura nanseni	.06	.01	.03	.01
Dinocras cephalotes	0	0	0	0
Capnia pygmaea	.01	0	0	0
Nemoura sp.	0	0	0	0
Rhyacophila nubila	0	.01	0	.01
Hydroptila sp.	0	0	0	0
Arctopsyche ladogensis	0	0	0	0
Hydropsyche nevae	0	0	0	0
Apatania stigmatella	0	0	0	0
Lepidostoma hirtum	0	0	0	0
Polyc. flavomaculatus	0	0	0	0
Limnephilidae	0	0	0	0
Trichoptera, p.	0	0	0	0
Tipulidae, l.	0	0	0	0
Simuliidae, l.	0	.01	0	0
Chironomidae, l.	.16	.45	.46	.57
Chironomidae, p.	0	0	0	0
Ceratopogonidae, l.	0	.01	0	0
Empididae, l.	0	.03	0	0
Sialis sp.	0	0	0	0
Dytiscidae	0	0	0	0

samples) were also calculated from quantitative data sets (as in Table 4), using the average Euclidean distance coefficient (Table 2, Romesburg 1984) and the Bray-Curtis dissimilarity measure (Bray and Curtis 1957).

To illustrate the relative faunal similarity between stations, the resulting resemblance matrices were clustered following the unweighted pair-group method of arithmetic averages (=UPGMA method, Sneath and Sokal 1973, Romesburg 1984). The values from the resulting tree were compared with the resemblance matrix by the Pearson correlation coefficient. This gives the so-called cophenetic correlation coefficient (**r**) of Fig. 2 and Fig. 3. It ranges from 0 to 1, with 1 indicating perfect similarity. For the tree to represent the resemblance matrix, a value of **r** above 0.8 is acceptable (Romesburg 1984).

Calculations and the UPGMA clustering was done at the SYSTAT.3 PC software package.

Resemblances between stomach contents were measured from the Schoener diet overlap index (Table 2, Schoener 1968, Wallace 1981). This is really a similarity coefficient, ranging from 0 to 1, where 0 means no taxa in common and 1 means perfect similarity in stomach contents. The Schoener indices were calculated from proportions of food items by volume (as in Table 8), which is really the V % divided by 100.

Results and discussion
Bottom fauna – qualitative analyses

Since 1980, 17 species of Ephemeroptera, 17 species of Plecoptera and 13 species of Trichoptera have been recorded at the stations A4, A8, A12, A16 and E1. Table 3 shows the presences (1) and the absences (0) of these species. The stations were compared to each other using six different resemblance coefficients, and the resulting dendrograms are shown in Fig. 2. All dendrograms exhibit the same pattern: the stations A12 and A16 are most similar to each other, then A4 and A8 forms a separate group, and E1 differs from the four other stations. The dendrograms are based on repeated samples from nine years at different seasons. It is therefore thought that the result tells something about the dissimilar conditions between the stations: some are able to carry a species and some are not. The reasons for this may be physical (water current speed, temperature, ice-covering, substratum) and/or biological (inter-/intraspecific competition, food availability, fish predation). Terms such as habitat
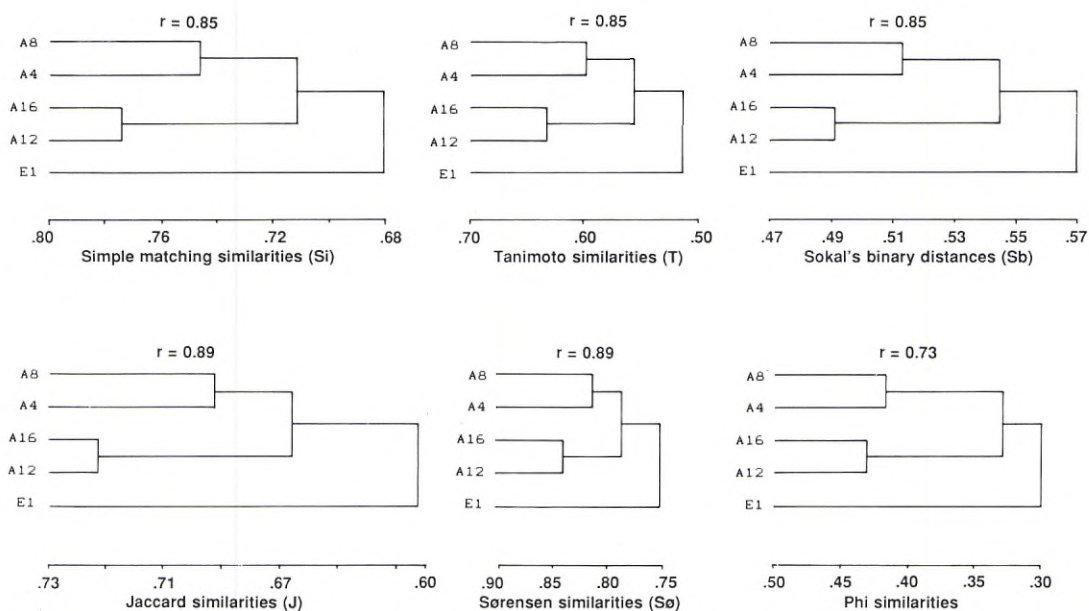
Fig. 2. Dendrograms(trees) showing the relative faunal similarity between 5 localities in Alta River and Eiby River. The trees were produced by UPGMA-clustering (Sneath and Sokal 1973) of 6 different resemblance matrices, calculated from Table 3. **r**=cophenetic correlation coefficient (see text).

segregation and niche come into account. An important aspect (which is easy to forget) are the conditions for the adult insects to survive and reproduce. The stations A12 and A16 are located in the Šavčo canyon. Here the climate is somewhat different from A8 and especially A4, which exhibits a more coastal climate. In the inland canyon there are cold winters and hot summers, and the river bottom substratum is more settled due to higher stream velocity. The smaller tributary Eiby River (E1) may again set other conditions for the zoobenthos. This general pattern seems to be reflected in the dendrograms (Fig. 2).

In this particular study, it is quite obvious that all recorded species in the Alta River should have the opportunity to occupy and exist at all stations. At least, there exist no biogeographic reasons why they should not. Therefore it here seems logical to allow **d** (the common absence of a taxon at two stations) as well as **a** (the common presence) to contribute to similarity. In any case, **a** does not tell anything about the abundances of the taxon. However, in most ecological studies **d** is not included, and the Jaccard and

Sørensen coefficients are widely used. This "double-zero problem" is discussed in Legendre and Legendre (1983) and Romesburg (1984).

The Jaccard (**J**) and Sørensen (**Sø**) coefficients were found to be monotonically related, i.e. the two equations are related by an unequality (Fig. 4a). The simple matching (**Si**), Tanimoto (**T**) and Sokal's binary (**Sb**) coefficients are also mathematically related (Fig. 4b). **Si** is always greater than **T** and **Sø** is always greater than **J**. The relationships are easy to calculate and give

$$T = \frac{Si}{2-Si} \quad \text{or} \quad Si = \frac{2T}{T+1} \quad \text{and}$$

$$J = \frac{Sø}{2-Sø} \quad \text{or} \quad Sø = \frac{2J}{J+1}$$

The similarity between the **Si**, **T** and **Sb** dendrograms (Fig. 2) should be interpreted as a result of the related coefficients rather than because of the data. However, the position of the stations in relation to each other is strenghtened by the similarity between the **J** and **Si** dendrograms (Fig. 2).
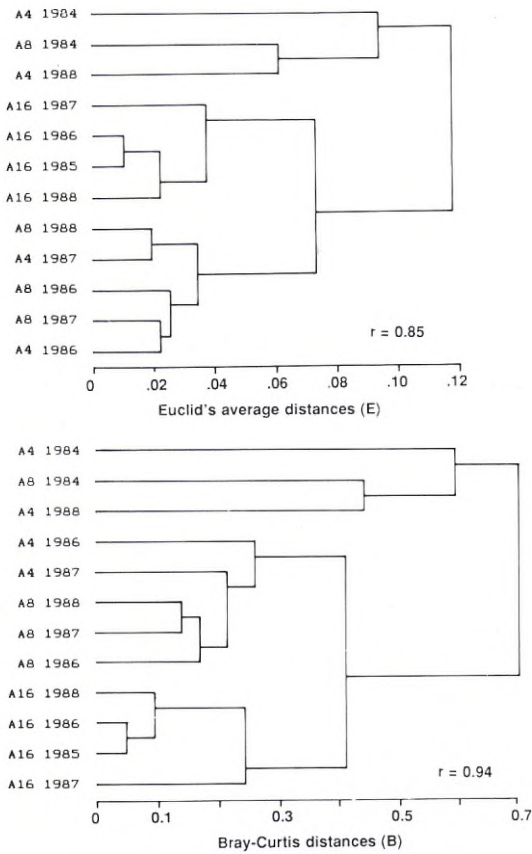
Bottom fauna – quantitative analyses

Twelve different quantitative data sets of bottom samples (as the four in Table 4) were compared to each other using Euclidean distances and the Bray-Curtis measure. The resulting resemblance matrices are shown in Table 5. The matrices were then cluster-analyzed (Fig. 3) to see the pattern of similarity between stations and between years. Both dendrograms show the same pattern: Three distinct clusters were formed. One is containing the samples from A16 in four successive years, the other two combines the samples from A4 and A8. A4 1984, A8 1984 and A4 1988 differ clearly from the rest, and they are also quite unequal to each other. What then, do these differences and similarities consist of? So far, after 5 years of sampling, it becomes clear that it is not possible to see any trend in the development of the fauna. Especially it is not possible to say what differences before/after 1987 are due to the dam construction. It is here suspected that repeated samplings for at least 20 years before regulation had been necessary to catch up natural changes in the fauna composition. In that respect, the title of this paper might have been: "Repeated samplings in Alta River – an epitaph".

The Sokal's binary distance (which includes **d**) is equivalent to the Euclidean average distance when the data are restricted to values of 0 and 1, and the Sørensen coefficient (which excludes **d**) is

Fig. 3. Trees showing the relative faunal similarity in May between bottom samples from 3 localities in Alta River, at 5 different years. The trees were produced by UPGMA-clustering of the resemblance matrices in Table 5. **r** = cophenetic correlation coefficient (see text).
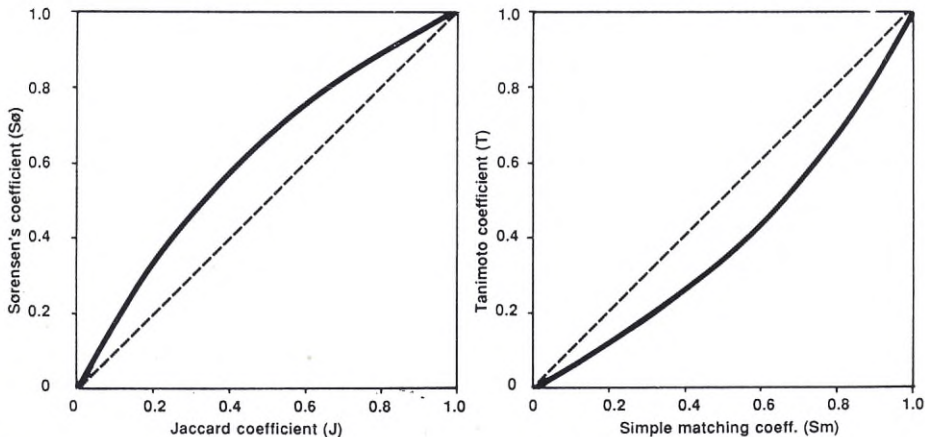
Fig. 4. Idealized monotonic relation between the Sørensen index and the Jaccard index (a), and between the Tanimoto and Simple matching indices (b).

Table 5. Resemblance matrices with the resemblance coefficients (lower left half) between 3 localities at 5 different years (bottom samples). a) calculated from the Euclidean average distance, b) from the Bray-Curtis distance. After clustering, the corresponding values from the trees (Fig. 3) were found, and are shown at upper right half.

a)

	A484	A486	A487	A488	A884	A886	A887	A888	A1685	A1686	A1687	A1688
A484	—	.118	.118	.096	.096	.118	.118	.118	.118	.118	.118	.118
A486	.126	—	.035	.118	.118	.027	.022	.035	.074	.074	.074	.074
A487	.121	.047	—	.118	.118	.035	.035	.021	.074	.074	.074	.074
A488	.101	.093	.085	—	.063	.118	.118	.118	.118	.118	.118	.118
A884	.090	.066	.079	.063	—	.118	.118	.118	.118	.118	.118	.118
A886	.125	.030	.031	.091	.075	—	.027	.035	.074	.074	.074	.074
A887	.131	.022	.034	.097	.079	.024	—	.035	.074	.074	.074	.074
A888	.134	.040	.021	.100	.087	.027	.023	—	.074	.074	.074	.074
A1685	.157	.090	.052	.128	.126	.072	.074	.052	—	.011	.039	.022
A1686	.157	.096	.056	.127	.127	.077	.081	.059	.011	—	.039	.022
A1687	.137	.073	.033	.101	.099	.054	.060	.039	.032	.031	—	.039
A1688	.170	.114	.074	.142	.144	.095	.098	.076	.025	.020	.050	—

b)

	A484	A486	A487	A488	A884	A886	A887	A888	A1685	A1686	A1687	A1688
A484	—	.712	.712	.601	.601	.712	.712	.712	.712	.712	.712	.712
A486	.720	—	.269	.712	.712	.269	.269	.269	.413	.413	.413	.413
A487	.700	.340	—	.712	.712	.226	.226	.226	.413	.413	.413	.413
A488	.640	.710	.590	—	.440	.712	.712	.712	.712	.712	.712	.712
A884	.560	.510	.790	.440	—	.712	.712	.712	.712	.712	.712	.712
A886	.790	.280	.290	.770	.600	—	.180	.180	.413	.413	.413	.413
A887	.760	.170	.210	.710	.550	.180	—	.150	.413	.413	.413	.413
A888	.750	.260	.160	.720	.550	.180	.150	—	.413	.413	.413	.413
A1685	.830	.480	.310	.800	.690	.400	.380	.270	—	.060	.251	.100
A1686	.820	.530	.360	.790	.740	.440	.430	.360	.060	—	.251	.100
A1687	.750	.470	.280	.680	.610	.380	.360	.230	.250	.230	—	.251
A1688	.830	.580	.410	.800	.790	.500	.480	.370	.100	.100	.270	—

equivalent to the complement of the Bray-Curtis measure (Romesburg 1984). The Euclidean and the Bray-Curtis measure were therefore found not to be mathemathically related. Besides, the Euclidean measure varies with **n**, the numbers of taxa included. However, in practice both resemblance coefficients give essentially the same result. This can be seen from Fig. 5, where the almost linear relationship becomes clear. When clustered, the resulting dendrograms will be fairly similar (as in Fig. 3).

A clustering procedure

The Euclidean measure is widely used in many research fields. The Bray-Curtis measure is widely used in marine ecological studies, and is according to Romesburg (1984) accepted as "ecologically meaningful" by many researchers. Both measures are mathematically simple and easy to understand. Which of them to choose may in practice be a matter of taste, but the Euclidean distance should be preferred only when **d** (common absence of species) is considered to contribute to similarity. The clustering method now widely used is the UPGMA method (Sneath and Sokal 1973). Its mathematical properties are generally accepted (Strauss 1982, Romesburg 1984), and there seems to be no reason why freshwater biologists should not use it for general ecological studies. Given the choice of a resemblance coefficient (see above), the treatment of the raw data matrix will conclusively influence the final result. It is possible to compute the resemblance
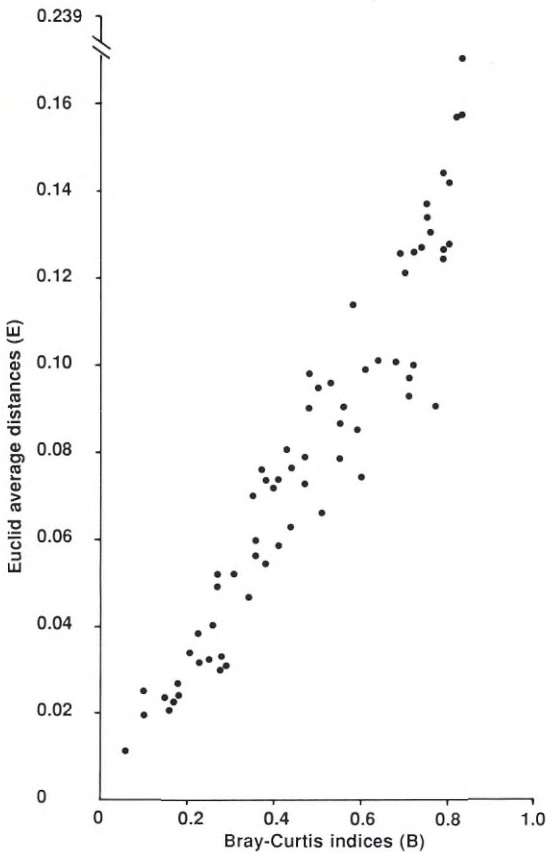
Fig. 5. Corresponding values of the Euclidean average coefficients and the Bray-Curtis coefficients in Table 5.
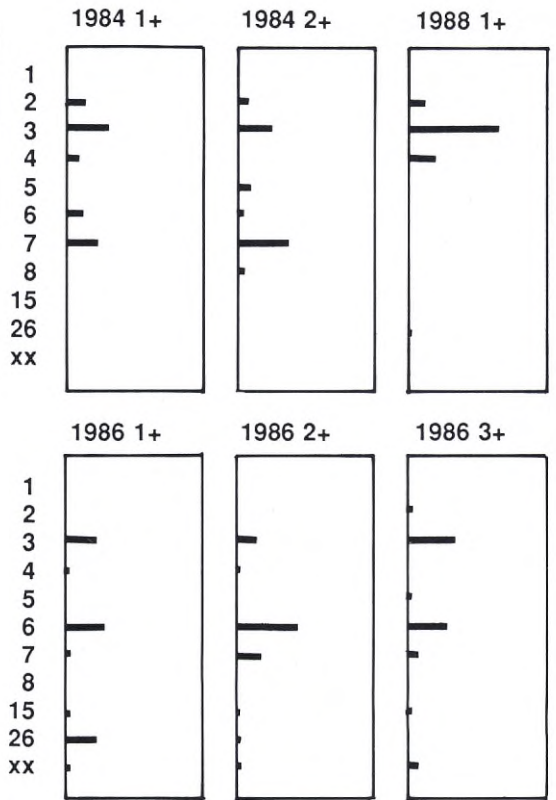

Fig. 6. Contribution by volume (V %) of 11 different taxa in salmon fry stomachs at A4, May.

1 = *Ephemerella mucronata*, 2 = *E. aurivillii*, 3 = *Ameletus inopinatus*, 4 = *Baetis* spp., 5 = *Heptagenia dalecarlica*, 6 = *Capnia pygmaea*, 7 = *Diura nanseni*, 8 = *Arcynopteryx compacta*, 15 = *Apatania stigmatella*, 26 = Chironomidae, larvae and pupae, xx = Others.

coefficient values directly from it, or it can be transformed in many ways (standardized, square rooted, log-transformed or converted into proportions as done in this study). This must be the decision of each researcher, but it should be explained carefully to the reader what is actually done. In most studies the treatment of the data matrix and the choice of a resemblance coefficient will be dependent on to what extent the faunal density or the faunal composition (or both) shall contribute to overall resemblance.

To sum up, a simple and meaningful clustering procedure may be the following:

a) Convert the raw data matrix into proportions (0–1 scale), 0–10 scale (cover values much used in botany) or a percentage scale (0–100). The scale choice is important only when a resemblance coefficient containing products are chosen! When computing the resemblance values, then dominating species will influence the result more on a 0–100 scale than on a 0–1 scale.

b) Choose the Euclidean distance measure (E) when **d** (common absences of species) is considered to contribute to similarity, or else use the Bray-Curtis measure (B). Be aware that E is a similarity coefficient and B is a dissimilarity coefficient!

c) Compute the resemblance values into a resemblance matrix.

d) Execute the clustering following the UPGMA method.
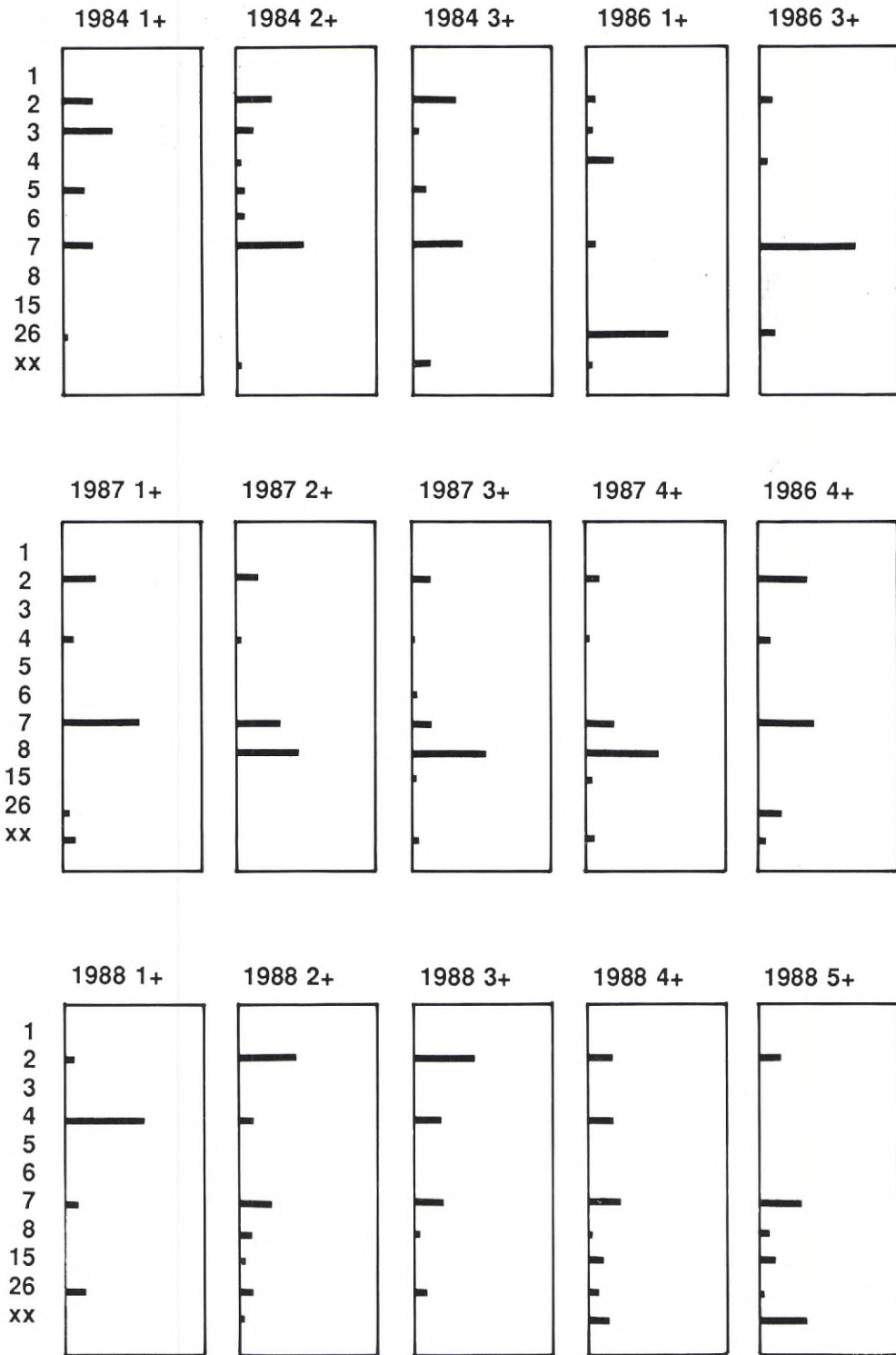
Fig. 7. Contribution by volume (V%) of 11 different taxa in salmon fry stomachs at A8, May. Legend: see Fig. 6.
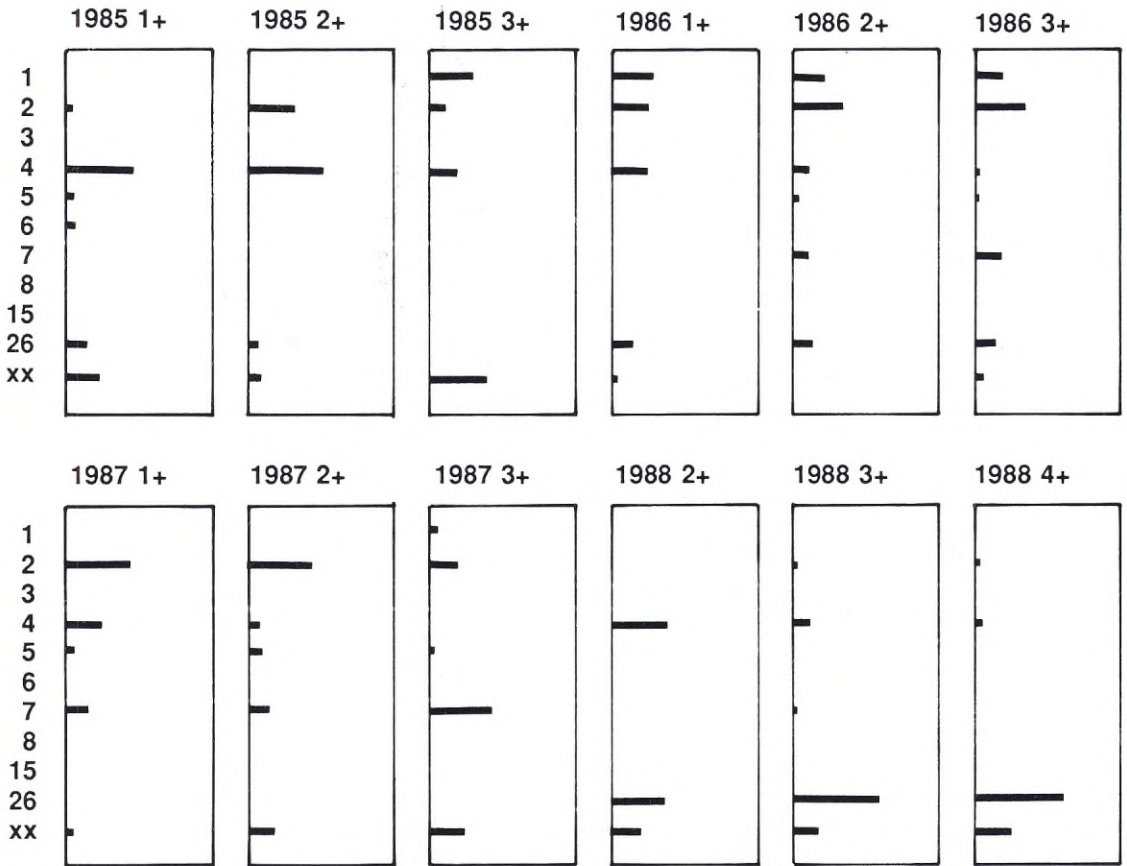
Fig. 8. Contribution by volume (V%) of 11 different taxa in salmon fry stomachs at A16, May. Legend: see Fig. 6.

e) Compute the Pearson cophenetic correlation coefficient to ensure that the dendrogram represents the resemblance matrix (values above 0.8 are acceptable).

f) If possible, rearrange the raw data matrix from the dendrogram to see the important differences between the clusters or the similarities within each cluster.

Table 6. Schoener diet overlap indices between years (May).

| | A4 | | A8 | | | | A16 | | | |
	1+	2+	1+	2+	3+	4+	1+	2+	3+	4+
84–86	.46	.46	.21	—	.46	—	—	—	—	—
84–87	—	—	.49	.64	.31	—	—	—	—	—
84–88	.60	—	.18	.51	.55	—	—	—	—	—
85–86	—	—	—	—	—	—	.44	.50	.36	—
85–87	—	—	—	—	—	—	.34	.46	.32	—
85–88	—	—	—	—	—	—	—	.46	.21	—
86–87	—	—	.22	—	.25	.41	.55	.60	.56	—
86–88	.32	—	.46	—	.45	.58	—	.26	.24	.24
87–88	—	—	.25	.65	.32	.44	—	.11	.13	—
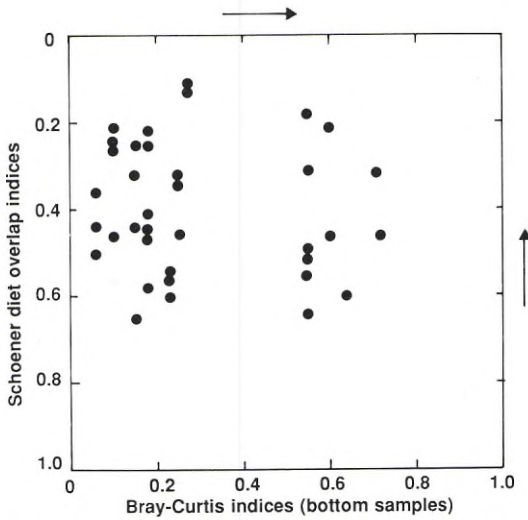
Fig. 9. Bray-Curtis indices from bottom samples plotted against Schoener diet overlap indices (May only), calculated from salmon fry stomachs collected at the same place and time. Arrows indicates increasing dissimilarity.

Stomach analyses

Some of the results from the stomach analyses are presented in Figs. 6, 7 and 8 (May only). The points method of Hynes (1950) proved sufficient to roughly quantify the relative importance of the food items.

Through the season, about 10 species of benthic insect larvae, the snail *Lymnaea peregra*, the simuliids and the chironomids were considered to be the most important food items for the sal-mon fry. Surface insects were eaten very infrequently. At any given time, usually 2–4 species dominate the stomach content. These very often proved to be in their rapid growth period, and were frequently eaten 1–2 months before emerging and during the emerge. After the emerge of an important food prey, the diet is dependent on the new fauna composition and prey availability. This varies to some degree from year to year and between stations, and different year-classes also respond differently to the new situation. In addition, some insects are perennial and may occur in several size-classes of larvae simultaneously. The emerging time of some insects may vary from year to year, and some insects have an extended period of egg hatching. This complex picture was partly revealed in Bergersen (1987), where a number of selection indices (Strauss 1979) were calculated. A taxon highly positively selected for at one station was often found to be negatively selected at the other stations, and this situation might be reversed the following year. At all seasons the food of the youngest salmon fry seemed most to reflect the composition of the bottom fauna (Bergersen 1987). The older year-classes became more selective in their choice of food items.

Within each year-class, Schoener indices between years were calculated for A4, A8 and A16 (May only, Table 6). An attempt was made to cluster-analyse the Schoener-indices. The resulting dendrogram was impossible to interprete,

Table 7. Schoener diet overlap indices between year-classes (May).

	A4		A8				A16			
	1984	1986	1984	1986	1987	1988	1985	1986	1987	1988
1+–2+	.70	.67	.67	—	.64	.34	.56	.75	.80	—
1+–3+	—	.70	.62	.35	.35	.44	.24	.62	.56	—
1+–4+	—	—	—	.34	.42	.42	—	.57	—	—
1+–5+	—	—	—	—	—	.17	—	—	—	—
2+–3+	—	.72	.73	—	.70	.87	.33	.85	.68	.52
2+–4+	—	—	—	—	.77	.59	—	.72	—	.45
2+–5+	—	—	—	—	—	.53	—	—	—	—
3+–4+	—	—	—	.67	.76	.71	—	.75	—	.85
3+–5+	—	—	—	—	—	.44	—	—	—	—
4+–5+	—	—	—	—	—	.64	—	—	—	—

Table 8. The standard set-up for the calculation of Schoener diet overlap indices (Schoener 1968) between fry samples (May only).

The example below is from May A8 1988, and shows the proportional contribution of each taxa by volume.

	Year-classes				
	1+	2+	3+	4+	5+
Ephemerella mucronata	0	0	0	0	0
E. aurivillii	.06	.42	.45	.18	.16
Ameletus inopinatus	0	0	0	0	0
Baetis spp.	.70	.11	.20	.19	.01
Heptagenia dalecarlica	0	0	0	0	0
Capnia pygmaea	0	0	0	0	0
Diura nanseni	.08	.23	.22	.24	.30
Arcynopteryx compacta	0	.10	.03	.03	.06
Leuctra hippopus	0	0	0	.03	0
Taeniopteryx nebulosa	0	0	0	0	0
Protomemura meyeri	0	0	0	0	0
Dinocras cephalotes	0	0	0	0	0
Isoperla obscura	0	0	0	0	0
Nemoura spp.	0	0	0	0	0
Apatania stigmatella	0	.03	0	.11	.11
Hydropsyche nevae	0	0	0	0	0
Arctopsyche ladogensis	0	0	0	0	0
Rhyacophila nubila	0	0	0	0	0
Polyc. flavomaculatus	0	0	0	0	0
Chaetopteryx spp.	0	0	0	.05	.30
Trichoptera, p.	0	0	0	0	0
Empididae, l.	0	0	0	0	0
Tipulidae, l.	0	0	0	0	0
Simuliidae, l.	0	.02	0	.08	.02
Psychodidae, l.	0	0	0	0	0
Chironomidae, l./p.	.16	.09	.10	.09	.02
Sialis sp.	0	0	0	0	0
Surface insects	0	0	0	0	.01

since no systematic trend between the stations nor between years was apparent. The dendrogram is therefore not presented here. In other words, the trends which were found from the bottom samples (Fig. 3) were not reflected in the stomach contents. This is also evident from Fig. 9, where no correlation between the Schoener indices and the Bray-Curtis indices is apparent. As a preliminary conclusion, it seems difficult to use stomach contents as a tool to measure the bottom faunal resemblances between years. Presumably this has to do with the developmental stages of the insect larvae, which may vary from year to year. Also, minor differences in fauna composition may cause major effects on the selection of prey items. This effect is strenghtened when sampling occurs before/after (or during) the emerge of an important prey insect species.

Schoener diet overlap indices (Schoener 1968) between year-classes are presented in Table 7, calculated from the standard set-up in Table 8. Diet overlap indices between year-classes for May, August and September are presented in Fig. 10a, and shown from left to right with decreasing similarity in stomach content (5+ not included). In general, the year-classes 3+ and 4+ appears to have the most similar stomach content, followed by 2+ and 3+. Naturally, 1+ and 4+ had eaten the most dissimilar food items. An attempt was made to visualize the general distances in food choice between the year-classes
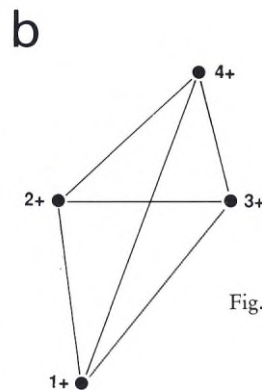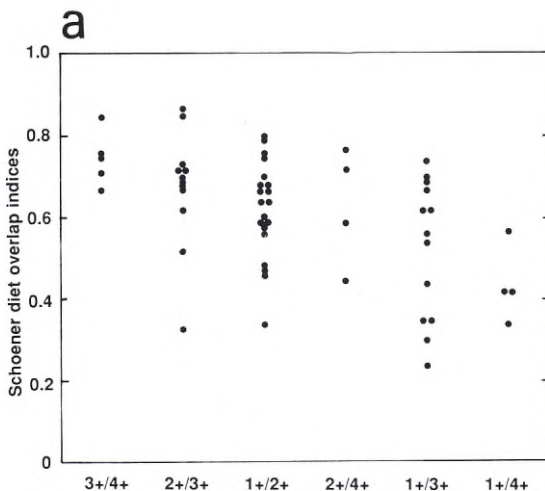

a

b

Fig. 10. a) Schoener diet overlap indices between year-classes (same place and time) for May, August and September. b) Idealized picture of the Schoener distances between year-classes, calculated from the mean values of a).

in Fig. 10b. The distance used was the complement of the Schoener index (1 – Schoener index). In fact, this distance was found to be equivalent to the Bray-Curtis measure, when the denominator of the Bray-Curtis equation (Table 2) is 2. In other words, when the Bray-Curtis measure is used on percentages or proportions, it is equivalent to the complement of the Schoener index. The geometric distances between the year-classes in Fig. 10b are the averages of the values from Fig. 10a, and were simply drawn by a pair of dividers. Some distances between 0+ and 1+ in August/September were also calculated, showing that the gap between these yearclasses was considerably larger than between 1+ and 2+. From this the preliminary conclusion is that the salmon fry switch their prey to a progressively smaller extent as they grow older. Very likely this is correlated with the relative size increment of the fry, and not with the absolute size increment.

Alta River through the season

Where no others are cited, the following is based on own material and Huru (1984).

Though there are great natural changes in fauna composition from year to year (especially at A4 and A8), the general features in the development of the fauna through the season became apparent. From the stomach analyses, it is concluded that the all-year food of the salmon fry are chironomids and the univoltine mayfly *Heptagenia dalecarlica*. Also the mayfly *Ephemerella aurivillii* and the stonefly *Diura nanseni* occur in the river most of the year, and were frequently eaten. Presumably the abundance and life cycle of these taxa permit them to become the most important food items on a yearly basis. Predation on other taxa was strongly time dependent, and closely followed the development of the fauna through the season.

When judging the most important prey for the salmon fry through the year, it became clear that at least 20 species of benthic invertebrates should be accounted for. These 20 species are referred to below. The occurrence and abundance

of the benthic evertebrate fauna in Alta River are remarkably in accordance with that in other large North Norwegian rivers (Huru 1984) and also Vindelelva, Northern Sweden (Ulfstrand 1967, 1968).

Three species of stoneflies emerges before the spring flood, which occurs between medio May and medio June. These are *Taeniopteryx nebulosa*, *Capnia pygmaea* and *Arcynopteryx compacta*. *T. nebulosa* emerges first, in the end of April when the river is still ice-covered. This species is sparsely represented at all seasons, but present almost everywhere in the river.

Capnia pygmaea is a lowland species, seldom found above the tree line (Lillehammer 1974b). In the lower parts of the river, *C. pygmaea* occurs in wast amounts when it emerges in primo May. Along open leads it may turn the ice completely black, and occasionally it "invades" nearby housings. This conspicuous species has therefore adopted different local names. In August and September the numerous young larvae appear, being important prey for larger invertebrate predators. Though not investigated, *C. pygmaea* presumably is an important food for the salmon fry during the winter months. In April/May it is a major food item.

Arcynopteryx compacta emerges in May, and already in June the river has a stock of small larvae. This stock is severely reduced during the summer months. It is quite surprising that the larvae one finds in September are not much bigger than they are in June. The main growth seems to occur in April/May, when it is of some importance as food for the salmon fry.

In May and June the mayfly species *Ameletus inopinatus*, *Ephemerella aurivillii*, *Ephemerella mucronata*, *Parameletus chelifer* and the stonefly *Diura nanseni* have rapid growth, and they are then important prey. *D. nanseni* emerges in June, soon after the spring flood. Being the most common carnivore stonefly species in Norway (Lillehammer 1974b) it occurs everywhere in the river, but especially at localities in fast-flowing parts. Already in July the small larvae appear, and these presumably were hatched in late winter/ early spring. It is well known that the eggs may not be hatched the first year (H. Huru, pers.

com.), and Ulfstrand (1968) stated that the species may have an annual and a two-years life-cycle simultaneously. *A. inopinatus* is winter-active (Ulfstrand 1968) and has a long period of sustained growth towards the emerge in July. In September the young nymphs appear. However, it seems that this species may have a strategy analogous to *D. nanseni*, since some small nymphs found in June presumably were hatched in early spring. According to Gledhill (1959) these nymphs grow quickly towards the emerge; the life cycle of *A. inopinatus* is therefore presumably annual.

Ephemerella aurivillii clearly shows an annual life cycle, as in Vindelelva (Ulfstrand 1968). It emerges in June/July, and in August the young nymphs appear. Except for July and August it is always important prey for the salmon fry. *E. mucronata* and *Baetis muticus* also emerge in July.

The blackflies (Simuliidae), being almost absent from the May samples, occur in wast amounts in June when they are the major prey. After the emerge in July they are very poorly represented in samples from late summer and autumn.

In July there is rapid growth of the stonefly *Leuctra fusca* and the caddisfly *Apatania stigmatella*. Especially the latter is a very important fry food towards the emerge, which mainly occurs in September. In August larvae of the water bug *Oreodytes sanmarki* (A4 only), pupae of the caddisfly *Arctopsyche ladogensis*, small *Baetis rhodani* (which now occur in wast amounts), *A. stigmatella* and chironomid larvae are important prey. In September most of the chironomids have emerged. This month is the main swarming period of the caddisfly *Hydropsyche nevae*.

The life-cycles of the caddisflies *Rhyacophila nubila* and *Mystrophora intermedium* and the mayfly *Heptagenia dalecarlica* are as yet unknown. At all seasons, larvae of *H. dalecarlica* show up in several sizes simultaneously. However, in May there are two fairly well defined size-classes. Other studies have shown that *H. dalecarlica* may possess a very complicated life-cycle (Ulfstrand 1968). The occurrence of relatively medium-sized nymphs through the whole year apparently makes this species the "daily bread" for salmon fry of all ages.

Special attention should be paid to the occurrence of *Dinocras cephalotes*, especially the stock at A16. In North Norway, the distribution of this big, carnivorous and territorial stonefly species is now restricted to a few small and isolated populations (Huru 1987).

Acknowledgments

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The Ecology of Smelts (Genus *Osmerus*): A Literature Review

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Abstract

The smelts of the genus *Osmerus*, have an obscure taxonomy with representatives in both fresh (land-locked) and marine waters (anadromous). The different populations exhibit a range of population parameters such as maximum age from 1–2 years to over 15 years, maturation from first year to 6–7th year and a variety of growth rates. The smelts have an ability to establish large populations, which in combination with their eurythermal life history might have an impact on other fish species both directly (predation) or indirectly (competition). The degree of this impact is still under debate.

This review aims to evaluate the present state of knowledge about smelt ecology in view of possible introductions to Swedish lakes. It is concluded that new introductions of the species should be limited and carried out first after a thorough inventory of the biota in question.

Introduction

The smelts of the genus *Osmerus* have an almost circumpolar distribution and over this range they live under various ecological conditions. The populations show a wide ecological variability manifested for instance in the age structure of the populations, rates of reproduction and quantitative indices of growth. They occur in a range of salinities from fresh water to marine waters of at least 30 ‰ S, and in temperatures from below 0°C to more than 20°C. The populations consist of anadromous and landlocked forms as well as dwarf and normal sizes. The smelts have been introduced to different inland waters and in some of them, for instance the Great Lakes, they have become one of the most abundant species. Due to the creation of new reservoirs and introductions the range of the smelts is gradually expanding. Their role in these new ecosystems has caused a debate about whether their introduction has been beneficial or not. The smelts were often introduced as forage fish for different salmonid species and in this respect they have many times fulfilled that role. But their impact on the native species in the lakes is under debate and some authors are strongly against new introductions.

This review aims to evaluate the present state of knowledge about the ecology of smelts of the genus *Osmerus*, as it has been suggested that *O. eperlanus* could be introduced to improve fisheries in northern Swedish lakes (Svärdson 1976, Svärdson et al. 1988). Many of these lakes have already been stocked with crustacean "glacial relicts" (Fürst 1981, Fürst et al. 1985, Hill et al. in press).

Earlier "reviews" on smelt comprise that written by Kendall (1927) for material published before 1925, and the Synopsis of biological data on smelt by Belyanina (1969). This review therefore mainly concentrates on publications from the mid 1960s and onwards. Many theses on smelt have not been available to the author and he regrets that an apparent gold mine of smelt biology, in the form of publications in the Russian language, was not able to be investigated properly.

Taxonomy
Species level

The taxonomy of smelts of the genus *Osmerus* is very confusing. The picture from morphometric and meristic studies contradicts that from electrophoretic results.

Weitzman (1967) compared the ethmoid bones of some fishes of the order Salmoniformes, and removed the family Osmeridae from the suborder Salmonoidei to a separate suborder, the Osmeroidei.

The classification of the different forms to species and subspecies has differed through the years and ichthyologists in North America and Europe have differing opinions about the status of these forms. Among North American ichthyologists the genus *Osmerus* was for many years considered to contain three species, European smelt *Osmerus eperlanus*, northeastern North American smelt *O. mordax* and North Pacific and Arctic waters smelt *O. dentex* (Scott and Crossman 1973). The Soviet ichthyologist Berg (1962) considered *O. dentex* and *O. mordax* to be subspecies of *O. eperlanus*. He considered two or three species to be present including *O. attenuatus*, which is now classified as *Allosmerus elongatus* (McAllister 1963). McAllister (1963) made a revision of the smelt family, Osmeridae, where he considered that the genus *Osmerus* contained one species with two subspecies: *O. eperlanus eperlanus* and *O. eperlanus mordax*. McPhail and Lindsey (1970), in their paper on freshwater fishes of Northwestern Canada and Alaska, concluded that *Osmerus* probably formed a systematic complex which was not yet understood and thought it best to apply the term "*O. eperlanus*" complex. Klyukanov (1975, 1976) considered two species of smelt, *Osmerus eperlanus* and *O. mordax* with two subspecies *O. m. mordax* and *O. m. dentex*.

The above divisions are based only on meristic and morphological characteristics. The first electrophoretic investigation covering all three forms was by Luey et al. (1982). They calculated the genetic distances based on data from 13 loci. The results indicated a relatively large genetic distance between the Pacific and the Atlantic groups. The distance between the European and the east North American type was smaller than expected for congeneric species. On the other hand the Alaskan samples and the Atlantic samples were in the range expected for congeneric species. From the life history characteristics of smelt from Alaskan waters Haldorson and Craig (1984) suggested that the Pacific-Arctic and At-

lantic populations had evolved divergently, and that a division into subspecies was appropriate.

The electrophoretic results of Luey et al. (1982) contradict the migration routes and differentiation of the species proposed by McAllister (1963). However the results are in agreement with the distribution routes proposed by Klyukanov (1975, 1976). He proposed a Pacific origin for *Osmerus*, as well as McAllister (1963), but suggested that the smelts migrated into the Polar basin at the end of the Pliocene period and eastward into the Atlantic. The encroachment of the glaciers thereafter isolated the Atlantic from the Pacific forms and led to the development of the "*eperlanus*" and "*mordax*" forms. In postglacial time *O. eperlanus* migrated eastward while *O. dentex* moved westward from the Pacific into the White Sea, and according to Klyukanov (1975, 1976) both forms, distinguished by osteological and morphological features, live sympatrically in the White and Barents Seas, which indicates that they should be considered to be two species.

A new species of smelt, the pygmy smelt *Osmerus spectrum*, was described from four North American lakes by Lanteigne and McAllister (1983). They concluded that it was a sibling species to the rainbow smelt and distinguished it from the latter by higher gillraker counts, a relatively larger eye, lower lateral scale counts, and a smaller maximum size. The spawning time does not overlap with that of the rainbow smelt when both are present in the same lake. The range of distribution of the pygmy smelt is uncertain at present but reports of dwarf and giant forms in other lakes (Kendall 1927, Zilliox and Young 1958) should be investigated.

To resolve the confusing picture of smelt taxonomy future systematic research should include electrophoretic data for a large number of loci and for all forms of smelt.

Different forms, races or populations of smelt

The picture of the species complex is even more complicated due to discussions about a normal and a stunted form of smelt. These two forms

have been found by different authors to live both in allopatry and in sympatry. It has been proposed that the forms evolved as a result of geographical isolation and that they spread thereafter during different periods of deglaciation. For instance populations of large and small smelt were found living allopatrically and sympatrically in some Swedish lakes (Svärdson 1958, 1961), four groups of populations were identified in Poland (Rembiszewski 1970) and three types were found in Ostpreussen (Willer 1926). Two races were found in Lake Champlain, USA (Greene 1930, Zilliox and Young 1958), two sympatric smelt populations inhabited Lake Heney, Quebec (Legault and Delisle 1968), one of which was the pygmy smelt according to Lanteigne and McAllister (1983), and two sympatric smelts occurred in New England (Brooks and Deevey 1963).

Rupp and Redmond (1966) carried out transfer experiments in eight lakes in Maine to determine which characteristics of the parent population would be altered after the transfer to a new environment. They concluded that growth, length and abundance in a given environment were dependent mostly on the physical and biological characteristics of the particular environment and that the large and small smelts were not hereditarily different forms. Only the time of spawning was shown to be under the control of the genotype. These studies were later complemented and extended by Copeman and McAllister (1978). In these studies meristic characters were also included i.e. gillrakers and vertebrae. They concluded that the initial phenotype exhibited in the first study should not be considered as characteristic. In the second phase, when the populations reached equilibrium the growth characteristics returned to those of the parental populations. They therefore concluded that it was not possible to refute the hypothesis of at least two hereditarily different forms of smelt. Lanteigne and McAllister (1983) noted that gillraker count was the best meristic character for diagnosing the forms.

After the construction of the Rybinsk Reservoir in the U.S.S.R. in 1944 a type of landlocked and stunted smelt, the "snetok" or "stint",

penetrated the reservoir from Lake Beloye. In the new environment the "snetok" began to differ slightly and by the mid sixties this smelt had become more similar to the river smelt (Ivanova et al. 1969). The smelt now grew older, reaching 4 to 6 years of age, spawned repeatedly, had more stabile populations and was piscivorous. The smelt from Rybinsk later penetrated into the lower reaches of the Volga River to the Gorkiy and Kuybyshev Reservoirs. Here the populations changed back to the Lake Beloye "stint" type with a short life span (Kriksunov and Shatunovskiy 1979). This shows the plasicity of the species.

Copeman (1977) used multivariate analysis for 32 mensural and meristic characters on 13 samples of North American smelt, including anadromous and landlocked populations, and came to the conclusion that there were three distinct groups of smelt. One of the groups, stunted smelt, was regarded to fulfill the criteria for species status, while the anadromous and normal smelt were suggested to be subspecies. The stunted smelt from some North American lakes was, as stated earlier, studied more closly by Lanteigne and McAllister (1983) who gave it the name pygmy smelt, *O. spectrum*.

Significant differences in size and growth data of smelt from the Central and Eastern basins of Lake Erie were examined by MacCrimmon et al. (1983 a). Based on meristic, morphometric and electrophoretic data they concluded that the growth and size differences were attributed to differences in limnological conditions between the basins.

There are indices that interbreeding between closely related populations of smelt is rare. Using variation in biological characters Frechet et al. (1983 a) separated anadromous smelt from Quebec waters into three geographical groups and suggested a fourth group. In a second paper Frechet et al. (1983 b) stated that this hypothesis was supported by the distribution of 3 smelt parasites i.e. *Glugea hertwigi, Diphyllobothrium sebago* and *Echinorhynchus salmonis*. From differences in average vertebral number in Miramichi River smelt populations McKenzie (1964) concluded that the smelt consisted of different

schools or groups and not one homogeneous stock. In western Lake Superior three discrete populations of smelt were suggested by complementary evidence from an electrophoretic study (Schreiner et al. 1984) and from a study of length-frequency distributions, fecundity and growth (Luey and Adelman 1984).

Altukhov and Yerastova (1974a) stated that because the smelt was a fish that migrated little, it had separate ecological groups in different coastal bays. Fedorova (1974) concluded that morphometric characters of smelts from Lakes Seliger and Ilmen confirmed the view that these smelts were ecological forms of the Baltic Lake smelt.

Volodin and Ivanova (1973) investigated smelt in Rybinsk Reservoir and Lakes Ladoga and Beloye, and found that the relative magnitude of individual morphometric characters changed appreciably as the size and age of the fish increased in connection with the irregular rate of their growth. According to Kriksunov and Shatunovskiy (1979) the adaptive significance of the dwarf state lay mainly in the sharp increase in the rate of reproduction of the population, which allowed it to survive successfully under unfavourable conditions. They concluded that in no fish species, except the smelts, did the species range expand actively due to the dwarf form. The dwarf form was also an adaptive mechanism contributing to an expansion of the species range and to an increase in its abundance.

Distribution
Worldwide

Anadromous smelt of the *eperlanus* type occur along the coasts of western and northern Europe. The southern limit is Virgo, W Spain (Berg, 1962). They occur in the Bay of Biscaya at the mouth of the river Loire, France (Lardeux 1986). They have been recorded in 29 river systems in United Kingdom and Ireland (Hutchinson 1983) and the population in the river Thames has increased lately, probably due to the improved

water quality (Wharfe et al. 1984). On the west coast of Ireland smelts are found in the Shannon estuary (Kennedy 1948) and the estuary of the Foyle (Vickers 1974). They are found along the coasts of the Netherlands (Hadderingh et al. 1988), Germany (Lillelund 1961) and Denmark (Jensen 1949) and in the whole Baltic (Nordqvist 1910, Rembiszewski 1970, Enderlein 1981). They are also found from the coastal areas of the White Sea and eastward to the river Pechora (Klyukanov 1975).

Landlocked populations occur in England, Denmark (Jensen 1949), Norway (Ekman 1922), lower parts of the Baltic countries (Nordqvist 1910, Ekman 1922, Willer 1926, Leskien 1942, Svärdson 1966, Rembiszewski 1970, Degerman and Nyberg 1987) and in the USSR (Lakes Ladoga and Onega, River Volga and the drainage area of River Pechora) (Berg 1962). In the Volga, due to the building of reservoirs, the smelt is now found at Volgagrad, which means that the southern boundary of its distribution has moved almost 3,000 km (Ivanova 1982a, Volodin and Ivanova 1987).

The *dentex* type consists only of an anadromous form (Klyukanov 1975) which is found in the White Sea and eastward along the Siberian coast into the Pacific, where it occurs along the coast down to Korea (Berg 1962). In North America it occurs on the Pacific coast from Vancover Island north to Yakutat (McPhail and Lindsey 1970)

The *mordax* type is anadromous along the eastern North American coast from New Jersey to Labrador (Scott and Crossman 1973).

Indigenous landlocked smelt occur widely in North American inland waters, such as those of New Hampshire, Maine, New Brunswick, Nova Scotia, Insular Newfoundland, Labrador, Quebec and eastern Ontario (Scott and Crossman 1973). Following their introduction to Crystal Lake in Michigan (Van Oosten 1937b) they have spread into all the Great Lakes, except for Lake Ontario, where they are thought to come from elsewhere (Scott and Crossman 1973, Bergstedt 1983). Smelt were introduced to reservoirs in the Mississippi River Basin and are now found close to the mouth of the river in Louisiana (Mayden et al.
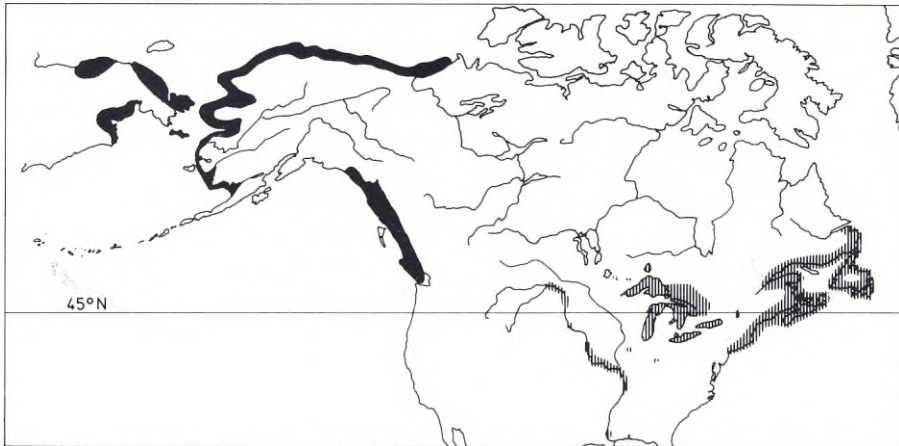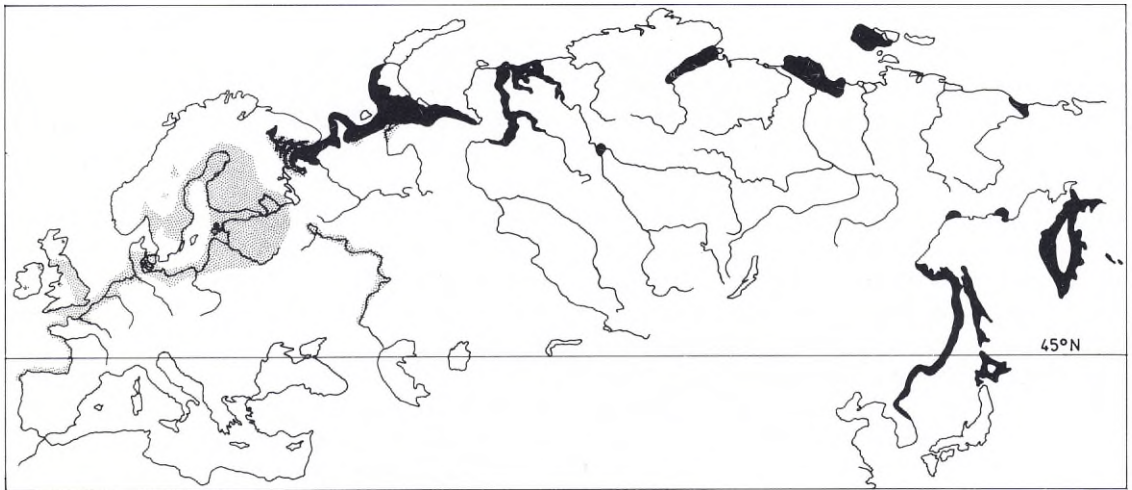
Fig. 1. Distribution of three forms of smelt ☐ E. eperlanus, ■ E. dentex and ▥ E. mordax. The distribution of smelt in the lower Missouri and middle/lower Mississippi is based on scattered observations.

1987). The species is still expanding its range (Evans and Loftus 1987).

The worldwide distribution of the smelts is indicated in Fig. 1.

Seasonal and spatial distribution

The smelt is generally considered to be a cold-water fish, and consequently its seasonal movements and depth distribution may be thought to be determined by water temperature. This view is contradicted by investigations in the Great Lakes where smelt, especially the yearlings, appeared to be rather eurythermic (MacCallum and Regier 1970, Evans and Loftus 1987). The latter view is also supported by Rupp (1959) who found smelt in 51 of 327 typical warmwater lakes in Maine.

Dahlberg (1981) studied the vertical and horisontal distribution of fish in Cayuga Lake, New York, to estimate temperature preferences. During summer the smelt showed a mean occupied temperature of 10.4–14.4°C. When the near-shore temperature exceeded 13°C the smelt

moved offshore. Greene (1930) mentioned 15°C as a higher avoidance temperature for Lake Champlain smelt. In Lake Michigan, Wells (1968) found smelt mostly at temperatures ranging from 6 to 14°C.

The seasonal distribution of the landlocked smelt in the Rybinsk Reservoir was investigated by Ivanova et al. (1970). The entire population remained in the estuarine area of the reach in summer. At other times of the year the population was spatially segregated into age and size groups. The young fish were in the lake portion and the older fish in the riverine areas of the reach. The older and larger the fish, the greater was the distance they ascended the reach.

In western Lake Huron, rainbow smelt larvae dominated in late spring and early summer and were most abundant from 2 m to at least 6 m beneath the surface (O'Gorman 1983). Nursery areas were in bays and off irregular coastlines.

The distribution of smelt in Lake Superior was investigated using bottom trawls and gillnets (Dryer 1966). Age groups 0 and I were taken mostly in the upper 18 m and few were caught below 35 m. The adults were rather evenly distributed between 18 and 71 m. The smallest trawl catches were in summer for all age groups. The gillnet catches in summer indicated an offshore movement in age group II and older fish and a movement off the bottom.

In the largest lake in Norway, Lake Mjøsa, Sandlund et al. (1985) studied the vertical distribution of fish with the use of gillnets and echo sounding. Smelt was the dominating species in the gillnet catches (40 % by number). The benthic catches from one of the stations indicated that smelt mainly utilized the bottom profile from 10–50 m and were caught at 50–80 m only during autumn. The smelt were caught in the littoral zone in significant numbers only during spring, close to the spawning time. In the pelagic nets the smelt was caught in large numbers only from August to November which coincided with the maximum zooplankton biomass.

Dembinski (1971), used gillnets and echo sounding to investigate the vertical distribution of fish in some Polish lakes. The smelt congregated in the epilimnion and metalimnion at night

from June to October. July to August are probably the time of optimal feeding activity for smelt. Daily vertical feeding movements by smelt were observed between July and October. The fish moved from 25–40 m depth to warmer upper layers richer in plankton. The migrations were discontinued in November during autumnal mixing. During the autumn overturn the smelt were caught at the bottom (30–40 m), but at the same time numerous fish were present in the upper water layers. Due to the poor fishing success of gillnets during daytime, it was hard to correlate the results with those from echo sounding. In winter smelt did not occur in water colder than 2°C.

Spatial distribution during ontogeny

The smelt are segregated in their habitat according to age and size, which may reduce intraspecific competition.

Evans and Loftus (1987) found that the rainbow smelt in lakes had a eurythermal life history. They occurred in the nearshore zone from 0 to 60 m in three temperature strata, with young-of-the-year (YOY) in warm water, yearlings in cool water and adults in cold water habitats. This habitat response could be due to ontogenetic changes in preference for temperature and to intraspecific interactions related to light levels and fish size, as Hamrin (1986) found for vendace, *Coregonus albula*.

In a diving investigation in Georgian Bay, Lake Huron, Emery (1973) observed smelt larvae mainly at 2–4 m depth during the day. At night they were distributed throughout the water column down to 15 m, but were concentrated 2 to 3 m above the bottom. The larvae swam in schools in daytime but not during night. In western Lake Huron, O'Gorman (1983) found the highest abundance of smelt larvae from 2 to at least 6 m beneath the surface. In Lake Michigan, the newly hatched larvae were distributed in shallow water for a short period and were widely dispersed from June, but then gathered inshore in late August within the 15 m contour (Tin and Jude 1983). During September an

offshore migration probably occurred. The larvae were most common at water temperatures of 10 to 16°C. Dunstall (1984) also reported that the smelt larvae rapidly dispersed offshore to deeper strata.

In Lake Erie, young-of-the-year smelt frequented shallow epilimnial waters and were at times greatly concentrated near shore (Ferguson 1965). They were not present in the hypolimnion. In July yearlings were extremely abundant inshore at about 6 m. Offshore at the same time small numbers were present in mid-water at about 6–9 m. These latter individuals were larger than those inshore. In October yearlings were abundant offshore at about 18 m and their distribution began overlapping that of the adults. In the same lake, MacCallum and Regier (1970) found that the YOY smelt inhabited the inshore waters shallower than 18 m in spring and that by late autumn they were dispersed throughout the eastern two-thirds of the lake. Yearlings were spread throughout the lake in spring and appeared to move into shallower waters after the spawning period. In mid June many occurred in the sharp thermocline, even though oxygen concentrations were adequate below it. The adults were dispersed throughout most of the lake in winter and spring. After spawning runs in April the adults moved offshore and in summer most were found in the thermocline, possibly because the hypolimnion in the central basin was deoxygenated. Argyle (1982) found that the smelt caught at mid-depths were smaller on average than those caught in the bottom trawls. In Lake Michigan, YOY smelt were caught in the upper water layers until fall, when at least some moved to the bottom (Wells 1968). The yearlings were either at mid-levels or at the bottom and the adults were mostly at the bottom.

In the Miramichi Bay larvae of anadromous smelt were carried back and forth by the tide and most larvae were always found close to the bottom. The juveniles were found in the Bay and outer estuary during summer while the adult smelts were chiefly found in the outer estuary. The larger smelt were farthest out (McKenzie 1964). The larvae of anadromous smelt in arctic waters were most abundant near

the surface in the warmer (10–15°C) and less saline (11–13 ‰) waters above the halocline (Ratynski 1983). This distribution differs from that in the Miramichi River and is probably caused by the lower temperature (near 0°C) and the higher salinity (26–29 ‰) near the bottom.

Diel vertical migrations

Like many zooplanktivorous fish species e.g. herring, sprat and vendace, the smelts display a diel behaviour pattern.

In Lake Superior the density and abundance of smelt were highest in water shallower than 50 m. The smelt made vertical migrations from the bottom, where they were during daylight, to near surface water, of 2–30 m depth, at night (Heist and Swenson 1983). In Lake Erie, Ferguson (1965) found the adult smelt concentrated near the bottom at about 45 m during the day. In late afternoon they started to rise from the bottom and they dispersed into the epilimnion during the night.

Heist and Swenson (1983) also found that the distribution of smelt within a given depth interval was strongly influenced by water temperature. During summer nights the highest densities of smelt occurred in water where temperatures were from 11 to 16°C. Brandt et al. (1980) also found the highest densities of smelt in the above temperature interval in September in Lake Michigan. During the day the adult smelts were widely distributed between 7 to 18°C, but maximum concentrations occurred at temperatures of 7–8°C. The larval smelt showed a different and opposite distribution picture, though they were caught at all temperatures. During the day the mode occurred at 13–14°C and at night the maximum occurrence was at temperatures of 5–6°C.

In the Missouri River reservoir, Lake Oahe, South Dakota, the summer distribution of smelt was assessed with hydroacoustic methods (Burczynski et al. 1987). Their distribution was found to depend on temperature, with no fish found in areas without a hypolimnion. In daytime the smelt stayed close to the bottom and at night

they migrated towards the thermocline. Some young smelt moved slightly into the epilimnion.

Rogers (1940) found the greatest concentrations of smelt larvae in the middle estuary of the Miramichi River. The smelt larvae were negatively phototrophic such that more larvae were found in deep water in light and more were found in shallow areas during darkness.

Spawning and hatching

Spawning run (time, water temperature, population structure)

In spring the anadromous smelts leave the sea and ascend freshwater streams. The migration to spawning areas can be as long as 1,000 km from the river mouth, as reported for the smelt in Yenisei River (Tyurin 1924 cited in Gritsenko et al. 1984). The landlocked forms also ascend freshwater streams but can also spawn at the shoreline of the lake. Deepwater spawning appears to be less common but has been reported from Lake Heney, Quebec (Legault and Delisle 1968) and from Lake Champlain (Plosila 1984).

Hudd and Urho (1985) reported that in the Northern Quark, Gulf of Bothnia, the spawning sites in the rivers were probably lost because of acidification of the water. Spawning was therefore restricted to the estuaries of the rivers.

Smelt use a wide variety of spawning substrates, from gravel to mud and underwater vegetation, though gravel and sand may be preferred (Rupp 1959, Ivanova and Polovkova 1972).

The timing of spawning in 114 Maine lakes was investigated by Rupp (1959). He suggested that certain phases of spawning behavior were subject to the "law of heterogenous stimulus summation" which was termed by Fabricius (1950). Spawning in the Miramichi River system, New Brunswick, lasted from late April to early June (McKenzie, 1964). The time of entry of spawning runs into the various streams from year to year was so regular that it was possible to classify the brooks as early, midseason and late-spawning streams. The early spawners were found in the larger headwater streams at tem-

peratures of 4–5°C and the later runs were found in the small brooks at slightly higher temperatures of 6–7°C. After spawning the smelts migrated downstream at least to the outer part of the estuary. In autumn they were found in the larger rivers but when these became ice-covered the smelts moved down to the Bay. The smelts usually ascended to the spawning site at night and left it at dawn. More than 80 % of the spawning in the Miramichi River occurred at night (McKenzie 1964). Spawning also seemed to occur at night in Lake Simcoe, Ontario (MacCrimmon et al. 1983 b).

Spawning normally occurs close to the ice-out period. During special conditions spawning also occurs offshore. The sex ratio and the size range normally change during spawning. Lillelund (1961), in his study of anadromous smelt in the River Elbe, proposed that the timing of spawning was related to water temperature at the spawning ground. The older age groups ascended to the spawning grounds first. The males stayed longer at the spawning grounds and the greater the water flow the higher was the upstream migration.

Belyanina (1969) stated in her review that throughout their great range the smelts begin to spawn when the water temperature is about 4 ± 1–2°C. In the Miramichi River spawning starts at 4–5°C in larger tributaries and at 6–7°C in the brooks (McKenzie 1964). Sharp decreases in water temperature may interrupt spawning. In the Northern Quark, Gulf of Bothnia, the ascent of smelt was most intense when the temperature had reached 3–4°C (Hudd 1985a). In the River Cree, SW Scotland, the smelts ascended the river on 10 March 1980 and 1981 at a water temperature of more than 5°C (Hutchinson and Mills 1987). In both years the spawning stock was dominated by the 1978 year class. The mean length of the fishes changed during spawning but was different during the two years. In 1980 the mean length tended to increase as the run progressed but in 1981 the trend was the opposite, and smaller specimens were found at the end of the run. In the Miramichi River the average length of the spawners gradually declined during spawning and even the average size

within each age group declined as the season progressed (McKenzie 1964). In the River Amur, Podushko (1970) found that the larger the smelt, the higher they ascended the river. He also found that when the stock was more numerous the fishes ascended higher up the river.

In Sakhalin rivers Gritsenko et al. (1984) found three groups of spawning populations distinguished by spawning characters. The first group spawned some 100 m, the second 1 km and the third tens of kilometers from the river mouth. The spawning period of the two first groups lasted 1.5 months while that of the third group lasted only 10 days. The first two groups entered the rivers at a water temperature of 7–14°C and the third group at 2–3°C. In spite of the different lengths of the spawning migrations spawning and egg incubation occurred at practically the same water temperature (10–14°C). Kuznetsov (1976) reported that the smelt in the Kuybyshev Reservoir (middle Volga) spawned at temperatures above 10°C.

Ivanova and Polovkova (1972) found two forms of spawning grounds in the Rybinsk Reservoir, lake and river. They concluded that the fish maturing for the first time, aged 1 + and 2 +, used the lake spawning ground and that the repeat spawners used the river spawning grounds. It was thought that migration against the current to the upriver spawning grounds presented great difficulties for the younger and smaller fish. In the Miramichi River, larger smelts were found farther up the the spawning streams than the smaller fish (McKenzie 1964).

Tagging experiments on anadromous smelt in the Parker River estuary, Massachusetts, indicated a homogeneous spawning stock, as individual fish utilized several spawning sites (Murawski et al. 1980).

The different populations mature at different ages. Anadromous forms mature relatively late, just before their second year of life or older. It is thought that among the freshwater smelts the populations of small smelt mature in their first or second year of life and that these populations often inhabit relatively shallow bodies of water. Smelt populations maturing at a later age inhabit deeper cold-water bodies (Ivanova and Volodin

1981). Arctic-Pacific smelt in the Beaufort Sea mature at age 6–7 years (Haldorson and Craig 1984).

Ivanova and Volodin (1981) carried out experiments in ponds to examine the influence of temperature and feeding on maturation during the first summer. They came to the conclusion that maturation in the smelts depended not only on food supply but was largely determined by the temperature during larval development. If the sum of heat during the period of larval development exceeded 600 degree days, mass sexual maturation occurred in the first year of life.

Alm (1917) reported that in Lake Hjälmaren, Sweden, smelt spawned for the first time at two years of age. In the Bothnian Bay most of the smelts (79 %) spawned for the first time at two years of age (Timola 1978). None spawned in their first year of life.

Hatching (time and success)

The hatching time for smelt eggs varies with temperature, as in other fishspecies. In the Miramichi River, eggs deposited early took three weeks to hatch, while the eggs that were deposited late took 10 days (McKenzie 1964). The hatching success ranged from 0.03 to 0.6 %. The more crowded the egg masses the lower was the hatching success. At densities greater than 12,000 per ft^2 (130,000 per m^2) the result was even fewer larvae. A significant negative correlation was also found between precipitation following spawning and larval production. Altukhov and Yerastova (1974b) stated that it took 25–30 days or 161 degree-days for the eggs to hatch at temperatures between 0.2 and 11.3°C. Lillelund (1961) found the eggs of smelt to be fertile up to a salinity of 16 parts per thousand and the upper temperature tolerance to be in the range of 17.7°C and 20.7°C for the first stages. The mean duration of incubation was 15 to 29 days depending on temperature.

Rothschild (1961) investigated smelt in a tributary to Branch Lake, Maine. He found a survival of 24 % in eggs at the prehatching stage and indicated that mortality was 99.5 % to the

prolarval stage. He also suggested that time had a greater influence on egg mortality than did egg density. Rupp (1965) investigated shore spawning in the same lake and found a mean survival rate to hatching of 1.07 %. MacCrimmon et al. (1983b) estimated the survival rate of eggs to be 7.2 % in Lake Simcoe.

Johnston and Cheverie (1988) found a diel and seasonal drift in eggs and larvae of anadromous smelt in West River, Prince Edward Island, Canada. Of the drifting eggs 45% were unfertilized or in early development and 41 % were dead. There was a diel drift with a peak around midnight, probably caused by spawning activity during the dark. The peak in the drift of larvae at night suggested nocturnal hatching, which could be an adaptive mechanism to avoid predation. It was also shown that smelt eggs and protolarvae could tolerate a salinity of 22 ‰ S.

After hatching in streams the larvae drift downstream. In the Miramichi River they were found close to the bottom (McKenzie 1964). Even at night most of the larvae were found in the deeper layers. The diurnal behaviour of the negatively phototrophic larvae was suggested to be the factor that kept them in the estuary (Rogers 1940). The larvae were transported inwards by the inflowing bottom water. The dispersion and retention of smelt larvae were studied by Ouellet and Dodson (1985a) in the estuary of the St. Lawrence River. They found indications of a 24 hour hatching periodicity and a daytime accumulation of larvae at the mouth of the natal river. This accumulation was thought to be a result of the negative phototaxis exhibited by the small larvae and the incorporation of patches of smelt into the estuarine watermasses once every night following high tide. Ouellet and Dodson (1985b) later found evidence of a synchronous nighttime hatching of larvae that was independent of water temperature and river hydrodynamics. They concluded that the riverine transport and mixing of yolk-sac larvae with the estuarine water mass were controlled principally by the hydrodynamics of the system and the nighttime hatching and specific gravity of the yolk-sac larvae. In June and July the slightly larger larvae were found near the surface during flood tides and nearer the bottom during ebbs. The older larvae used the current more efficiently and were found further upstream in July than in June (Laprise and Dodson 1989). The smelt larvae in the middle of the St. Lawrence River estuary were associated with a highly productive planktonic community that provided an abundant source of food (Dodson et al. 1989).

From the distribution of the larvae it was strongly suggested that the population richness of this species was defined at the early life-history stages (Sinclair and Iles 1988).

Population dynamics, age, growth and mortality

The different populations of landlocked and anadromous smelt show a great variability in size structure, age structure and population dynamics. Belyanina (1969) has an extensive compilation of data on the fecundity and population dynamics of different smelt populations. Some additional data on fecundity is presented in Table 1.

Table 2 shows recent data on growth rates and age at first maturity in different parts of the world. The anadromous smelt populations often mature late, grow to a large size and have a rather stable population. The smelts in larger, colder and deeper lakes have a similar life history, but smelts from shallow, warm lakes mature early, live for a few years and have fluctuating populations.

Because smelt segregate by age and show major variations in year-class strength as well as seasonal shifts in spatial distribution the estimation of mortality can be complicated (Schaefer et al. 1981b).

The number of surviving one-year-old smelts in the River Elbe was found to be correlated with the hydrographical conditions on the spawning grounds in the year of birth and with the environmental conditions for the brood (Lillelund 1961). These environmental conditions were later validated in a model that simulated the influence of three basic environmental

Table 1. Fecundity of different smelt populations (E) Eperlanus, (M) Mordax, (D) Dentex.

Population		Size of fish (mm)	Number of eggs (1000) per fish	Number of eggs per g of fish	Number of eggs per g of gonad	Author
Landlocked						
Rajgrod Lake	(E)	74-101	4.1- 9.0			Czeczuga 1959
Syam Uzera	(E)	108-157	7.5- 20.0			Sterligova 1979
Lake Superior	(M)	185-224	22.3- 40.9	980-1030		Bailey 1964
Lake Erie	(M)	97-132	5.5- 15.3	380- 656		Nsembukya-Katuramu et al. 1981
Anadromous						
Northern Quark	(E)	130-250	4.- 57			Hudd 1985b
Bothnian Bay	(E)	120-199	10.4- 29.2			Timola 1978
White Sea	(E)	150-200	25.7- 35.6			Altukhov & Yerastova 1974b
River Cree	(E)	185-279	40.1-105.9	844-1718		Hutchinson & Mills 1987
Sakhalin rivers	(D)	150-340	16.9-207.9			Gritsenko et al. 1984
Akkeshi, Hokkaido	(D)	140-220	17.5- 72.5	491-1063	2850	Horikawa 1988
Mori, Hokkaido	(D)	170-240	23.6-109.9		3091	-"-
Kushiro, Hokkaido	(D)	180-240	17.6-125.9		3605	-"-

Table 2. Length (mm) of age-groups from different populations of smelt. (E) Eperlanus, (M) Mordax, (D) Dentex.

Population		1	2	3	4	5	6	7	8	9	10	11	12	13	Age at first maturity	Author
Landlocked																
Lake Beloye	(E)	65	98	101											(1)-2	Volodin & Ivanova 1987
Rybinsk Reservoir	(E)	64	86	98	123										2	-"-
Gorkiy Reservoir	(E)	58	103	108											1	-"-
Kuybushev Reservoir	(E)	75	126	151											1	-"-
Wigry Lake	(E)	93	111	125											2-3	Leskien 1942
Rajgrod Lake	(E)	79	93	111											1-2	Czeczuga 1959
Miedwie Lake (small)	(E)	71	87	112												Rembiszewski 1970
Miedwie Lake (large)	(E)			143	173	195	212	224							3	-"-
Syam Ozera	(E)	82	111	126	148	167	182								2	Sterligova 1979
Gull Lake	(M)	60	150	163	188	198	187								2	Burbidge 1969
Lake Superior	(M)	64	126	162	184	203									2	Schæfer et al. 1981b
Lake Superior	(M)	66	151	191	211	229	249								3	Bailey 1964
Anadromous																
River Elbe	(E)	71	135	174	212	238		185							(2) 3-4	Lilleund 1961
Gulf of Finland	(E)				149	160	170	300							2-3	Berg 1962
White Sea	(E)		140	200	224	270	311									Altukhov & Yerastova 1974
Miramichi River	(M)		137	157	176	194									2	McKenzie 1964
Parker River	(M)	120	189	216	239	248									2	Murawski & Cole 1978
Colville River	(D)				157	192	197	228	246	256	272	285	291	293	(1)-2	Halgorson & Craig 1984
Amur	(D)	42	119	166	190	230	262	244							6-7	Podushko 1970
Yenisey River	(D)	46	98	141	176	203	223	239	255						(2) 3-4	Berg 1962

parameters (Borchardt 1988). The correlation between the by-catch on the coast of Schleswig-Holstein and the index by Lillelund proved to be significant for the one-year-old smelt during a period of 31 years.

Ivanova (1982b) studied the life span and population dynamics of smelts from one pond, two lakes and one reservoir with different biological and physiological characters. She used the number of circuli formed in a given year on the scales as a natural mark to determine which specimens lived to the maximum age characteristic of each population. In the cold and comparatively oligotrophic Lake Ladoga the smelt grew slower than in any of the other bodies of water. These smelt lived up to 7–9 years and the fish that grew most during the first year, i.e. those that had 6–8 circuli, were those that lived three years or more. The slower growing smelt, i.e. those with 2–5 circuli, were the first to die. In the experimental pond, on the contrary, fish with a lower growth in the first year lived to the third year. In Lake Beloye, where smelt lived for 1–2 years and rarely for 3 years, the rapidly growing fish had lower survival after the first year. These fast growing specimens matured early and perished shortly after the first spawning (Ivanova 1980).

Anadromous rainbow smelt from the Beaufort Sea ranged in age from 1 to 13. Most were age 2 and ages 6 to 8 and 62 % were estimated to be age 7 or 8 (Bond 1982 cited in Hopky and Ratynski 1983).

The growth rate of smelt is connected with changes in the abundance of the spawning stock (Podushko 1970) which has also been shown for other fishes (Svärdson 1953, for whitefish). Normally the larger the size reached in the first year of life the slower the smelt grows in the following two years (Podushko 1970). In Lake Miedwie, Poland, the highest growth rate was observed in the first year of life and it then decrased in the second and third year. In the fourth and fifth years of life the growth rate increased again (Trzebiatowski and Gaj 1978).

Garnås (1982) studied the age and growth of smelt in Lake Tyrifjorden, Norway. Females were larger than males. The smelt grew about 60 mm the first year and 220–230 mm the second and third years. The oldest smelt was 7+.

Female smelts have been found to grow somewhat faster than males. Ivanova et al. (1969) concluded that this was because the females were more predatory in autumn during their last years. A somewhat faster growth in females was also found in the Gulf of Bothnia (Hudd 1985a) and Lake Hjälmaren, Sweden (Alm 1917).

Ivanova et al. (1969) concluded that the transition of the older age groups of the stunted "snetok" smelt to a diet including young fishes led to an extension of its life cycle. In Lake Syamozero the weight increment increased considerably from the third year of life when the smelt changed over to a predatory diet (Sterligova 1979).

Mass mortality of smelt has been reported from landlocked populations of smelt. One of the first reports (Van Oosten 1947) was from Lakes Huron and Michigan during fall and winter of 1942–43. He concluded that the mortality could only be caused by a disease. Extensive die-offs occurred in Lake Superior during several springs after the smelts had spawned (Schaefer et al. 1981a). The age structure of the dead smelt was similar to that of the spawning population. The most probable cause was thought to be temperature stress and a consequent increase in susceptibility to the fungus *Saprolegnia* sp. Mass mortalities have also occurred in Lake Erie. Nsembukya-Katuramu et al. (1981) thought that death might be caused by a low tolerance to rapid changes in temperature. High summer temperatures can also have severe effects on smelt populations. The smelts in many lakes in the NW USSR suffered high mortalities during the hot summer of 1972 (Ivanova 1980). During that summer the slow growing smelt and the 1971 year-class were most severely affected, because they had small fat reserves (Ivanova 1980). In the Miramichi River, smelts were found to die during spawning. Most of these were males, and the fishes were covered with fungus. The mortality, not mentioned as mass mortality, was greatest in relatively dry warm years (McKenzie 1964).

Ivanova (1988) concluded that populations of

freshwater smelt (stint) mature early, at the age of 1–2 years, and are characterized by mass post-spawning mortality. An increased energy metabolism and the absence of food resources, i.e. larger prey, to meet the losses incurred by intensive development of the sex products lead to severe depletion of energy reserves during winter and spawning.

Schaefer et al. (1981b) estimated the annual mortality rate of the combined sexes of smelt in Lake Superior to be 40 % between ages 3 and 4 and 69 % between years 4 and 5. The annual mortality rate was 77 % for males and 42 % for females. Murawski and Cole (1978) investigated anadromous smelt population dynamics in the Parker River, Massachusetts during the spawning run and estimated that 72 % of the adults died each year. They also found fewer males than females during the post-spawning period. In some areas a higher mortality among male smelt may also be the result of a heavy fishery during the early period of the spawning run, when there are more males (Bailey 1964).

Walter and Hoagman (1975) found the year-class strength of smelt in Green Bay, Lake Michigan, to be positively correlated with the size of the spawning stock and suggested that the abundance of young smelt was not primarily regulated by intraspecific competition with the adult fish.

Cannibalism of YOY smelt by 1 year old smelt was thought to explain the alternating dominance of year-classes in Lake Erie between 1963 and 1974 (Henderson and Nepszy 1989).

Food and feeding

Larvae and O-group

The availability of the food to the fish larvae during their first months of life is extremely important, and the survival rate during this period determines the strength of the year-class to a great degree (Siefert 1972, Strelnikova and Ivanova 1982).

McCullough and Stanley (1981) investigated an oligotrophic lake in Maine and found that the food of smelt larvae consisted of microplankton,

largely rotifers. Many of the larvae, especially the smaller ones, had empty guts. They suggested that initiation of feeding may pose a serious problem for larval smelt and limit their survival. They thought that the larvae had passed a critical period for starvation mortality at 12 mm length. Siefert (1972) found that larval smelt in Lake Superior absorbed their yolk-sacs before they reached 7 mm length. The first-feeding fish selected *Cyclops bicuspidatus*, copepod nauplii and diatoms. Thereafter, as they grew, they first rejected the nauplii and then *Cyclops*, and developed a preference for larger calanoid copepods. *Cyclops cuspidatus* was the principal food until the fish reached 21 mm.

Strelnikova and Ivanova (1982) studied the feeding of smelt larvae in the Rybinsk Reservoir. Nauplii, copepodites and some rotifers were the first food items eaten by smelt of 9.5–12 mm length. At lengths of 11–16 mm the main food was copepodites and adult copepods. In contrast, Naesje et al. (1987) found that phytoplankton, mainly pennate diatoms, were important as initial food for the larvae in Lake Mjøsa, Norway. This may have been caused by the diatom bloom that occurred simultaneously with the start of feeding by smelts. In the River Elbe estuary smelt larvae (7–9 mm) fed mostly on rotifers and thereafter on nauplii and copepodites. Copepods were the main food of the young-of-the-year (Kühl 1970).

The food of YOY smelt in Lake Tjeukemeer, the Netherlands, was mainly restricted to the pelagic zooplankton (van Densen 1985). The smelt selected the larger sizes of *Daphnia* and cyclopoids during the course of June, except for the beginning of June, to October. They also showed that YOY smelt were capable of preying on the oppossum shrimp *Neomysis integer*. In Saginaw Bay, Lake Huron, YOY smelt ate mostly crustaceans, and copepods were eaten more than cladocerans (Gordon 1961).

Postlarvae-adults

Whether or not the adult smelt is a serious predator on larvae and young fish has long been a

subject of discussion. Many reports do not support the idea, at least as regards the effect on commercially important fish species (Kendall 1927, Greene 1930, Schneberger 1937, Gordon 1961, Ferguson 1965, Burbidge 1969, Lackey 1969, MacCrimmon and Pugsley 1979), while some other reports do (Loch et al. 1979, Loftus and Hulsman 1986).

There are indications that fish eggs and larvae disappear rapidly in the stomachs of smelt and alewife (Crowder 1980). Larvae may be unrecognizeable within an hour. This means that traditional gillnetting cannot be recommended as a method for collecting smelt for stomach analysis. It also means that quick preservation of the stomachs is necessary.

Foltz and Norden (1977a) found a marked increase in piscivorous food habits in smelt longer than 180 mm. Ferguson (1965) found few fishes in the stomachs of smelt, but the smelts were in the size range of 150–165 mm, which may be too small for piscivory. Schneberger (1937) reported from Green Bay, Lake Michigan that *Mysis* was found regularly in smelt stomachs but that only 6.5 % of the stomachs contained remains of fish. The size of the investigated smelts was not mentioned. In Saginaw Bay Gordon (1961) found that in age-group I and older smelt, insects made up the bulk of the food, 46–63 %, and that fish made up 25–49 % of the total volume from July to September. In November the stomachs contained nearly only *Mysis*.

MacCrimmon and Pugsley (1979) found that the feeding of adult smelts in Lake Simcoe, Ontario, was selective and varied with fish size, sex and season. Food intake was minimal before the spawning period and females resumed feeding more quickly than males after spawning. Fish, mostly YOY smelt, were eaten by smelt 156 mm or more in length. Foltz and Norden (1977b) studied the consumption and energy content of smelt in Lake Michigan. Smelt had empty stomachs during the spawning run in April, had maximum stomach contents in June and least stomach contents during winter and early spring. Altukhov and Yerastova (1974b) also reported that smelt scarcely fed at all in the spawning run. Stedman and Argyle (1985) studied the

feeding of smelt during October in Lake Michigan. Of the fish that had eaten, 56 % had eaten YOY fish. The frequency of occurrence of YOY fish in the diet was highest in the large smelt. The diet was related to the availability of prey at the depths where the smelt were caught.

In his study of the River Elbe estuary Kühl (1970) found that the smelt fed mostly on amphipods, mysids, *Crangon*, and fish (20–80 mm long smelts, herring and gobids). The smelt fed in all months, even when water temperatures were low. In the lower part of the River Elbe, smelt was the fish species that showed most dependence on zooplankton, especially the copepod *Eurytemora* (Ladiges 1935). During autumn when there was less plankton they changed to bottom feeding. Higher up in the River Elbe Stadel (1936) found a similar pattern of feeding.

In oligotrophic Twelve Mile Lake, Ontario, less than 41 % of the smelts were feeding at or close to the time of spawning, and the following increase in feeding activity coincided with the increase in the number of spent individuals (Loftus and Hulsman 1986). Larval coregonids, zooplankton and dipteran pupae were the most frequently observed food items. The frequency of occurrence of coregonid larvae reached a peak (93 %) in mid April and dropped to 25 % in the beginning of May. The results supported the hypothesis that the primary cause of recruitment failure in the whitefish population was predation by smelt.

Smelt in Lake Miedwie, Poland, were typical plankton feeders in the first year of life, but older individuals switched to predation, including cannibalism (Trzebiatowski and Gaj 1978). In terms of weight, fish appeared to be the most important component of smelt food (93.1 %). Czeczuga (1959) found that the smelt in Lake Rajgrod had a marked food selectivity and that they fed on their own species in their 3rd year of life.

Garnås (1983) studied the feeding of 80–160 mm long smelt in Lake Tyrifjorden, Norway. Zooplankton dominated the diet from July to February, while benthic insect larvae and nymphs were more important from March to June. Cladocerans were preferred to copepods during

most of the year. During the spawning run 80 % of the stomachs were empty.

In the brackish Bothnian Bay, smelts less than 150 mm in length fed mainly on cladocerans, copepods and mysids, while those longer than 150 mm fed mainly on mysids and fish (Timola 1980a). He concluded that smelt predation on fish populations must be regarded as being of some significance as the larger smelts constituted a large proportion of the population.

The daily feeding pattern of 175–250 mm long anadromous smelt in Nyyskiy Bay, Sakhalin, was found to be monocyclic during June and July (Churikov 1976). The feeding rate rose in the evening and peaked at night (2 and 6 am in June and July respectively). In June the food consisted mainly of mysids and in July it consisted of herring. On a daily basis, the food intake was 2.2 % and 1.6 % of body weight in June and July respectively.

Predators

Predators on smelt include different kinds of sea mammals, birds and fish.

Möller and Klatt (1988) studied the role of smelt as a transmitter of the seal worm *Pseudoterranova decipiens* in the River Elbe estuary. They assumed that each individual seal had a daily consumption of about 9 smelts in the 16–18 cm size class.

Piersma et al. (1988) studied the predation on smelt by great crested grebes, *Podiceps cristatus*, in a shallow lake in the Netherlands. The food of the grebes consisted almost exclusively of smelt and the grebes foraged only for about two hours during dawn and dusk. Sonar registrations showed that during these periods the smelt moved to the water surface, while they were concentrated near the bottom in the daytime and at night. It was thought that the smelts foraged during the twilight periods and that they were not schooling at that time which made them more easily captured by the grebes. Cormorants in Lake Ontario have little effect on smelt populations, as the smelt are below their diving range,

and as the cormorants are not present in the area during the smelt spawning run (Christie et al. 1987). In Finland, Caspian terns (*Hydroprogne caspia*) were found to prey on smelt to a small extent (Koli and Soikkeli 1974).

Greene (1930) mentioned 9 species of fish from lakes Champlain and Upper Saranac that had smelt in their stomachs. The great importance of smelt as food for stocked salmonides in the Great Lakes is evident. The diet of yearling pink salmon, *Oncorhynchus gorbuscha*, in western Lake Huron consisted of 45 % by weight of smelt, mostly 1+ smelt which had the same vertical distribution (Kocik and Taylor 1987). In Lake Michigan large stocks of salmonides rely heavily (48–79 %) on alewives and to a lesser degree (4–11 %) on rainbow smelt (Eck and Brown 1985, Eck and Wells 1986, Jude et al. 1987). In Lake Ontario smelt was the second most common prey eaten by salmon and trout (Brandt 1986). In the same lake Elrod (1983) found that the diet of lake trout consisted of 27–69 % by weight of smelt during July–August. Smelt was thought to contribute to the improved growth of salmon (*Salmo salar*) in two Fish River Lakes, Maine (Warner and Incerpi 1969) and in Schoodic Lake, Maine (Havey 1973).

An example of the importance of smelt as food for species other than salmonids comes from Lake Michigan (Wagner 1972). During spring, the contribution of smelt to the food of northern pike (*Esox lucius*), walleye (*Stizostedion vitreum vitreum*) and burbot (*Lota lota*) was 76 %, 94 % and 76 % respectively.

Adult alewife may be an important predator on young smelt, as they occur together. There is no strong evidence for this from the contents of alewife stomachs, but this might be due to very rapid disintegration of young smelt in the stomachs (Smith 1970). De Nie (1987) found that eels 250–350 mm long in the shallow Lake Tjeukemeer, the Netherlands, became piscivorous when YOY fish (bream, roach and smelt) were available towards the end of June. There was size-selective predation by eels on smaller individuals in the YOY fish population during summer and autumn. Large eels were important predators on YOY smelt and YOY percids. In

Lake Vänern, Sweden, smelt appeared to be the most important food for sander, burbot and landlocked Atlantic salmon (Nilsson 1979). Smelt was also the dominating fish prey for lake trout and perch in Lilla Ullevifjärden, Lake Mälaren, Sweden (Hammar 1968). Vøllestad et al. (1986) found that smelt was the most important food item for pike (*Esox lucius* L.) in Lakes Bjørkelangen and Rødenes, Norway. They were also important as food for pike in Lakes Øgderen and Tyrifjorden.

Interrelationships

The smelts act mostly as planktivores and may therefore have the ability to restructure the zooplankton community.

Reif and Tappa (1966) were able to study the zooplankton community in Harveys Lake, Pennsylvania, before and after the introduction of smelt. The circumstantial evidence pointed to a reduction or disappearence of larger zooplankton such as *Leptodora kindtii* and *Daphnia pulex*, and their replacement by smaller species such as *D. dubia*. In Gull Lake, where smelt prey on *Chaoborus* and *Daphnia pulex*, Lane (1978) proposed that the indirect benefits to most of the zooplankton population were larger than the harm caused to prey by direct smelt predation. The establishment of a large population of smelt in the south part of Lake George, New York, appeared responsible for the difference in the abundance of large-bodied crustacea between the north and south basins of the lake (Siegfried 1987). Gannon and Beeton (1971) thought smelt to be one of the most probable reasons for the decline of the large copepod *Limnocalanus macrurus* in Lake Erie. The smelt was found to undergo the same seasonal and diurnal vertical migration as the copepod.

There is evidence that smelt affect other fish species by predation on eggs and young.

The decline in the whitefish population of Lake Syam, Lake Onega basin, was caused by excessive fishing, eutrophication and predation on its eggs and young by smelt and ruffe (Sterligova and Pavlovskiy 1985)

In Lake Michigan, the disappearence or low abundance of 9 native fish species with pelagic eggs and larvae was probably caused by predation by alewife and smelt (Stewart et al. 1981, Magnuson and Crowder 1984).

Large smelt prey on young alewife during fall when they occupy the same watermasses (O'Gorman 1974).

Selgeby et al. (1978) studied the possible predation by smelt on lake herring larvae in Lake Superior and concluded that, though the smelt consumed 3.3–11 % of the herring larvae, they were not the major factor suppressing the population.

Recruitment failure in 3 of 21 walleye stocks in the Great Lakes coincided with an increase in the abundance of rainbow smelt. The small effect of predation by individual smelt could have been magnified greatly by the high density of smelt. Even if the smelt did not play an important role in the decline of the walleye stocks, they may have been important in preventing their recovery (Schneider and Leach 1977).

MacCrimmon and Pugsley (1979) thought that competition with smelt for specific food items that were required at some critical stage in early development, had a greater effect on other fish species than did predation by smelt on these species. Evans and Waring (1987) suggested that there was a negative interaction between YOY and yearlings of smelt and lake herring in Lake Simcoe. In their analysis intraspecific effects accounted for 29 % of the total variation in the catch, which indicated that there was an interaction between YOY and yearling smelt. This may have been caused by predation or competition for food.

The decline in the population of lake herring *Coregonus artedii* in western Lake Superior was evaluated by Anderson and Smith (1971). They suggested that competition for food, during the larval stage, by smelt and bloater, *Coregonus hoyi*, was the major reason for the decline. The more abundant smelt population probably had the largest influence.

Gordon (1961) thought that the smelt in Saginaw Bay, Lake Huron, competed for food with the young of all the associated fish species and

with the adults of some. The study did not indicate smelt to be a significant predator on commercially exploited species, with the possible exception of smelt itself. Brandt and Madon (1986) studied the food of smelt in Lake Ontario and inferred that rainbow smelt may compete with juvenile lake trout (*Salvelinus namaycush*) for slimy sculpin (*Cottus cognatus*).

Other fish species can also have a negative effect on smelt populations.

Interactions between alewife, smelt and stocked salmonides in Lake Ontario were studied by O'Gorman et al. (1987). During the study, the growth of smelt declined and was directly related to the recovery of alewife population, in which growth also declined. The decline in smelt growth probably resulted from the reduction of zooplankton by alewife. The large alewife population probably increased the survival of older smelt as the probability of the smelt being encountered by a predator would have decreased. When alewife were hyperabundant the quantity of YOY fish decreased, which in turn slowed the growth of yearling brown trout and coho salmon.

In their study of thermal habitats of fish in Lake Michigan Brandt et al. (1980) stated that the most abundant fish species occurred at different temperatures. Adult smelt were found just to the cold side of the thermal distribution of alewife. It was not clear whether the smelt preferred this temperature or if they had shifted their thermal distribution in response to the abundant alewives. The study was later complemented by an examination of the diet of five fish species (Crowder et al. 1981). Adult alewife and smelt had the most similar diets, but tended to segregate on the basis of thermal habitat. The authors suggested that the native species that had declined during the increasing abundance of alewife and smelt, were those that had similar food and habitat requirements. When the abundance of bloater increased during 1977–79, smelt may have shifted to slightly warmer water (Crowder and Magnuson 1982). In Sparkling Lake, young cisco may have occurred at the same depth as older cisco because they avoided rainbow smelt (Rudstam and Magnuson 1985).

Johnston and Cheverie (1988) found little overlap in the spawning and hatching times of anadromous smelt and blueback herring in the West River, Prince Edward Island. Johnston and Morse (1988) discussed the possible interaction between alewife and smelt in the same area, as they both spawned in the streams and the early juveniles were not separated in habitat and time. The faster growth rate of smelt suggested that interactions between the species could be reduced by the use of different sizes of prey i.e. smelt turning to the larger size of food.

Courtois and Dodson (1986) found that competition between smelt, capelin and herring larvae was minimal, as they mainly occurred in different water masses in a Canadian estuary. They were of different sizes and therefore exploited different sizes and species of prey.

Evans and Loftus (1987) summarized 35 studies of the introduction of smelt in inland lakes in the Great Lakes region. Declines in the recruitment of lake whitefish occurred in 13 of 24 cases and declines in the recruitment of lake herring occurred in 5 of 19 cases. In eight lakes lake whitefish and/or lake herring were relatively successful in the presence of smelt, but they were absent in two lakes with large indigenous smelt populations. In two lakes that continued to support coregonines the indigenous smelt populations were rare or had disappeared. An observed increase in growth rate of lake trout and Atlantic salmon associated with smelt invasion in 10 cases provided relatively convincing evidence of the effect of smelt as prey.

Interactions between smelt and other fish species have also been documented in European lakes.

Lammens et al. (1985) studied the resource partitioning and niche shifts of bream and eel in Lake Tjeukemeer, The Netherlands. The resource partitioning was related to the variation in abundance of *Daphnia hyalina* and chironomids. Niche shifts in bream and eel populations were related to the abundance of young planktivorous fish, particularly smelt, as these preyed selectively on large *D. hyalina*. This caused the bream to switch to benthic feeding (chironomid larvae), which in turn caused the

eels to switch from chironomid pupae to a diet of smelt. The size of the smelt population in the lake was to a great extent determined by the hydrological regime, which controlled passive immigration. Synchronous fluctuations in the abundance of *Daphnia hyalina* and the mean size of *Daphnia* in some Frisian lakes, The Netherlands, were considered to be mainly caused by the varying densities of YOY smelt and YOY perch (van Densen and Vijverberg 1982). A high abundance of YOY smelt facilitated the onset of piscivory by YOY pikeperch and also buffered the latter from predation by adult pikeperch.

In Polish lakes, bleak *Alburnus alburnus*, smelt and vendace occupied different water layers in summer, which seemed to limit interspecific competition (Dembinski 1971).

Interactions between cisco and smelt in Swedish lakes were suggested by the low degree of sympatry. In 110 lakes in northern Sweden, 71 contained cisco, 51 contained smelt but only 13 lakes had both species (Svärdson 1966). In 23 Swedish lakes with smelt, the catch of smelt per unit effort was significantly negatively correlated with the number of species in the lakes (Degerman and Nyberg 1987). The spatial distribution of these species was studied in Lambarfjärden, Lake Mälaren, Sweden by Northcote and Rundberg (1970). Their methods made it difficult to determine the extent to which cisco and smelt were spatially segregated. They concluded that the vertical distributions overlapped considerably in summer, although adult smelt were not taken near the surface. They recommended that future studies should be more detailed.

In Lake Vänern, Sweden, smelt and cisco overlapped to a large extent, but the smelt was more confined to deeper water (Nilsson 1974). There was size segregation in both species with the smaller specimens in the upper 20 m and the larger ones in deeper water. Nilsson concluded that the results confirmed the theory of competition between the species, which results in the segregation of habitat and food. He proposed that the cisco was the stronger competitor and that the smelt population relied on the crusta-

cean "glacial relicts" in the lake to withstand the competition for food. These results were later confirmed in two other investigations (Appelberg 1977, Almer 1979).

The food competition between herring, smelt and cisco was investigated in the Bothnian Bay (Enderlein 1981). The fish species were very rarely found together, probably due to their different salinity tolerances. Only the large smelt were piscivorous. Large food items, such as mysids, were eaten by smelt and to a lesser extent by herring. It was thought that abiotic factors e.g. the brackish water, probably interact, resulting in a system dominating by two species, herring and cisco, instead of one, the cisco.

In another large Swedish lake, Lake Vättern, more than 50 % of the food of smelt consisted of "glacial relicts" (Svärdson et al. 1988). It was suggested that smelt, cisco and *Mysis* constituted a rather stable sort of feed-back system for char, trout and salmon. The concept of smelt as a "buffer species" was introduced by Svärdson (1976). Smelt may play such a role in reducing intraspecific predation in pikeperch in the Fresian lakes, The Netherlands (van Densen and Vijverberg 1982) and rainbow smelt and alewife may buffer bloaters from predation by lake trout in Lake Michigan (Eck and Wells 1986).

Parasites and diseases

Data on the parasite fauna of fishes in the Canadian waters of the Great Lakes have recently been put together in a catalogue edited by Nepszy (1988). The four lakes concerned, Lakes Superior, Huron, Erie and Ontario, are presented separately in the catalogue in chapters written by different authors (Dechtiar and Lawrie 1988, Dechtiar et al. 1988, Dechtiar and Nepszy 1988, Dechtiar and Christie 1988 respectively).

In the oligotrophic Lake Superior the prevalence of parasites in smelt was 91 %. One digenetic trematode, one nematode and two acanthocephalans infested the smelt, all with light to medium intensity (Dechtiar and Lawrie 1988). In Lake Huron the prevalence of parasites in

smelt was 95 %. One digenetic trematode, two cestodes, one nematode, three acanthocephalans and one leech infested the fish, all with light to medium intensity (Dechtiar et al. 1988). In Lake Erie the prevalence of parasites in smelt was 97 %. Two digenetic trematodes, one cestode and three acanthocephalans had a light to medium intensity of infestation, while the protozoan *Glugea hertwigi* had a heavy intensity of infection (Dechtiar and Nepszy 1988). In Lake Ontario the prevalence of parasites in smelt was 95 %. One fungus, two digenetic trematodes, two nematodes and two acanthocepalans had a light or medium intensity of infestation, and *G. hertwigi* had a heavy intensity of infection (Dechtiar and Christie 1988).

Infection by the protozoan parasite, *Glugea hertwigi*, has been found to be lethal for smelt and has even led to mass mortality in YOY and adult smelt (Dechtiar 1965, Nepszy and Dechtiar 1972, Nepszy et al. 1978). Haley (1953) suggested that *Glugea hertwigi* contributed to the decline of the smelt population in the Great Bay region, New Hampshire. He also suggested that the parasite entered with the food.

Sherburne and Bean (1979) found smelt infected by *Glugea hertwigi* in four of five Maine lakes and in all of 16 Massachusetts and Canadian maritime localities. Overall, 25 % of the landlocked smelt and 8% of the anadromous smelt were infected. Jimenez et al. (1982) found that 13.4 % (range 0–18 %) of the smelt from six Massachusetts rivers were infected by *Glugea hertwigi*. Chen and Power (1972) compared the infection of smelt by *Glugea hertwigi* in Lakes Ontario and Erie. In Lake Ontario the prevalence was much lower (5.2 %) than in Lake Erie (62.7 %). They also found a striking difference in the fecundity of the two smelt populations which was attributed to the replacement of ovarian tissue by the cysts of the parasite. There was a seasonal fluctuation in infection which seemed to be correlated to the maturation process.

Legault and Delisle (1967) studied dead specimens of rainbow smelt found on the beaches or floating in Lake Clay, Quebec. The smelt were heavily infected with *Glugea hertwigi*, which was thought to be the cause of death. Delisle

(1969) followed up the above study with the aim of determining the tolerance of the YOY-smelt to *Glugea hertwigi* in Lake Henney, Quebec. From June to September 1967 the prevalence of infection increased from 6.7 to 93.2 % and the number of cysts also rose from 0.08 to 57.44 during the same period. There was a period of time, mainly from the end of August, that favoured the multiplication and growth of the cysts. This coincided with the period of greatest growth in the smelt. After considering the results from other lakes, he suggested that some populations of smelt possessed a certain physiological resistance to *Glugea*.

Muzzall and Peebles (1988) found seven parasitic helminth species in smelt from lakes Huron and Michigan, with a prevalence of at least 97 %. Amin (1981) studied the distribution of the acanthocephalan *Echinorhynchus salmonis* in smelt in Lake Michigan. He found no seasonal periodicity in infection but suggested that it was primarily determined by climatic and other ecological conditions affecting the heterogeneity in the temporal and spatial distribution of infection sources and in the feeding behaviour of rainbow smelt.

In Newfoundland Threlfall (1981) found that 97 % of the landlocked and 86 % of the anadromous smelt were host to metazoan parasites. The two populations shared only one of the ten parasites found and none were unique for smelt.

Belyanina (1969) lists 30 parasites of smelts in the USSR. Of these, the microsporidian *Glugea hertwigi*, the cestode *Triaenophorus nodulosus*, the copepod *Eryasilis sieboldi* and the branchiuran *Argulus foliaceus* could cause mass mortality in fish, and the trematode *Diplostomum spathaceum* could cause blindness and mortality.

Most of the work on parasites and diseases in European smelt comes from the River Elbe and from Finland. Köhler and Hölzel (1980) found that intestine and liver of young smelt were less damaged than the organs of older fish. Juvenile smelt showed serious pathological changes of the organs only ten weeks after the hatching of the smelt and they suggested that the disease was caused by toxic compounds in the food of the smelt. Möller (1984) investigated diseases of 22

fish species in Germany from Hamburg to the open North Sea. The highest prevalence (12.7 %) and the largest variety of disease occurred in smelt. The incidence of diseases increased in larger (older) fish. Spawning papillomatosis was observed in adult smelt (>110 mm) during the spawning period. Pharyngeal granuloma were found in 8.8 % of fish larger than 110 mm. Neither pollution nor lack of oxygen were the main triggers for the outbreak of diseases. Anders and Möller (1985) suggested that the virus that caused spawning papillomatosis had an affinity with the Herpes group. Herman (1988) investigated tumours in smelt from a small pond in Maine, USA. He concluded that although the tumours were found during the spawning period they were distinct from the spawning papillomatosis described by Anders and Möller (1985). The cause and significance of the tumour remains to be determined. Anders and Möller (1987) found that granulamatosis in the buccal cavity was caused by spines and leg fragments of amphipods. The incidence of damage was lower in very large smelts, probably due to a change in feeding habits.

Jarling (1982) studied the helminth fauna of smelt in the River Elbe estuary. He found 11 species (3 trematodes, 1 cestode, 2 acanthocephalans and 5 nematodes). The dominating parasites were the cestode *Proteocephalus longicollis* and two species of the nematode *Thymnascaris*. Smelt was the intermediate host for 7 of the 11 parasites. Möller and Klatt (1988) found that the nematode *Pseudoterranova decipiens* infested 10 % of the 0-group, 36 % of the I-group and 76 % of the adult smelt. Infestation took place after the migration of the smelt from the spawning areas.

In the coastal waters of Finland, Voigt (1981a) found 9 species of parasitic worms in smelt and in another paper (1981b) he mentioned 25 species of parasites found in smelt from the Baltic Sea. Timola (1980b) identified three species of acanthocephalans in the alimentary organs and one species of nematode *Cystidicola farionis* in the swimbladder of smelt from the Bothnian Bay. The incidence of infestation by all four parasites increased sharply up to a fishsize of 150 mm.

Valtonen (1983) looked at the prevalence and intensity of infestation by two acanthocephalans in 30 species of fish in the Bothnian Bay. Female smelt were more heavily infested than male smelt, but the fish were free of parasites for the 3–4 last months studied. Valtonen et al. (1988) found a low (1.4 %) incidence of infestation by the nematode *Contracaecum osculatum* in smelt from the Bothnian Bay. In Lake Suvasvesi, Finland, the prevalence of the eyefluke *Diplostomum spathaceum* in smelt was 75 to 100 % (Ruotsalainen and Ylönen 1987). No blind or dim-eyed fish were found.

The introduction and spread of smelt

Smelt have been introduced on purpose or by accident to different lakes in North America and Europe. The main purpose has been to increase the growth of different predatory sport and commercial species, mainly salmonids (Warner and Fenderson 1963).

Svärdson (1976) held the opinion that smelt was a "buffer species" that reduced interactions between whitefish and char in Lake Vättern and between sander and perch in Lake Hjälmaren, Sweden, on the basis of the observation that smelt were the most sought-after prey for char, sander and large perch. He proposed that the smelt could be introduced to southern lakes and mountain lakes for fishery management.

The introduction of smelt into the Great Lakes serves as a good example of its ability to spread. After introduction to Crystal Lake, Michigan in 1912 (Van Oosten 1937b) smelt spread to the Great Lakes. They were found in Lake Michigan in 1923, Lake Huron in 1925, Lake Superior in 1930 and Lake Erie in 1935. As smelt were found in Lake Ontario in 1929, before they were first recorded in Lake Erie, they probably spread from the Finger Lakes, New York where they were introduced after 1917 (Youngs and Oglesby 1972, Bergstedt 1983). They are thought to have spread to Lake Ontario via Cross Lake, Seneca River and Oswego River (Scott and

Crossman, 1973). Smelt were introduced to Lake Sakakawea, in the Missouri River drainage area, in 1971 (Burczynski et al. 1987) and were accidentally introduced into Lake Oahe, 400 km downriver in 1974 (Mayden et al. 1987). In four years they became the most abundant fish species and spread down the Missouri River to the next reservoirs. About 7 years after the introduction to Lake Sakakawea they were found in the lower Missouri River. Another route of dispersal was from Lake Michigan via the Chicago canal and the Illinois river to the Mississippi river (Burr and Mayden 1979). Juvenile smelt have now been found in the lower Mississippi River, about 32 miles north of Baton Rouge, Louisiana (Suttkus and Conner 1979).

A proposed canal system, The Garrison Diversion, was to divert water from the Missouri River Basin into North Dakota. This would have an impact on Canadian waters such as Lakes Manitoba and Winnipeg, by way of the Rivers Souris and Red. The possible impact of movements of exotic fish species, in particular rainbow smelt, gizzard shad and Utah chub, into the Hudson Bay Basin was examined by Loch et al. (1979). They believed that that if smelt spread to the Basin they would cause the collapse of lake herring populations and have a negative impact on the lake whitefish fishery.

From his experience of the results of the introduction of smelt to the Great Lakes, Van Oosten (1937a) maintained that it would be a good policy never to introduce an exotic fish species but rather to cultivate the highly prized native species. Current debate over the introduction of smelt to the Great Lakes also revolves around the question of whether it is most important to maintain the diversity of the indigenous fish communities or to promote commercial and sport fisheries for the large salmonid species (see chapter Interrelationships).

Kircheis and Stanley (1981) regarded landlocked smelt to be more valuable than alewife for introduction in New England, because the distribution of smelt within the water column more closely matched that of coldwater predators such as Atlantic salmon. However, the extreme fluctuations in the abundance of smelt were thought to limit their reliability as a primary forage-fish.

Evans and Loftus (1987) advocated caution with regard to the introduction of smelt, in view of the potentially serious effects on indigenous species. Lack of information on the specific effects of smelt on recruitment succes of most other species necessitates a cautious management approach.

Other aspects

Skurdal et al. (1985) studied mercury accumulation in the muscle of fish and set up four requirements for a test organism.

(1) The species should be monomorphic with respect to sex, growth rate, age at smoltification, age at sexual maturation, and mode of migration.

(2) Age determination of the species should be easy and reliable.

(3) It should be possible to catch sufficient numbers of the species during all life history stages.

(4) It should be possible to catch the species before or after the growth season to eliminate the effects of accumulation throughout the season, i.e. a fixed point for comparison.

Of five fish species, they considered smelt to be the most suitable indicator of mercury contamination. Sandlund et al. (1987) found a significant increase in mercury in the muscle of smelt as the age of the fish increased from 1 to 10 years.

In Canada, MacCrimmon et al. (1983c) had earlier suggested that smelt was an indicator of mercury contamination. The lake trout in Tadenac Lake showed a pronounced acceleration in growth rate when they started feeding on smelt and at the same time there was an increase in the accumulation of mercury. There was also a positive relationship between the mercury levels in smelt and trout in nine Ontario lakes. It was reported that smelt might act as a vector of mercury uptake in lake trout in Maine lakes.

Lake trout had higher mercury levels in lakes containing smelt than in lakes without smelt (Akielaszek and Haines 1981 cited in MacCrimmon et al. 1983 c).

Evans and Loftus (1987) argued against the introduction of smelt to softwater areas where the bioaccumulation of naturally occurring mercury could be accelerated by lake trout feeding on smelt.

Large numbers of power plants and their use of water for cooling may have a certain local impact on fish populations. For instance van Densen and Hadderingh (1982) believed that entrappment mortality could have a considerable influence on the density of larvae of smelt and percids at the beginning of the growing season in the Bergumermeer, the Netherlands. In a study of the entrainment of larval fish in Lake Huron, Kelso and Leslie (1979) found that power plants appeared to concentrate larval fish and that there was some selection of particular species.

Recommendations

Li and Moyle (1981) stated that introduction of new species into aquatic communities has often created more problems than it has solved. They suggested loop analysis as a tool of systems analysis to be useful in predicting systems behaviour once a introduction is made. They also drew up the following modified roles for use in fisheries management.

(1) No introductions should be made into the few aquatic systems left that show little evidence of human disturbance.

(2) Introductions should be considered mainly for systems that have been so altered by human activity that it is necessary to create a new community to take advantage of the production.

(3) Introductions should be considered mainly for bodies of water that are sufficiently isolated that uncontrolled spread of the introduced species is unlikely. If the body of water is not isolated, the connected waters should be analyzed for potential effects of the introduction in the same way the target waters are analyzed.

(4) Any system being considered for an introduction should be inventoried thoroughly.

(5) From the inventory, a species list should be developed that organizes the species into functional groups by habitat and trophic position (pelagic piscivores, benthic detritivores, etc.

(6) Estimates should be made from the information available for the functional groups with which the proposed introduction is likely to interact. The arithmethic signs of the possible interactions should be determined and loop analysis used to obtain a range of possible answers.

(7) Studies should be conducted to fill in data gaps revealed by the loop analysis and to determine the intensity of the possible interactions.

(8) Oligotrophic systems or nutrient-poor systems are not good sites for species introductions.

They also suggested the following criteria for the species that is the candidate for introduction.

(a) The species should be part of a coadapted trophic assemblage, members of the assemblage already being present within the system.

(b) It should have a narrow niche breadth including being stenophagus.

(c) It should have a low vagility, so that should it escape from the original site of introduction, there will be a good chance of controlling its spread.

(d) It should be free of diseases and parasites exotic to the system.

Smelt cannot be said to be a suitable species for introduction according to points (b) and (c).

Ryder and Kerr (1984) stated that for north-temperate oligotrophic waters the greatest likelihood of success lay in the use of species that had co-evolved in glacial refugia but may have become allopatric through the vagaries of redistribution following glacial recession. A resulting high level of niche complementarity of the candidate species with the various components of the native community would increase the likelihood of success of an introduction. In the process of considering a species for introduction

three concepts were thought to have particular application at the community level, i.e. interactive segregation (Nilsson 1967), dominance-subordinance (Svärdson 1976), and resource partitioning (Schoener 1974).

In Lake Storsjön, Sweden, introduced smelt became an important food resource for lake trout, and the growth rate of the lake trout increased. In spite of this, Nilsson et al. (1987) recommended against new introductions of smelt into Swedish lakes.

Conclusions

For resolving the taxonomic problems of the genus *Osmerus*, studies of the morphometric and meristic characters must be complemented by more electrophoretic studies, where an international collaboration is required.

More studies of the diel and seasonal distribution of smelt during their whole life span are needed, possibly with the use of new hydroacoustic methods. Detailed studies of the co-occurrence of smelt with other fish species on a daily and seasonal basis are needed to get a better picture of their impact on these species.

There is a need for food studies on the diet of larvae and large adults in particular. For these studies active sampling methods should be used to obtain fresh stomachs and to avoid breakdown of the contents.

Bioenergetic analyses and models of feeding and growth efficiency could provide an explanation for differences in age structure between populations, and for the occurrence of mass mortality after spawning.

Introductions to Swedish lakes should be avoided or limited in accordance with the roles of Li and Moyle (1981). Introductions should only be carried out after a thorough investigation of the abiotic and biotic parameters of the lakes in question.

Acknowledgments

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GUIDELINES TO AUTHORS

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