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N

ORDIC JOURNAL *of*  
FRESHWATER  
RESEARCH

*A Journal of Life Sciences  
in Holarctic Waters*

No. 74 • 1998

# **N**ORDIC JOURNAL *of* **FRESHWATER RESEARCH**



National Board of Fisheries  
Institute of Freshwater Research  
Sweden

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Nordic Journal of Freshwater Research is a modern version of the Report of the Institute of Freshwater Research, DROTTNINGHOLM. The journal is concerned with all aspects of freshwater research in the northern hemisphere including anadromous and catadromous species. Specific topics covered in the journal include: ecology, ethology, evolution, genetics, limnology, physiology and systematics. The main emphasis of the journal lies both in descriptive and experimental works as well as theoretical models within the field of ecology. Descriptive and monitoring studies will be acceptable if they demonstrate biological principles. Papers describing new techniques, methods and apparatus will also be considered.

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BLOMS I LUND TRYCKERI AB, 1998

# Postglacial Dispersal and Reticulate Evolution of Nordic Coregonids

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## Abstract

When the Weichselian ice-sheet withdrew from the Baltic basin, *Coregonus* species could colonize. The ice-sheet over Finland disintegrated from SE to NW and temporary ice-dammed lakes were formed. They first drained eastwards or northwards, later, when the ice sheet melted, westwards or southwards in the Ancylus Lake, about 9,500 BP. Four species of whitefish, including *Coregonus peled* and *C. pidschian*, used these routes and still live sympatrically in northern Sweden. Two came in a first wave, due to the earlier melting of the ice in the SE. They were the only ones to colonize parts of the Indalsälven river, since local obstruction by dead ice blocked the river for the second wave of colonists. Two species of vendace, *Coregonus albula* and *C. trybomi* survived, together with probably one whitefish species, in the South Baltic proglacial lakes. Their subsequent penetration northwards was temporarily blocked by the saline Yoldia Sea. Vendace arrived in the northern parts of the Ancylus Lake rather late and colonized the lower reaches of the drainages systems. *Coregonus lavaretus*, an anadromous species, colonized the Baltic area from the SW, via lake Vänern during the Ancylus Lake stage. It is a geographically restricted western species with a late Pleistocene ancestry different from that of the northern quartet of whitefish. A transgression of the Ancylus lake about 9,300-9,200 BP, by some 20 m, eroded two major outlets in the lake Vänern area. The rapids so formed, with a combined water flow of up to 20,000 m<sup>3</sup>/s and velocity of 5-7 m/s (Björck 1995) flushed freshwater fish, including the coregonids, from the Baltic basin into the Kattegat and Skagerrack. The sea currents carried these freshwater fish to southeast Norway, Denmark and the rivers on the Swedish west coast. Whitefish and vendace even reached southwest Norway, near Stavanger. During the postglacial period, the coregonids have undergone a reticulate evolution, by introgression between sympatric populations. The gene flow has varied according to lake size and the ecological niches occupied. Introgressed populations must be judged as incipient species, being a mixture of genes from several different species. Reticulate evolution by freshwater fish, in numerous isolated populations, could by later reunion result in species flocks. In glaciated areas, the reshuffling factor has been brutal and the species flocks are small, such as the ciscoes of the American Great Lakes. In tropical areas, where isolation and reunion are due to less dramatic water level fluctuations, the species flocks could be larger. The cichlids of African lakes may be an example.

Keywords: *Coregonus*, colonizing, postglacial dispersal, reticulate evolution, species flocks.

## Introduction

Europe's richest fauna of *Coregonus* fish lives in Fennoscandia and the adjacent parts of Russia. In northern Sweden, lakes may have four sympatric populations, with different body sizes,

gillrakers, spawning grounds and periods. They have usually been given local names by the indigenous people.

Chromosome studies have revealed that salmonid fish were probably old polyploids (Svärdson 1945). Moreover, two-days-old em-

bryos of whitefish showed more chromosome disturbances than other species, except for artificial *Salmo*-hybrid backcrossings, suggesting the presence of unbalanced gametes from meiotic dysfunction.

Svärdson (1949) pointed out early that the sympatric whitefish populations were biological species, which had not originated in their present lakes, but allopatrically. Final evidence for this interpretation appeared when a characteristic Russian whitefish species, *Coregonus peled*, was found to be one of the four native populations in the Storvindeln lake (Svärdson 1979).

Comparison of lakes within and between different rivers suggested genetic introgression which could explain the chromosome variations (Svärdson 1957, 1958, 1970, 1979). Despite that, the populations could be grouped into major entities, traced back to some original colonists. The taxonomic problems, however, were great. Local populations in the British Isles or in the Alpine region were described and named early on, while their relationships to the vast number of forms in Fennoscandia and Russia were unclear (Svärdson 1957, 1979).

Gradually, it was realized that the 'Coregonid Problem' was not so much a trivial systematic or taxonomic mess, but a case of interesting reticulate evolution. This kind of evolution is known from bacteria and plants but is thought to be rare in animals.

The molecular genetic methods were heralded with great hopes. However, the main result turned out to be the proven genetic similarity of sympatric populations, that suggested, to several authors (Vuorinen 1988, Sandlund et al. 1995) some sort of sympatric speciation. The similarity, however, is better explained by genetic introgression over long periods of time, whereas ecological characters are selected for their persistence. The selection pressure, by water temperature acting on different enzyme alleles (Vuorinen et al. 1991, Kirpichnikov 1992), should also tend to make sympatric populations more similar.

Obviously, if the colonization routes could be revealed from new quaternary geology data and compared with the morphological and ecologi-

cal traits in whitefish, more light would be shed on the reticulate evolution of coregonids.

## Material and methods

All samples were taken by gillnets and most fish were caught when spawning. Exceptions were the fish used for food studies.

Size of spawners is used as a short-hand parameter in the figures. Body size, of course, is a function of growth rate and age. Since the 18<sup>th</sup> century it has been well known that growth rates may explode when small-sized whitefish are introduced into lakes with no native whitefish populations (Hasselberg 1930, Olofsson 1934). More recent and drastic examples have been given by Svärdson (1949, 1950). In a balanced population, however, body size tends to stabilize (Olofsson 1934). Length of life, as well as diet preference, has a genetic basis, as proved by transplantation experiments (Svärdson 1979). Consequently, body size can, with some caution, be used as a character of homologous whitefish species (cf. Wagler 1937).

Some morphological traits, used in older coregonid systematics, were found to be allometric and correlated with growth rate (Svärdson 1950). The number of scales in the lateral line is influenced by the temperature during a formative stage (Svärdson 1952).

The gillrakers have grown almost to their full number ontogenetically when the young fish is some 10-12 cm in length (Svärdson 1952, 1965). Samples, taken in consecutive years from the same year-class, show an average increase of one raker up to old age. Gillrakers and food taken were correlated in a hybrid population derived from benthic and pelagic parent populations. 22-28 raker fish had a less pelagic diet than those with 29-36 rakers (Svärdson 1965, p. 111).

Gillraker numbers are intermediate in hybrids (Svärdson 1957, 1958, 1965, 1979) and respond to artificial selection. Out of a population with 36.0 rakers, two selected individuals, with 32 rakers, produced a progeny with 33.8 rakers (99 fish). Another selected pair, with 41 rakers, raised a progeny of 38.3 (40 fish).

A significant decline in gillraker numbers from the  $F_1$  to the  $F_2$  hybrid generations was proved in three experiments (Svärdson 1965). This was most marked in fish with high number of gillrakers. All the experimental results suggest that inheritance of gillraker number is polygenetic and additive.

Gillraker number does not change much over time, or in new environments (Svärdson 1979). After 92 years, most enzyme allele frequencies of a Norwegian population of vendace, *Coregonus albula*, transplanted to a lake at a 300 m higher altitude had changed significantly (Vuorinen et al. 1991), whereas gillraker numbers were virtually the same: 44.6 to 43.9 (Sandlund 1992).

For practical reasons, the Swedish names storsik, sandsik, älvsik, planktonsik and aspsik are used in the text. The names are not quite equivalent to normal species, since they cover a group of populations which are probably introgressed forms of one original colonist. The name blåsik (Svärdson 1979) is not used in this paper, since this species is no longer supposed to have existed as an independent form.

Some references to maps and tables are made to my 1979 paper, of which this one is a revision.

## Four sympatric species in northern Sweden

The presentation of the four northern sympatric whitefish species can best be done by comparing the lakes Storvindeln and Parkijaure (map in Svärdson 1979, p. 18). It should be remembered that the two lakes have been isolated for some 9,000 years.

	Lake Storvindeln	Lake Parkijaure
River system	Vindel	Lilla Lule
Altitude	342 m	295 m
Maximal depth	36 m	40 m
Size	5,500 hectares	4,000 hectares

The storsik is the largest fish found in both lakes (Figs 1, 2). It may reach over 50 cm total length and its weight can be 4 kg. Its food is benthic; *Gammarus*, molluscs and insect larva (Bergstrand 1982). Gillraker numbers are 18-29, with an average of 23 in Storvindeln but 20-32, average 27.6 in Parkijaure (Bergstrand 1977, Svärdson 1979).

Morphologically and ecologically the storsik of lake Storvindeln conforms to the Russian species *C. pidschian* (Shaposhnikova 1974) while the population in Lake Parkijaure fits less well, because of its higher number of gillrakers.

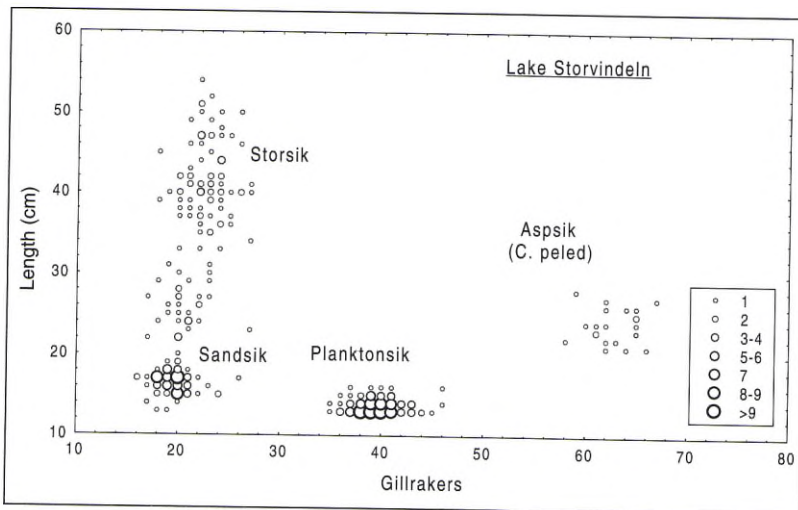


Fig. 1. Lake Storvindeln. Four whitefish populations live sympatrically, two of which conform to Russian species, viz. the aspsik, *Coregonus peled* and the storsik, *C. pidschian*.



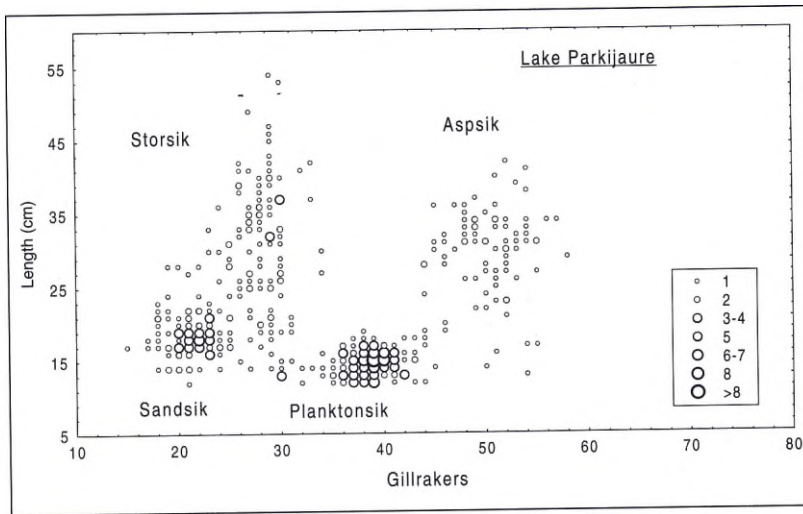


Fig. 2. Lake Parkijaure. 9,000 years of mutual introgression has made the storsik and aspsik more similar, but they still have different genomes.

The sandsik is almost a smaller copy of the storsik. Its diet is very much the same, but in every size-group it takes smaller items (Bergstrand 1982). In Storvindeln the spawners are less than 20 cm in length. On one spawning ground, at the mouth of a small stream from lake Gertsjaure, they spawn near the storsik. As suggested by Fig. 1, some stray (larger) hybrids may occur. Lake Parkijaure was fished during the summer. Again, stray individuals suggest that some sandsik can grow larger than the bulk of spawners (15-25 cm).

Gillraker numbers are 16-27 (average 20.5) in Storvindeln and 16-29 (average 21.3) in Parkijaure. The divergence in number to storsik is greater in Parkijaure than in Storvindeln.

The planktonsik of the two lakes are, again, almost identical. It is the most dwarfed population in both lakes, all spawners are less than 20 cm in length. Its diet is zooplanktonic and it lives pelagically. Gillraker numbers are 35-46 (average 39.9) in Storvindeln and 30-45 (average 38.7) in Parkijaure. There is no evidence of introgression to any other population in Storvindeln, but there might have been a slight gene flow to sandsik and aspsik in Parkijaure (Fig. 2).

The fourth species found in lake Storvindeln was a great surprise, when it was first identified in 1976 (Svärdsön 1979, p. 18-21). There could be little doubt that it conformed to the Russian species *C. peled* (called river *peled*), living in

river east of the White Sea. The high number of long gillrakers, 62.8, is outstanding, as also is the protruding lower jaw, very much like that of the vendace, *C. albula*. It must be pointed out that the *peled* is indigenous in lake Storvindeln and was known to the local people already in 1930. It has nothing to do with the recent introduction of Siberian *peled* (probably another species as discussed in Svärdsön 1979, p. 79) into eastern Europe in the 1960s (Reshetnikov 1988, 1992).

In lake Parkijaure the *peled* whitefish has become strongly modified, no doubt by mutual gene flow to the storsik. It is called aspsik in this lake, as well as in other Swedish lakes where the modified *peled* colonist lives. Firstly the species-identifying protruding lower jaw is lost and converted to a terminal mouth with a slightly shorter upper jaw than that of the storsik. Secondly, the gillrakers are heavily reduced in numbers from over 60 to just 50. They are also much shorter. Thirdly, growth improves and is almost as good as that of the storsik. Both species have converged to become more similar. Food habits, however, may be unchanged. In both lakes the *peled*/aspsik feed on plankton and surface food, viz. insect imagines. Strong vertical movements are suggested, since fish taken in deep water were found to have surface food in their stomachs. Bergstrand (1982) thought that the aspsik could only exceptionally feed on benthos.

Comparing the lakes, the gene flow between the sympatric species has been profound in lake Parkijaure but very restricted (if at all) in lake Störvindeln. There are probably  $F_1$ -hybrids storsik x aspsik in the Parkijaure catch, since large individuals with 33-34 or 44-45 rakers appeared (Fig. 2). When a species barrier has been broken by some gene flow, the isolating mechanisms, if inborn, should progressively become weaker, resulting in an accelerating formation of a hybrid swarm. But this has not happened. After 3,000 generations of whitefish in 9,000 years the storsik and aspsik still possess quite distinct gene pools. The *peled*, when transformed to aspsik, has lost some 12 gillrakers, i.e. 4 rakers in a 1,000 generations. The *pidschian* or storsik has acquired some more gillrakers, but only one raker in a 1,000 generations.

### Arjeplog lakes

The headwaters of a third river, the Skellefte with the famous Arjeplog lakes, are also inhabited by the same quartet of whitefish (Svärdson 1979, p. 38-43, map p. 18).

Here the storsik is large and benthic. Record size is 5.2 kg. Gillraker numbers are 19-20 on various spawning grounds. The sandsik is small, 15-25 cm and its benthic diet has been verified. Gillraker numbers are 20-21, in one locality even 24. The planktonsik is very numerous, in all three

major lakes. Gillrakers are most numerous (38) in the deep lake Hornavan, where spawning occurs even below 100 m depth. This species may gradually have become slightly introgressed with the local sandsik (of the same small size) and lives litorally. It has 33-35 gillrakers. The diet of fish less than 14 cm in length is zooplanktonic (*Bosmina*) but becomes more benthic at lengths of 16-17 cm (Lindström and Nilsson 1962). The aspsik is almost as large as the storsik, with 45 rakers, and spawns earlier, in streams. This species is mainly planktophagous (Nilsson 1958, Lindström 1962, Lindström and Nilsson 1962). It may prey on sticklebacks and takes surface food.

The rather similar spawning sizes of the storsik and aspsik may explain the appearance of stray storsik on the spawning grounds of the aspsik. Artificial hybrids were made between them in 1944 and later reared in another lake where they multiplied, just as a normal transplantation of whitefish does (Svärdson 1957, 1965, 1979).

### Lakes Vojmsjön–Dikasjön

Lake Vojmsjön is the headwater of the Vojmån stream, which is a tributary to the large Ångermanälven, a fourth major Swedish river (map in Svärdson 1979, p. 18). Three thousand whitefish from the lake have been studied (Svärdson 1979, p. 24-25), some of which are presented in Fig. 3.

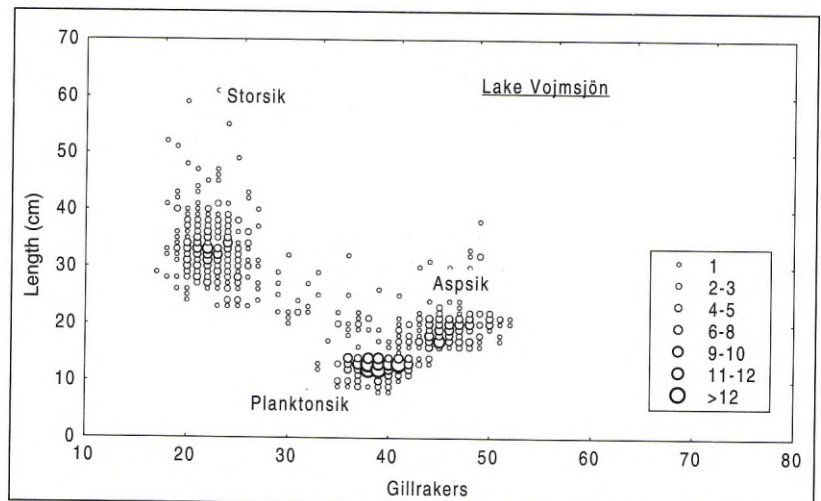


Fig. 3. Lake Vojmsjön. One member, the sandsik, is missing of the whitefish quartet.

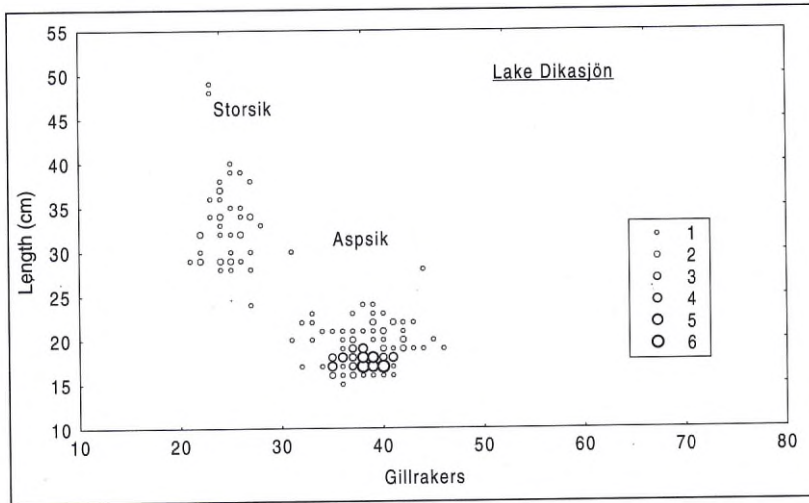


Fig. 4. Lake Dikasjön. In this shallow lake, upstream from lake Vojmsjön, only two introgressed species are left.

One of the species quartet seems to be missing here: the sandsik. The storsik, however, is more numerous than in most other lakes, suggesting genetic swamping to the normally abundant sandsik. The storsik grows to more than 60 cm, which, of course, indicates the dominance of genes from the storsik species. The planktonsik is, as usual, the smallest, 12-14 cm, with 38-39 gillrakers. It lives in deep water and was not known to the local people, which is otherwise the rule. The aspsik has 46 rakers and is relatively small, but clearly larger than the planktonsik.

Just upstream from the Vojmsjön lies a smaller and shallower lake, Dikasjön (Fig. 4). A short stream connects the two lakes. Nowadays, after damming, it is almost a sound. The two lakes indicate the importance of local topography for the direction and magnitude of mutual introgression. In the southern part of the Vojmsjön the aspsik has 47 gillrakers, in the northern part 45-46, and in the Dikasjön only 39. The storsik shows a converse trend. In southern Vojmsjön it has 21 gillrakers, in the northern part 23 and in Dikasjön 25-26 (Svärdsö 1957, 1958).

The planktonsik is missing from the Dikasjön, either because its deepwater niche is absent, or because genetic fusion with the aspsik population has taken place.

In 1967 the shrimp *Mysis relicta* was introduced into lake Vojmsjön, to produce more food for the fish population after the lake had been dammed for hydro-electric purposes. As in other cases in Scandinavia and North America, the shrimp turned out to be a serious competitor to the planktophagous fish (Northcote 1991). The dwarfed planktonsik was threatened (Hammar 1988). Older specimens, however, fed on the *Mysis*, grew better and became as large as the aspsik, with which introgression started. Of 612 specimens examined in 1949-81 an increase of gillraker number from 37.9 to 39.6 was documented (Hammar 1988).

The gene flow between the four whitefish species in lakes of the northern Swedish rivers creates a form of reticulate evolution, in which genes – from different genomes – become blended together. The introgressed populations evolve more rapidly from the incorporation of new chromosomes or gene sequences, than they could do only from new mutants and recombination within a single gene pool. Reticulate evolution creates incipient new species more rapidly than isolation of allopatric populations.

Introgression may be extremely small (lake Storvindeln) or moderate (lake Parkijaure), or lead to complete genetic fusion (probably so in lake Vojmsjön). Gillraker number correlate with diet. This indicator shows a change of 1-4 rakers

in 1,000 generations (Parkijaure). Transplantation of a population of älvsik into middle Sweden in 1870, provides another time-scale indicator. In lake Landösjön, in the river Indalsälven, the introduced species changed, by introgression into a native form, by 2.6 gillrakers in 50 years, i.e. some 15 generations (Svärdson 1979, p. 17). The Vojmsjön planktonsik developed 1.5 more gillrakers in 14 years, or over 4-5 generations of cohabitation with *Mysis relicta*.

## Colonization from the east and north

The four whitefish species, storsik, sandsik, planktonsik and aspsik, found in the large headwaters of the northern Swedish rivers could not have come from the west. There are no whitefish living in Norway in these latitudes. Moreover, the mountains lakes are either barren, or are

inhabited by Arctic char (*Salvelinus alpinus*), a species which is subdominant to whitefish (Svärdson 1976).

Dispersal from the south is improbable. The Baltic basin was occupied by the Yoldia Sea from 10,300 to 9,500 BP (Björck 1995) (Fig. 5). The ice front and the influx of salt water extended from the lake Vänern area, over the Åland islands to southeastern Finland. Fossil finds of harp seal, *Phoca groenlandica*, in the Stockholm area (Ekman 1922) suggest that a harsh environment prevailed. In the southern Baltic the water was previously fresh, during the Baltic Ice Lake stage. Its freshwater fauna, probably including one whitefish and two vendace species (see below), had to penetrate the salt water barrier in order to spread to the Bothnian area of the Baltic. When the ice sheet melted, fresh water began to replace the Yoldia Sea and the Ancylus lake stage (freshwater stage) of the Baltic began (Fig. 6).

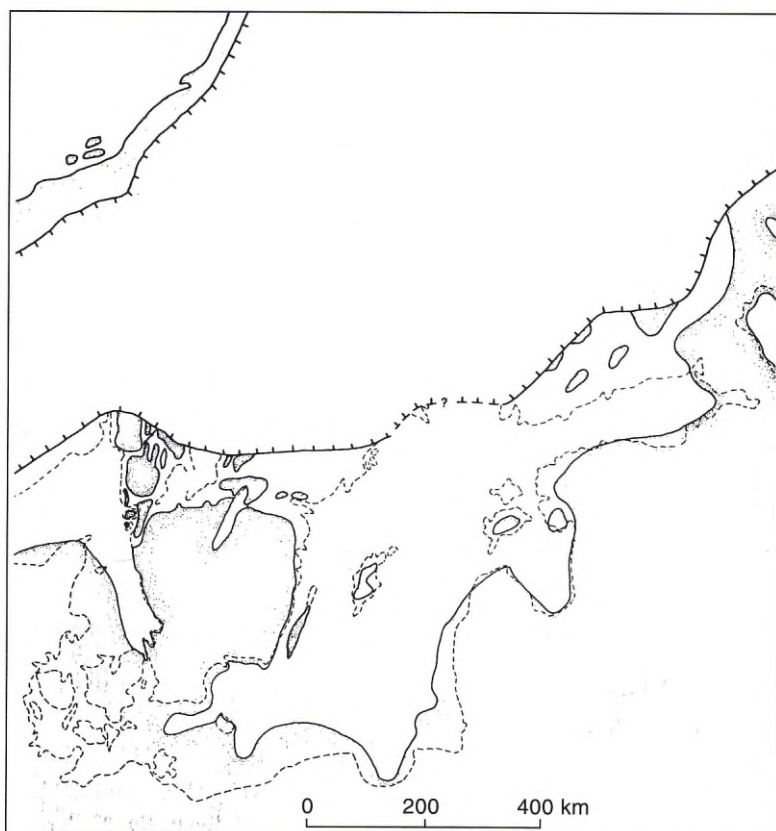


Fig. 5. The Yoldia Sea, about 10,000-9,900 BP. From Björck (1995).

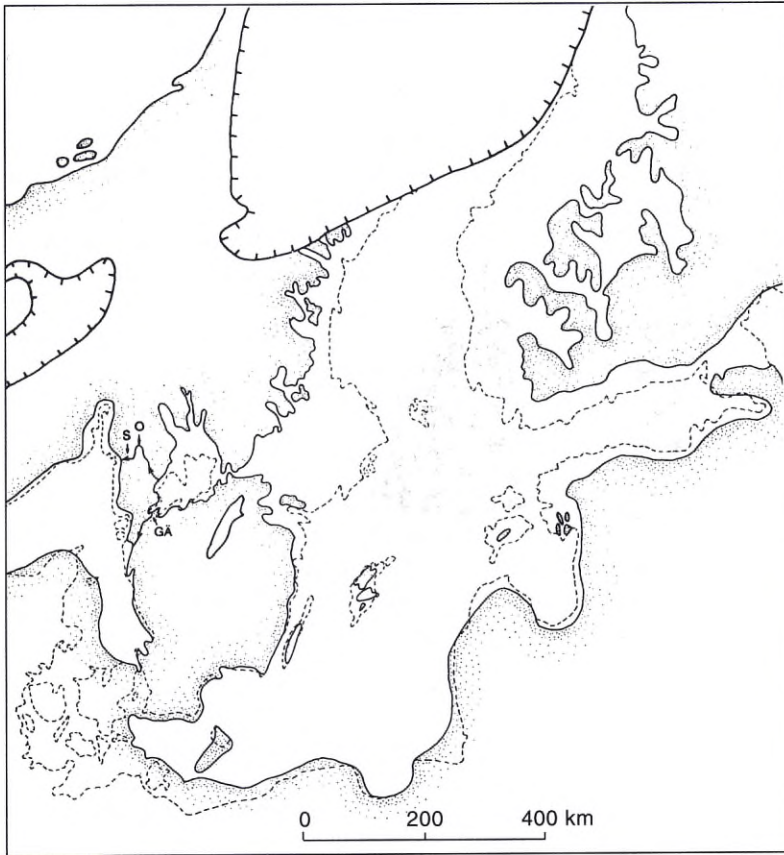


Fig. 6. The Ancyclus Lake when the transgression culminated, 9,300-9,200 BP. The outlets are rapids, with a water velocity of 5-7 m/s. Total water flow up to 20,000 m<sup>3</sup>/s. Freshwater fish, including coregonids, were probably flushed into the Kattegat and Skagerrack, and colonized the Swedish west-coast rivers, northern Denmark and southern Norway. From Björck (1995).

Temporary ice-dammed lakes formed between the melting ice sheet and the topographic water divide in eastern and northern Finland. These lakes first drained into the White Sea or Barents Sea, later more or less dramatically bursting into the Ancyclus Lake. Whitefish probably entered the eastern outlets of these lakes and were later flushed westwards down into the Baltic basin. At the present time no whitefish live close to permanent ice. Nevertheless biological productivity is high at the edge of melting ice sheets, both in sea water (Sakshaug and Skjoldal 1989) and in freshwater (Brundin 1956). In Alaska, analysis of lake sediments proves that the lakes there were more productive when just formed (Livingstone et al. 1958). The same was found for lake Inarijärvi, in northern Finland (Alhonen 1969). A rise to about a 7 °C higher air temperature (Alley et al. 1993, Fairbanks 1993) may also

have stimulated whitefish to colonize the ice-dammed lakes in summer time.

Saarnisto (1992) described the largest of the ice-dammed lakes. The Salla Ice Lake covered 3,500 km<sup>2</sup>, its outlet was to the White Sea. The water-level of this lake fell by 35 m (from 245 to 210 m) around 9,500 BP and it flushed water and fauna into the Ancyclus Lake. A series of smaller lakes appeared in the Ounasjoki valley (now the Kemi River) close to the present Swedish border. They first drained into the Barents Sea, later into the Ancyclus Lake (Saarnisto 1992, Kujansuu 1992). Sediments from other ice lakes are found in the Suomussalmi area (Kurimo 1979) as well as east of lakes Koitere and Pielenen in SE Finland (Saarnisto 1971). The first outlet from the great Saima complex was to the Bothnian Bay area of the Ancyclus Lake, later to the south and finally SE into Lake Ladoga (Hyvärinen 1966,

Saarnisto 1971). This tilting was caused by differential isostatic rise.

The main inference from these geological facts is that several different dispersal routes for whitefish existed. All provided eastern colonists with an opportunity to enter the Ancylus Lake around 9,500 BP. Those coming from east could arrive in the Ancylus Lake somewhat earlier than those coming from the north, since the ice sheet melted from SE over Finland during a period of 1,000 years (Lundqvist 1986b, Kujansuu 1992, Saarnisto 1992, Lundqvist and Saarnisto 1995).

The whitefish species which live in these areas now could be extant populations of the original colonists.

Järvi (1943, p. 34) concluded, after extensive studies on Finnish coregonids, that all whitefish with low numbers of gillrakers (21-24) known to him lived in northern Finland in lakes that run to the Barents Sea or the White Sea. In contrast, the stocks with many gillrakers (45-50) were found only in the lakes of central and eastern Finland.

Later studies (Järvi 1953) in lakes Päijänne, Peruvesi and Kivijärvi (Ilomantsi) revealed that the dominant, large-sized whitefish with many gillrakers, often found spawning in streams, had a smaller companion which had only 35-37 rakers. The stream-spawning stock in lake Koitere had the highest number (56) of gillrakers (Järvi 1928). On the Russian side of the border, in the River Vyg, lakes Vygozero and Segozero are inhabited by several whitefish forms, one of which has 50 or more gillrakers (Pravdin 1947, as cited by Berg 1962, p. 503).

Kallio-Nyberg and Koljonen (1988) reported two sympatric forms, with 31 and 57 gillrakers respectively, living in lake Pielinen and Heikinheimo-Schmid (1992) also two forms, with 31 and 53 gillrakers, in lake Paasivesi, which is part of the large Saima lake complex.

Two whitefish colonists, conforming to the Swedish names planktonsik and aspsik could therefore have been the first to arrive in the northern part of the Ancylus Lake.

In the northern Kuusamo area (Järvi 1943), there is a predominance of storsik, with 21-24 gillrakers. Some of the lakes, Kallunki, Suinunki

and Porontimo, are inhabited also by a second form, with 33-37 gillrakers. In lake Kallunki, the two forms were sympatric. All these lakes still drain, by the Oulanka river, into Lake Panajärvi and the White Sea. Panajärvi (in Russia) is also inhabited by stint (*Osmerus eperlanus*) and the crustacean relicts *Pallasea quadrispinosa* and *Pontoporeia affinis*, thus proving the existence of fresh or brackish water in the White Sea in early postglacial time. A central lake of the area, Kitkajärvi, also had a western outlet to the Baltic (Koutaniemi 1979).

The probable whitefish fauna of the Salla Ice Lake and the Ounasjoki valley ice-lakes is suggested also by the extant fish faunas of lakes Inarijärvi (Pasvik River) and Iijärvi (draining into the Varanger Fjord). Inarijärvi, before the recent introduction of vendace (*C. albula*), was inhabited by a large storsik (22-24 gillrakers), a dwarfed sandsik (locally called räpys) with 16-21 rakers and also a dwarfed planktonsik (locally called riika or reska) with 33-35 gillrakers (Järvi 1928, Toivonen 1960, P. Tuunainen pers.comm.). Lake Iijärvi (Tuunainen 1975) contains the same three species: storsik, sandsik and planktonsik. The first two have low numbers of gillrakers, the last has 34-35 rakers.

Three of the Swedish whitefish quartet, therefore, still live in northern Finland and could have been flushed into the Baltic basin when the ice-lakes burst. Two of the quartet still live in central and eastern Finland. One, the planktonsik, could have arrived from both directions into the Ancylus Lake. The period of time during which the immigrants lived in Finnish or Russian lakes, before being flushed into the Baltic basin, is of the order of 200-400 years. The *peled* (aspsik) species is nowhere in Finland or in the Kola-Carelia districts of Russia known to exist as a non-hybrid form (as in Storvindeln). The nearest "pure" population seem to be that in the river Mezen (Berg 1962, p. 370). This species, therefore, seems to be extremely prone to hybridize and lose its head shape character. The same is true in regard to the recent transplantation of Siberian *peled* into eastern Europe, after which widespread introgression started (Mamcarz 1992, Luczynski et al. 1995).

## Dispersal from the proglacial South-Baltic lakes

During the Weichselian glaciation there were some interstadials when the ice withdrew from most or part of the Baltic basin. The Jämtland interstadial (Lundqvist and Mook 1981, Lundqvist 1986a) was only 2-3 °C cooler than today and Sweden was almost completely deglaciated. Coniferous woods grew in central Sweden around 55,000 BP. Later on, at some 25,000 BP, the province of Skåne and the western coast near Göteborg were again ice-free, as was the whole of Denmark (Lundqvist 1986a).

When the glaciation culminated, 20,000-18,000 BP, various fauna elements from the Baltic became land-locked in the proglacial lakes. The ice sheet dammed all the northward-running rivers. Grosswald (1980) identified the Upper Volga lakes, the upper Dnieper lakes and a chain of lakes in the Warsaw-Berlin 'Urstromtal'. This system of valleys was eroded by freshwater flowing along the ice-front into the Dogger Lake (now the North Sea). The Dogger Lake drained south, through the English Channel, to the Biscayan Sea (Grosswald 1980).

It is generally agreed that relict crustaceans, with no ability to spread upstream, owe their present distributions in northern Germany and Poland to the existence of these proglacial lakes (Müller 1964, Dadswell 1974, Segerstråle 1982). Freshwater fish such as the stint (*Osmerus eperlanus*) and vendace (*Coregonus albula*) have roughly the same distribution pattern, probably for the same reason.

Vendace tends to eliminate planktophagous whitefish (Svärdson 1976) and only those populations which have few gillrakers may survive in the long run. The very same phenomenon has been noted in North America, regarding *C. clupeaformis* and *C. artedii* (Lindsey 1981). So, if vendace had become isolated in the proglacial lakes together with whitefish species, the latter would either have been eliminated or could have drifted downstream into the Dogger area, whence in the postglacial period, they could have ascended the Rhine river up to the Alps or into the fresh water Lough Hibernia (now the Irish Sea)

and into Irish and British lakes (Maitland 1970, Wheeler 1977).

Three forms of whitefish now live in the area formerly occupied by the proglacial lakes (Peters 1874, Thienemann 1922, Kulmatycki 1927, 1928, Wiese 1938, Wagler 1941). One is the anadromous *C. lavaretus* or Schnäpel, to be discussed later as a postglacial marine colonist to the Baltic from the SW. Another is a form with dense gillrakers, *C. generosus* (Thienemann 1928), which probably is an apssik that spread in Ancylus time into the area from the north. The third, however, may be a genuine survivor from some Weichselian lake refugium. It has few gillrakers and was named *C. holsatus* by Thienemann (1922). It occurs along the southern Baltic coast and also around Gotland. It may have introgressed to the Baltic *C. lavaretus* along the southeastern Swedish coast, as the 27-gillraker stock of the Skråbeån river, which offers the anglers catches of record-sized fish, of 4-5 kg. In the southeastern Baltic it is sympatric to *C. lavaretus*. The relationship of this form to the northern *pidschian* (storsik) remains to be studied but is probably close.

Thienemann (1933) described an aberrant vendace, sympatric to the usual form, in the small lakes Breiter and Kleiner Lucin and Zanzen in Mecklenburg. The population was named *C. albula lucinensis*. The lakes are situated within the 'Urstromtal' drainage. The two sympatric forms, which must be regarded as different species, may have drifted westwards in the chain of proglacial lakes. The origin of *lucinensis* could lie far to the east. It may have existed before the Weichselian glaciation.

The *lucinensis* feeds on *Mysis relicta* and is a deepwater form. It was presumed by Thienemann to be an autumn spawner, like *albula*. Svärdson (1979) speculated that it was a western form, that climbed the Elbe river during the postglacial. Since the two forms lived sympatrically, it would indicate that *C. vandesius*, the British vendace, was a separate species. But this hypothesis failed when Waterstraat (1990) proved that *lucinensis* actually spawns in May or June, thus conforming to the spring-spawning Baltic form *C. trybomi*. The *trybomi* species also inhabits some

eastern Finnish lakes, at a relatively high altitude. Its dispersal to the four known lakes in SW Sweden was discussed by Svärdson (1988).

The two vendace species were probably involved in the flush from the Ancylus Lake during the 9,300-9,200 BP transgression, to be discussed below. One vendace (*C. albula*) has also colonized the northern Baltic basin during the postglacial (Svärdson 1966). However, the lakes inhabited by the whitefish quartet generally lie at higher altitudes, which suggests that the vendace arrived rather late during the Ancylus stage. Vendace are more widespread in Finland, due to the lower altitudes of the lakes (below 300 m), which also means a more impoverished whitefish fauna, because of the competition.

Grosswald (1998) mapped the Younger Dryas re-advance of the Barents Sea part of the great Kara Ice Sheet. If the eastern least cisco, *C. sardinella*, had penetrated into the area before the re-advance, it could have become land-locked in the new proglacial lakes which united the Baltic Ice Lake with the Dwina and Pechora river drainages. That would have brought *C. sardinella* to lakes Ladoga and Onega during the postglacial, where, as *ripus* or *C. albula kiletz*, it lives sympatrically to the *albula* population (Michailowksy 1903, Pokrovsky 1956, Svärdson 1979, Dyatlov 1986). If so, all three species of vendace, viz. *C. albula*, *C. trybomi* and *C. sardinella* must have lived in proglacial lakes during part of the Weichselian glaciation or the Younger Dryas period.

### Colonization of the Indalsälven river by two waves of whitefish

In two tributaries, Långan and Hårkan, of the mighty Indalsälven river, a number of lakes are inhabited by only two whitefish species, both with dense gillrakers. The storsik and the sandsik are absent from all the lakes, which suggests a common cause. Downstream in the Indalsälven valley, a small lake, Övsjön, which now discharges into river Ljungan (further south), in early deglaciation time drained into the Indalsälven. It also has no storsik or sandsik. The outlets of

the Långan and Hårkan rivers were united by the temporary Lit Ice Lake, while Lake Övsjön was part of another ice-dammed lake, the Håsjön Ice Lake (Lundqvist 1973). In both cases the damming was probably caused by large chunks of dying ice.

Fig. 7 shows how far the Ancylus shoreline reached in the valleys. The Ancylus fauna must have penetrated the valley before the damming, since the relict crustacean *Pallasea quadri-spinosa*, which cannot spread upstream, lives in Lake Övsjön, some 20 m above the Ancylus shoreline (Nybelin and Oldevig 1944). Also, before the damming, the whitefish may have ascended the valley up to the Krokomb area (which became the second outlet from lake Storsjön) and become isolated in the Lit Ice Lake, which dammed the lower reaches of the tributaries Långan and Hårkan.

The situation is further complicated by the fact that lake Storsjön, the headwater of the river Indalsälven, is inhabited by the full whitefish quartet. Widegren (1863) found three species, Svärdson (1953) four populations, one of which, however, was later found to have been introduced (from lake Vänern) in the 1870s (Svärdson 1977).

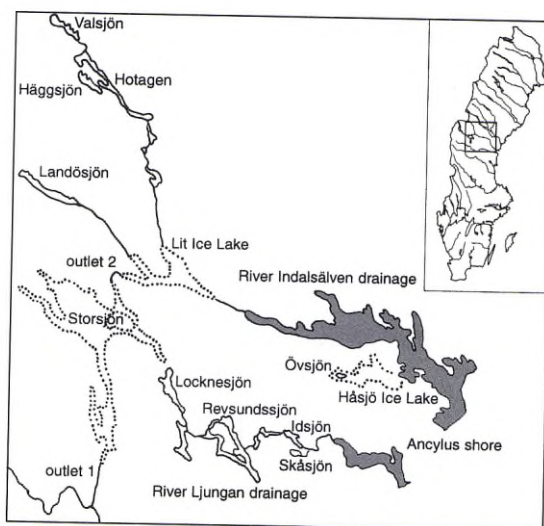


Fig. 7. Metachronic map of the Indalsälven and Ljungan drainage systems. All the lakes are still present, except the drained Lit Ice Lake and the Håsjön Ice Lake. Modified from Lundqvist (1973).



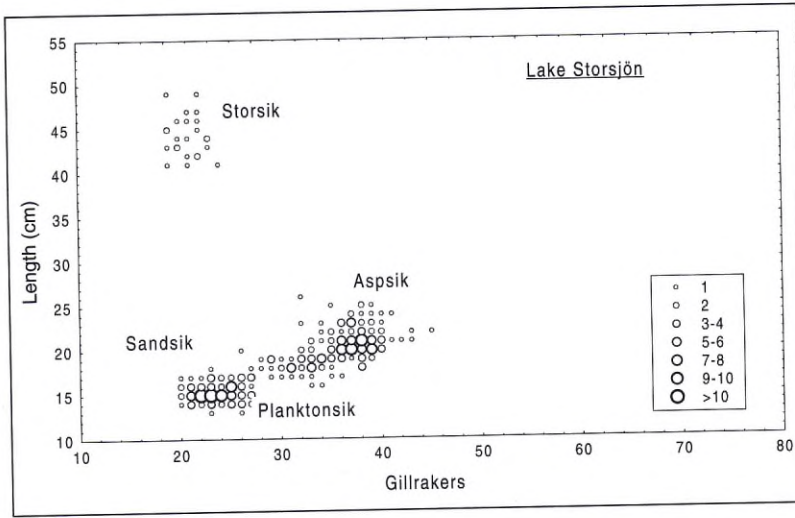


Fig. 8. Lake Storsjön. Four sympatric stocks of whitefish. A fifth species was introduced from Lake Vänern in the 1870's and from the Baltic coast in the 1960's (not shown).

The sandsik population in the lake was not found until the late 1950s (Fig. 8).

How then could the whitefish quartet have colonized the headwater of the river but not the three downstream tributaries, which only contain two members of the quartet? The extant whitefish distribution in Finland suggests the possibility of an initial arrival in the Ancylus Lake by two stocks with dense gillrakers. Lake Storsjön had its first outlet, southward, into the river Ljungan but later a second arose, at Krokum, into the Indalsälven preglacial valley. A second wave of whitefish colonists, including those with few gillrakers, could have ascended to Storsjön via

outlet 1, but were blocked by the Lit Ice Lake. When outlet 2 opened and the Lit Ice Lake emptied (Lundqvist 1973) (producing a heavy deposition of silt over the whole valley), the entrance to Långan and Härkan for the second wave of whitefish was probably difficult or impossible because of rapids and waterfalls. Similarly, Lake Övsjön became isolated, and later drained into the river Ljungan. When the Håsjö Ice Lake was emptied, no colonization by whitefish with few gillrakers occurred.

Fig. 9 illustrates the situation in lake Landösjön in the river Långan. The älvsik was introduced by man (the same stock as in lake Storsjön)

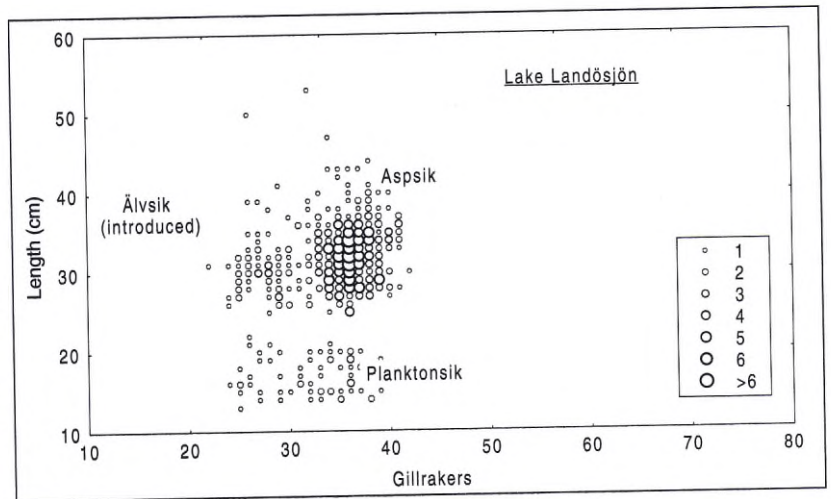


Fig. 9. Lake Landösjön. Summer samples from 1962. One introduced species hybridizes with the two indigenous stocks. The small-sized planktonsik is nowadays reduced in numbers after the introduction of the predator *Cristivomer namaycush* and the competitor *Mysis relicta*.

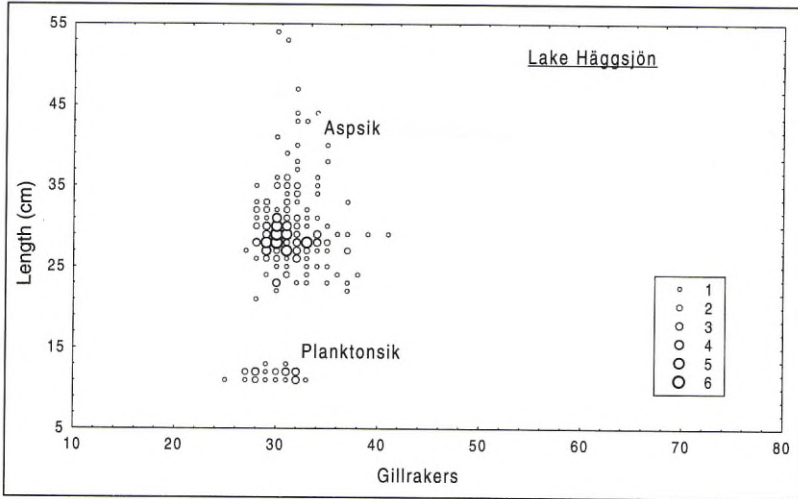


Fig. 10. Lake Haggjön, Hårkan river. Two whitefish species, early colonists, are the only ones found in the lakes within the Hårkan tributary of the Indalsälven river.

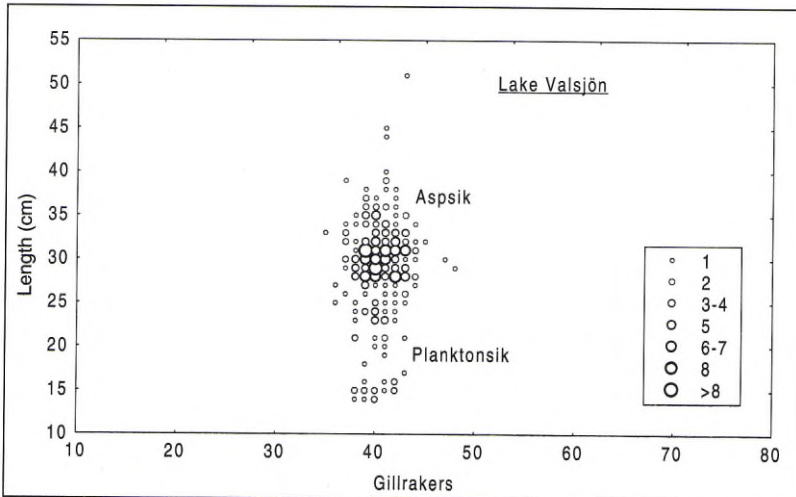


Fig. 11. Lake Valsjön, Hårkan river. The two species have introgressed so far as to have the same number of gillrakers, but are differently sized when spawning.

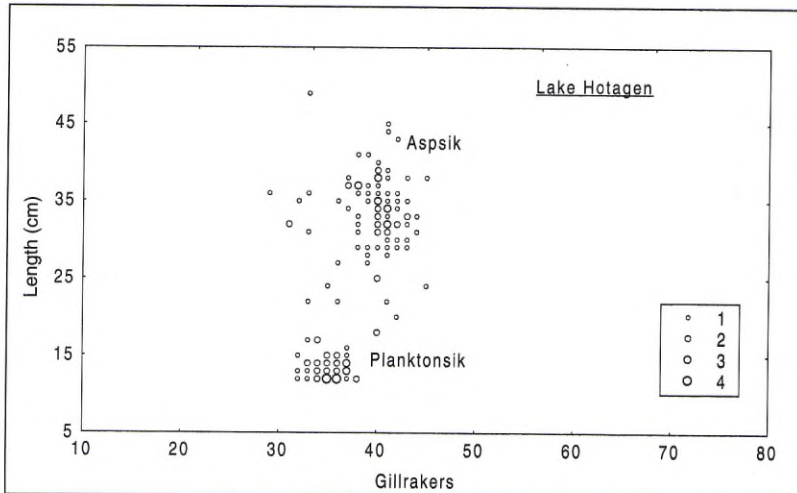


Fig. 12. Lake Hotagen, Hårkan river. The two species are less introgressed in this lake.

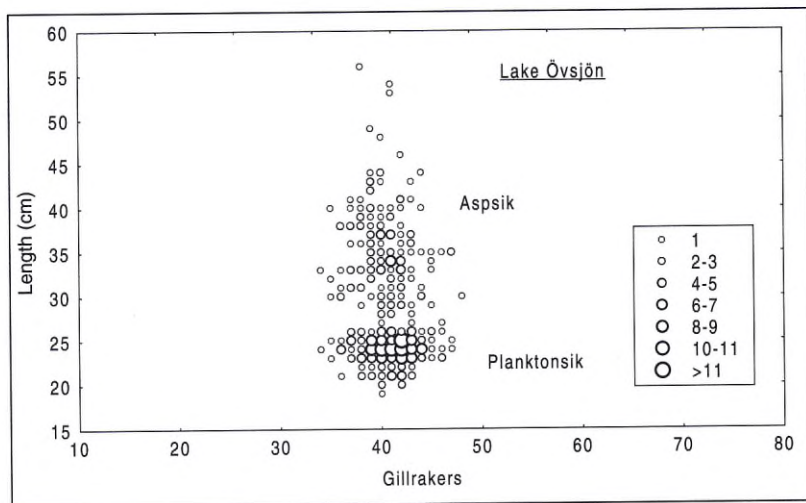


Fig. 13. Lake Övsjön. The same two species as in the Härkan river. They are similar in appearance, have the same number of gillrakers, but spawn on different grounds as 'large' and 'small'.

and has started to introgress with the indigenous aspsik, which is also large-sized. The planktönsik is a deep-living dwarf, which was very common until Canadian lake trout, *Cristivomer namaycush*, and the shrimp *Mysis relicta*, were introduced in the 1960s.

Figs 10, 11 and 12 present the situation in the lakes of the Härkan tributary. The gene flow between the planktönsik and the aspsik has pushed both species to the lower gillraker range in lake Höggsjön and to the higher range in lake Valsjön, while lake Hotagen probably more likely represents the situation at the time of the initial colonization.

The situation in lake Övsjön, finally (Fig. 13), has been an enigma for a long time (Svärdsö 1958, 1979), since the two populations, a large-sized and a dwarfed, had slightly different spawning grounds and periods and were well known to the local people. Svärdsö (1957, 1958) found the smallest spawners, below 20 cm, to have slightly more gillrakers (40.9) than the largest fish, above 35 cm (39.5). The growth rates of the two groups are different (Fig. 14), which also suggests differences in diet. So far, however, the diets could not be studied, since, in summer time, the species can only be separated arbitrarily, on a basis of their scale annuli. Spawners, however,

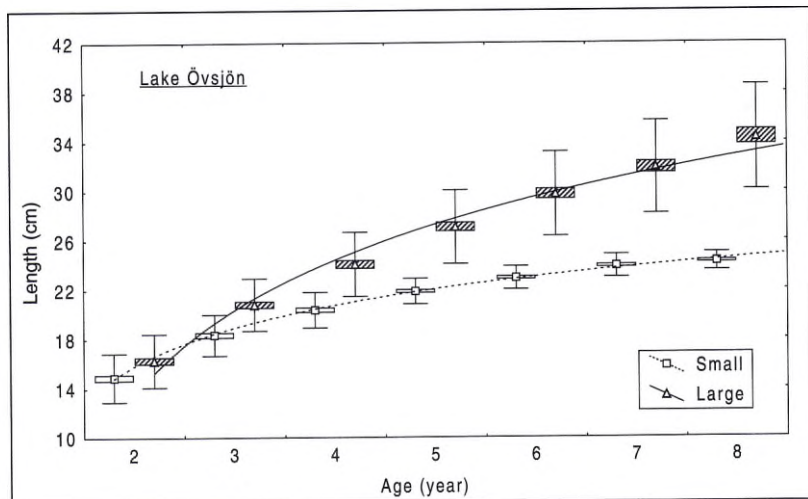


Fig. 14. Lake Övsjön. Reconstructed growth curves for the 'large' and 'small' species.

sort themselves out. It should be noted that planktonsik normally has fewer gillrakers than aspsik, whereas in Lake Övsjön the situation is reversed. The differences in growth rate and spawning size thus become the ultimate discriminating character indicating an advanced stage of introgression.

If the hypothesis of two waves of whitefish colonists is correct, then further cases should probably exist where the first two species to colonize have become the only species now present. Lake Vänjan in the Vanån tributary to the Dalälven river and Lake Tåsjön, in the Hotingån tributary to Ångermanälven river, may be such cases. Both lakes contain two sympatric species, neither of which conforms to storsik or to sandsik (Svårdson 1979, p. 27-29).

### *Coregonus lavaretus* - a Baltic marine colonist from the SW

The älvsik or river whitefish, *Coregonus lavaretus* L. is the predominant one in the Baltic Sea. It is often anadromous and may perform long-distance feeding migrations within the northern, Bothnian, part of the Baltic. Its diet is benthic and the species has a considerable economic value (Svårdson 1979, p. 13-17). Morphologically it is characterized by a more or less elongated snout, to which both the national and scientific names refer: 'Schnäpel', 'Näbbsik' or *oxyrhynchus*. In lake Vänern an alternative name is 'Fetsik', because of its fatness (Freidenfelt 1933).

The älvsik has about 30 gillrakers. The number is slightly less in lake Vänern (26) but higher in the southern Baltic (33). The fish may be poorly pigmented on the head, to such a degree that the brains are visible from above.

The general distribution strongly suggests a Weichselian survival somewhere in the former Dogger Land area of the present North Sea. The species formerly ran up the lower Rhine (Redeke 1933) and the Elbe. In the British Isles it was known as 'Houting'. It still survives in populations along the western coast of Jutland, but nowhere along the Swedish west coast.

To judge from the more developed 'beak' of the Vänern population than elsewhere in Fennoscandia (Fig. 15) the species colonized the Ancylus Lake via its Vänern outlet. Later it spread into the Baltic basin also through the new southern outlet, the Dana River, or through the Belt sounds.

In the southern Baltic there is a long-beaked population in river Schlei (Thienemann 1937) and more moderately nosed ones in Vorpommern (Thienemann 1935) and Poland (Wiese 1938).

The älvsik has a poor ability to colonize upstream lakes. Despite its name ('lavaret' in the French Lac Bourget) it is not one of the four whitefish found in alpine lakes (Wagler 1937, 1941). Linneus did not know much about whitefish and referred in his *Systema Naturae* to his friend Petrus Artedi, who knew the fish from his home in Anundsjö, close to the Mo River on the Baltic coast of Sweden. Apart from the sea, the älvsik lives only in the large lakes Vänern, Vättern, Mälaren and Siljan, all of which were once parts of the Ancylus Lake. Though running up rivers along the whole coast of Finland, it does not live in the inland lakes. When introduced by man, however, it is capable of establishing lake-dwelling populations in Sweden (Svårdson 1979, p. 15-17) as well as in Finland (Järvi 1940, 1953).

Since the älvsik is anadromous, it could, like the salmon (*Salmo salar*) and trout (*S. trutta*), possibly have reached the White Sea basin. Alleles, interpreted to prove a Baltic origin, have been found in some local White Sea populations of salmon and trout (Osinow 1984, Hamilton et al. 1989, Kazakov and Titov 1991). Indications of *lavaretus*-genes in the White Sea whitefish could possibly be the slightly higher number of gillrakers of the *pidschian* (Pyzhyan) in the area. Shaposhnikova (1974) found 24-26 gillrakers in several populations there, but only 19-22 in populations all the way from Pechora to Kolyma River in Siberia. Pyzhyan is most abundant in the southwestern part of the White Sea (Yershov 1989). Alternatively, the higher number of gillrakers in the White Sea *pidschian* population could be due to postglacial introgression with the local *peled* during the freshwater stage (cf. the modified storsik in lake Parkijaure).

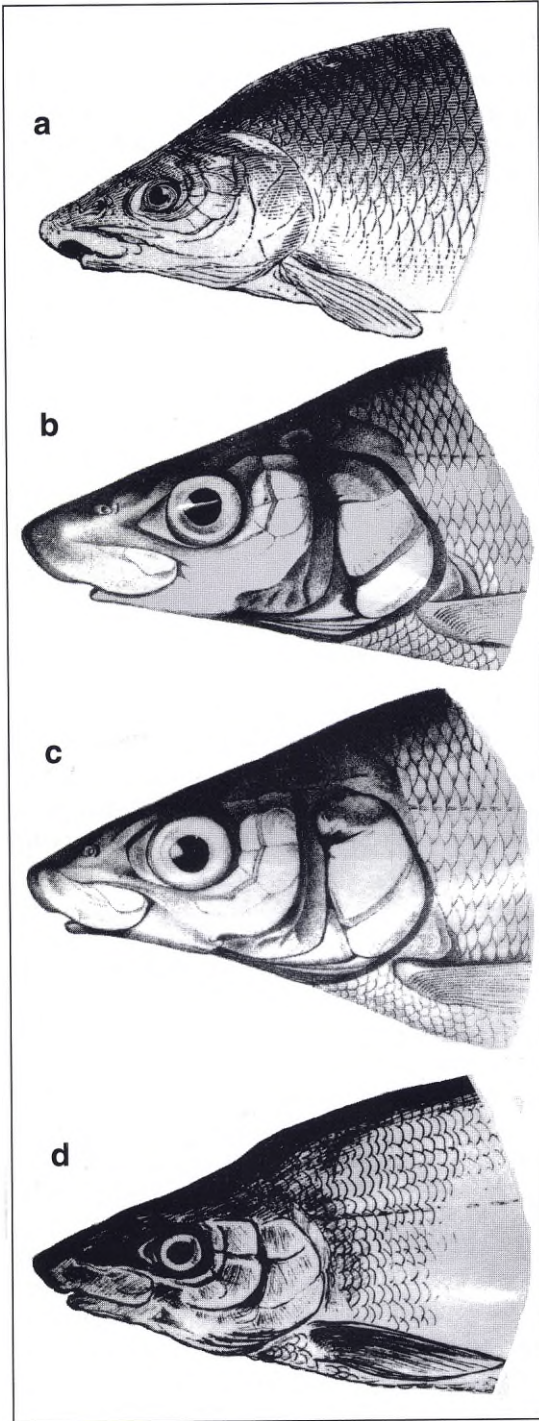


Fig. 15. *Coregonus lavaretus* or 'näbbsik' from Lake Vänern, according to a) Lloyd (1854), b) and c) Smitt (1886) and d) Svärdson and Freidenfelt (1974).

Passage from the Baltic to the White Sea (for salmon and trout) might have been provided by meltwater streams along the front of the decaying ice sheet in Yoldia or early Ancylus time. Alternatively, if they were already living in the Baltic Ice Lake, before the Yoldia stage, they could then have spread during the Younger Dryas period into the proglacial lakes in the Pechora and Dvina valleys (Grosswald 1998), as discussed above to explain the presence of *C. sardinella* in lakes Ladoga and Onega. In both alternatives, the älvsik must have ascended streams (into the Baltic Ice Lake or into the freshwater White Sea basin). The species, however, is a poor upstream colonizer. It may be associated with the habit of stream-spawning, in which the newly hatched fry drift downstream (Lindroth 1957).

Lake Saima in central Finland, with extant populations of Atlantic salmon, trout and Arctic char, as well as ringed seal (*Phoca hispida*) has no älvsik population. This fact suggests that the älvsik never reached the White Sea.

The most probable interpretation is that *Coregonus lavaretus* is a strictly western whitefish, phylogenetically separated from those in the Russian coastal drainages systems. The northern Swedish quartet of *Coregonus* species thus lie outside the late Pleistocene ancestry of *C. lavaretus*.

### Dispersal of *Coregonus* from the Ancylus Lake outlet

Lake Vänern is the third largest lake in Europe, covering an area of 5,500 km<sup>2</sup>. The total area of the Klarälven-Göta älv drainage system is 47,300 km<sup>2</sup>.

Six coregonid species are present in the lake. Vendace *C. albula* is dominant and in the 1990s the annual yield has fluctuated around 500 metric tons. The roe is sold as caviar. The five whitefish species together produce some 100 tons. Samples have been summarized in tables (Svärdson 1979, p. 33-35). Historical data were given by Svärdson and Freidenfelt (posthumously) (1974).

The älvsik, with its elongated snout (Fig. 15), is benthic and roams about in deep water (60 m)

in summer and spawns on exposed grounds in November. Fry of a local population, spawning in lower reaches of the Gullspångsälven river, were transplanted in 1870 to upper River Indalsälven, central Sweden, where the species ousted the Arctic char and later became widespread (Svärdson 1977).

The other four are those of the northern whitefish quartet. Storsik (local name 'lövsik' or 'blegsik') is the largest, 2-3 kg, with large eyes and predatory habits. The fishermen take it on long lines baited with vendace or stint, both of which are often found in the storsik's stomach. The fishermen say that it is not abundant because its big eyes enable it to avoid nets or seines. The species has some 30 gillrakers, a high figure.

'Sandsik' is a local name, which has been used nationally by the author. It is the smallest whitefish and is rare in commercial catches. It is benthic, littoral and has 23-26 gillrakers. Planktonsik, together with the älvsik, is the most abundant species. It is pelagic, spread all over the lake and has 32-34 rakers. It was called blåsik in Svärdson (1979) for reasons discussed below.

Aspsik is concentrated to the western part of the lake (local name 'Mårtenssik'). The average number of gillrakers is 40, some individuals have up to 55. Freidenfelt (1872-1936), who was a pioneer in the study of the whitefish in lake Vänern, caught a sample of ten specimens with an average of 44.3, the highest number recorded from Vänern proper. In the tables (Svärdson 1979) it was referred to as planktonsik for the following reasons.

Around lake Vänern a cluster of whitefish with dense gillrakers are to be found. In lake Hjälmsjön, to the east, now part of the eastern Norrström drainage, the whitefish has 40.6 gillrakers. Within the Klarälven drainage, three species are present in lake Femunden, in Norway (Svärdson 1979, Sandlund and Naesje 1986), one of which (the largest) has 45 gillrakers. Other lakes near Vänern are Stora Glan (39.4), Lelången (37.5), Storjungen (37.9), Knön (37.2) and Skagern (38.9 gillrakers).

Lake Tjele Langsø, in Danish Jutland, has a whitefish stock with 45 gillrakers (Otterström 1922, recent material in Svärdson 1979).

This mass of evidence suggested to Svärdson (1979) that a whitefish with many gillrakers had colonized the Vänern basin from the SW, like the long-nosed *lavaretus*, viz. from refugia in freshwaters somewhere in the Dogger area.

Since the aspsik of northern Sweden was the most extreme form and was related to populations in central Finland and the Russian lakes, it was probable that it had been brought into the Baltic 'by headwater transfer' (Svärdson 1979, p. 80). The existence of the ice-dammed lakes was not well-known at that time.

As a consequence there seemed to be two forms with many gillrakers, one northern and one southern. The former was called aspsik, the latter planktonsik. But, since there were also two such pelagic forms present in lake Vänern (and in lake Femunden, the headwater of the Klarälven river), the two Vänern stocks were identified as planktonsik and blåsik. The blåsik, however, is now not considered to be distinct, because the northern and southern aspsiks are thought to be one and the same, widespread species. So the 'planktonsik' from 1979 has been termed aspsik and the blåsik has become the true planktonsik.

There had been doubts for a long time, as to whether some stocks in lower reaches of northern rivers, with about 30 gillrakers, were dwarfed populations of the anadromous älvsik of the coast (Svärdson 1957) or were an independent (blåsik) species (Svärdson 1979). Now, it seems, none of these hypotheses is supported. Smaller lakes at low altitudes may receive whitefish genes, with the water flow, from the three or four sympatric populations found in the larger lakes upstream. The downstream drift is illustrated by the recent find of Siberian *peled* in the Swedish archipelago in the northernmost Baltic Sea. They are drifters from the Finnish lake reservoirs, Lokka and Porttipahta in the Kemi river, in which the species was introduced and is now spawning (Salonen and Mutenia 1992). They had drifted some 350 km downstream in the Kemi river and then been carried by the sea current to the Swedish side of the Baltic (Svärdson and Filipsson 1994). Jokikokko and Huhmarniemi (1998) found probable hybrids (with *lavaretus*) on the Finnish coast.

How then, to explain the abundance of aspik in the Vänern area, combined with an occurrence in Danish Jutland, since the stronghold of the species is in northern Sweden? Recent studies of the Ancylus Lake outlet (Björck 1995) seem to provide the key, not only to this but also other enigmas of the geographical distribution of the whitefish and vendace (Fig. 6).

Climat warming produced more meltwater than the Ancylus outlet could cope with. A transgression of some 20 m occurred in the period 9,300-9,200 BP. There were two outlets, the Steinselva river, just east of Halden (Norway) in the north and the Göta älv further south, which was broader but shallower. The combined water flow was up to 15,000-20,000 m<sup>3</sup>/s, with a velocity of 5-7 m/s (Björck 1995). In early summer, at the time of maximum flow, the sight must have been rather dramatic. The consequences for the Ancylus fauna were far-reaching.

The aspik is pelagic, but also takes food on water surface. It would therefore readily become concentrated in the outlet bay area of the former

great lake. With the accelerating water-flow it could have been flushed out in the salt water of the Kattegat or Skagerack, whence it ascended all the available freshwater streams in the neighbourhood. Sea currents could have carried it along the coast and over the sea to Danish or Norwegian streams.

Table 1 lists some whitefish populations of the Swedish west coast rivers. They should all owe their occurrence (as colonists from the sea) to the Ancylus outlets in 9,300-9,200 BP.

The vendace, *C. albula* lives in some small lakes in the Silkeborg area of Danish Jutland (Otterstrøm 1922), in a small lake on the Bjäre peninsula and formerly (now extinct) in lake Vombsjön in southernmost Sweden. Moreover, it lives, sympatrically with whitefish with few gillrakers, in the lake Orrevann, on Jaeren near Stavanger, Norway (Pethon 1974). All these localities could have been colonized by the Ancylus flush.

The vendace lives in several of the whitefish lakes listed in Table 1 and may be responsible,

Table 1. Numbers of gillrakers of the whitefish found in lakes in the Swedish west-coast rivers.

River	Storsik/sandsik		Planktonsik		Aspsik	
Rönne	-	-	-	-	Ringsjön	39.0
Lagan	Hindsen	23.4	-	-	Övringen	37.0
	-	-	Bolmen	33.5	Bolmen	42.9
	-	-	Allgunnen	27.5	Allgunnen	36.7
	-	-	-	-	Rusken	39.0
	-	-	-	-	Flåren	38.3
Nissan	-	-	Stengårdshultsjön	28.4	-	-
Ätran	Åsunden	24.3	Såken <sup>1)</sup>	32.3	Visen	38.0
	Sämsjön	21.0	Yttre Hallången <sup>2)</sup>	29.5	-	-
	Fegen	19.9	-	-	-	-
Viskan	Ärtingen	22.8	Tolken (Ås) <sup>3)</sup>	34.6	-	-
	Öresjön	23.1	Tolken (Mark)	28.4	-	-
	St. Holsjön	18.6	-	-	-	-
Kyrkälven	-	-	Södra Kornsjön	34.0	-	-
	-	-	Bullaren	33.0	-	-

<sup>1)</sup> Introduced about 1915, probably from Lake Bolmen. <sup>2)</sup> Introduced 1914, probably from Lake Allgunnen. <sup>3)</sup> Introduced 1930, origin not known.

because of competition for the plankton, for the erratic occurrences of whitefish. Three of the lakes, Åsunden and Fegen in the Ätran river and Stora Holsjön in the Viskan river are, or were, inhabited by two sympatric populations of vendace, *albula* and *trybomi* (Svärdson 1979). Only one further lake, Ören situated close to lake Vättern, is a known locality for *trybomi*.

The peculiar distribution of *C. trybomi* in Sweden was associated (Svärdson 1988) with an advance of the Öxnehaga glacier in the Younger Dryas period (Waldemarsson 1986). The glacier might have pushed some fish over the water shed and into western drainages. The Ancylus flush, however, is a more probable explanation.

Southeastern Norway has long been thought to have received its freshwater fish fauna from Sweden (Ekman 1922, Huitfeldt-Kaas 1923).

Lake Randsfjorden, in the Drammenselva river, NW of Oslo, is inhabited by two or three *Coregonus* species (Enge 1959). The 'grunnsik' is the largest fish, and with the fewest gillrakers, implying that either storsik or älvsik are probably involved. The 'strømsik' (stream-whitefish) has the highest number of gillrakers which suggest that the aspsik constitutes the bulk of the genome.

It remains for future studies to find out if the Ancylus flush could have brought freshwater fish even longer distances. Wheeler (1977) has discussed the colonization of the British Isles by freshwater fish species, where the fauna is richest in SE England.

Fig. 16 provides an overview of the presumed routes of colonists into the Baltic basin, as well as the secondary dispersals within and out of the basin.

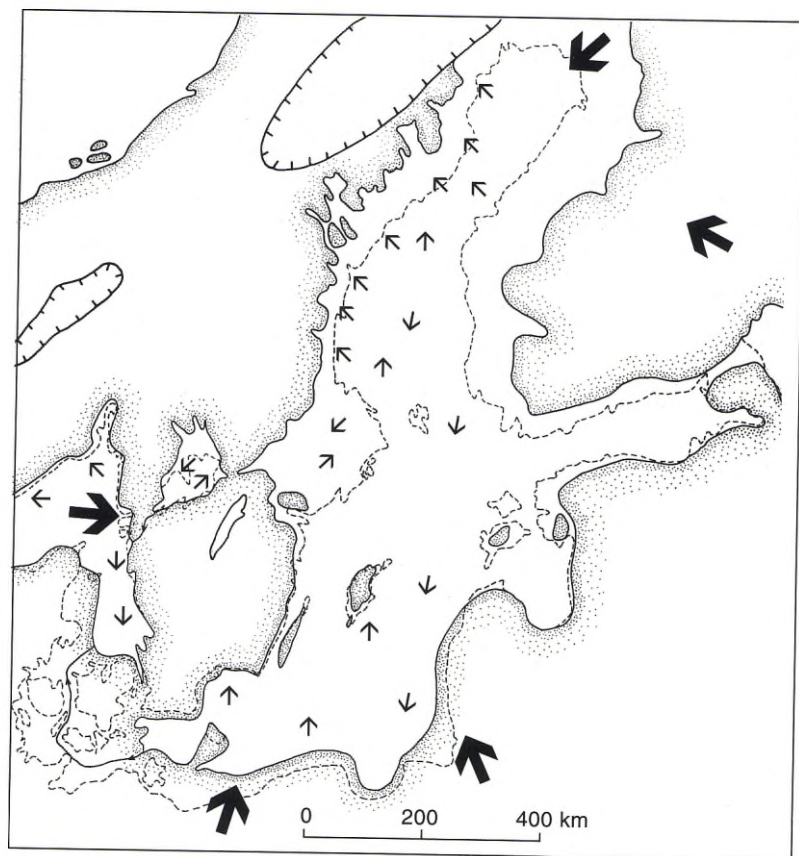


Fig. 16. The Ancylus Lake at 9,000-8,900 BP has tilted south because of higher isostatic rise of the land surface in the north. The Dana river has started erosion of the Darss Sill/Store Belt and lake Vänern has become isolated eastwards. Some 700-800 years later the sea water level rose above the Öresund sill and by 8,000 BP saline water also entered through the Store Belt. From Björck (1995).

Colonization and secondary dispersal of whitefish and vendace occurred before 8,000 BP when saline water finally filled the Baltic basin. During the Litorina period (7,000 BP-5,000 BP) the salinity was almost twice that of the present Baltic Sea.



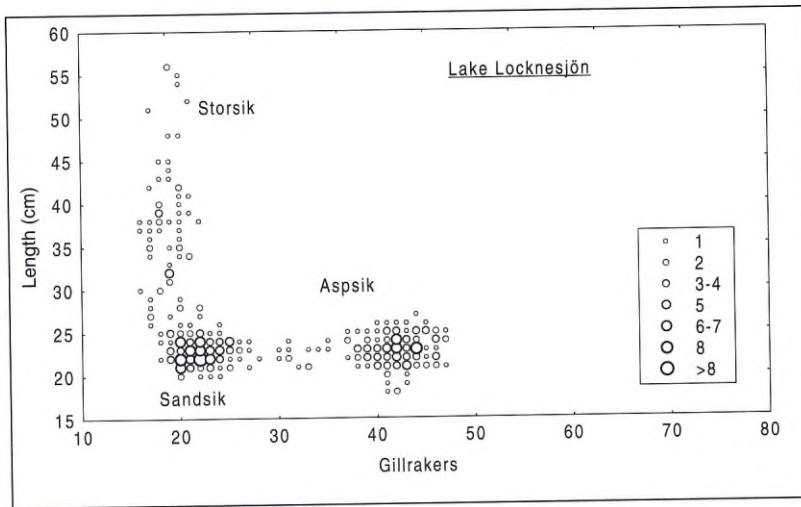


Fig. 17. Lake Locknesjön, Gimån river. Three whitefish species. The intermediate specimens, with 30-32 gillrakers, do not represent the missing planktonsik but are hybrids sandsik x aspsik caught within their resp. spawning groups.

## Reticulate evolution in the lakes in the river Gimån

Four of the most intensively studied lakes belong to the upper Gimån river system (Fig. 7). They all have three sympatric whitefish species, which have been used for transplantations and crossings.

Apart from the storsik, which is unmistakable in all four lakes, the two other populations should be sandsik, planktonsik or aspsik. One of these species is absent from every lake, but probably not the same one in each case.

Lake Locknesjön is an old impact lake and is the headwater of the Gimån. One thousand whitefish specimens from the lake have been caught and recorded (Svärdsö 1979, p. 9). Some data are presented in Fig. 17. Apart from the 50 cm storsik, there are two other species, both of equal body size, 20-25 cm. Since a difference in spawning size adds to genetic isolation, the intermediate specimens found in each spawning group, suggest that some gene flow has occurred. Nevertheless, after some 9,000 years of cohabitation, the gillraker numbers of the two stocks are distinct: 22 and 42 resp. Their diets are also different. The species with few gillrakers feeds predominantly on chironomid larvae, the other exclusively on zooplankton (Holmberg 1975).

The form with 22 gillrakers fits exactly into the sandsik concept. The population with 42 gillrakers should be an aspsik (though it was called planktonsik in Svärdsö 1979, for reasons already discussed in relation to the abandoned blåsik concept). So the genuine planktonsik seem to be absent from Lake Locknesjön. Of course, its colonization could have been blocked by the existence of some (shallow) rapids in the lake outlet.

Lake Revsundssjön lies downstream from the Locknesjön. Once again, the storsik with few gillrakers and a 50 cm spawning size is outstanding (Fig. 18). The next largest is a 30-35 cm population with 36-37 gillrakers. The third is a dwarf fish, 15-20 cm with 29.3 gillrakers (Svärdsö 1979, p. 68). None of them, except the storsik, is littoral or benthic. The sandsik possibly may have fused into the storsik.

Further downstream is the Idsjön lake, which has been discussed in a series of papers (Svärdsö 1953, 1958, 1970, 1979). Data for 5,000 specimens are listed in the tables (Svärdsö 1979, p. 70). The benthic storsik was reduced in numbers by annual fishing on the spawning grounds. The next largest is the *vaktfiskesik*, traditionally caught by the local fishers in cooperation. It is 25-37 cm long when spawning, has 36-37 gillrakers and could conform to the aspsik. Some specimens of this species were found among

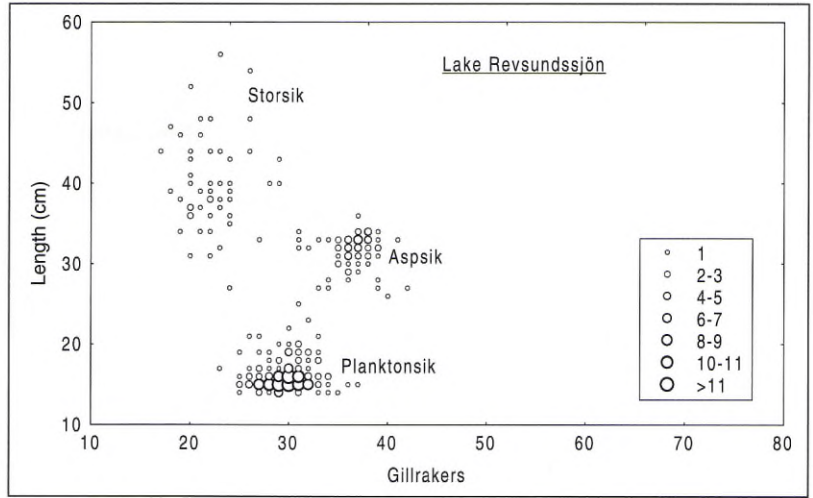


Fig. 18. Lake Revsunds-sjön, Gimån river. Three whitefish species. The sandsik is missing.

spawning storsik and, from scales studies, proved to have been 'shoal-trapped' for years (Svärdson 1953, 1970), a phenomenon which is also recorded for other lakes and is further discussed below in relation to shoal tenacity.

The dwarfed form in lake Idsjön has 26-27 gillrakers and is only 12-15 cm when spawning. It spawns in the inlet stream and was not known to the local people, who nevertheless are very keen on whitefish. It feeds almost exclusively on *Bosmina*. Both diet and size indicate that it is planktonsik, although it has very few gillrakers.

Finally, the small Skåsjön lake, lies close to

lake Idsjön and should have been colonized in the same period of time. Gillrakers and spawning sizes were investigated earlier (Svärdson 1979, p. 69). Two populations with few gillrakers and one with 37.4 live in the lake. The growth rate of the two differ (Fig. 20).

Lindsey (1981) called the whitefish 'chameleons', a reference to the gillraker variation. However, this variation is not environmental, since, when examined closely, gillraker number turn out to be firmly genetically based in polygenes. Their variation is a marker of the gene flow between former or present sympatric species.

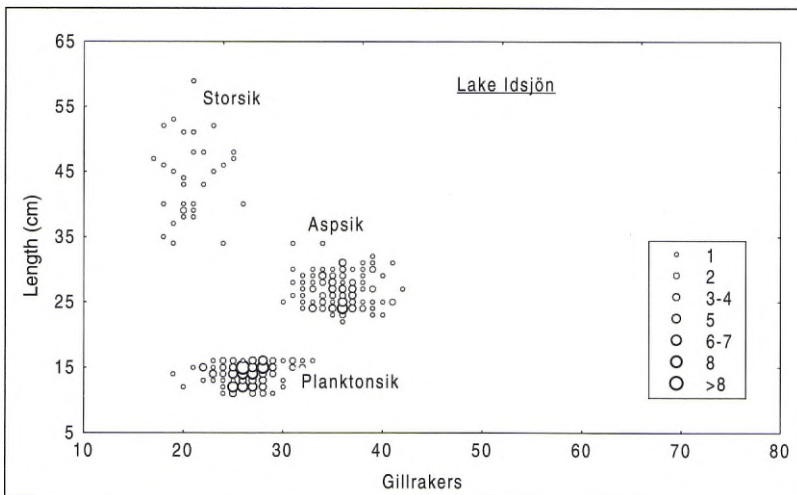


Fig. 19. Lake Idsjön, Gimån river. Three whitefish species. Is the sandsik or the planktonsik the missing member of the quartet?

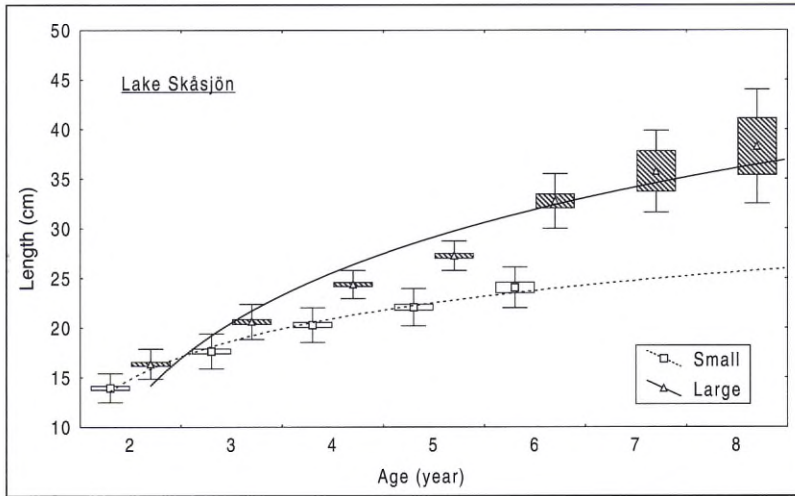


Fig. 20. Lake Skåsjön, Gimån river. Apart from the aspik there are two species, with few gillrakers, in the lake. Storsik and sandsik can only be separated by their different size when spawning. They also grow differently, as calculated from their scales.

Despite all the studies of the Gimån whitefish stocks, there is still a high degree of uncertainty about how to interpret the situation in each lake. Has the planktonsik never colonized the Gimån river in which case the populations of the Revsundssjön and Idsjön lakes are very modified sandsik, or has the sandsik completely merged into the storsik in Revsundssjön and Idsjön whereas it has not merged completely in the small-sized Skåsjön lake, with fewer ecological niches available?

Reticulate evolution, i.e. gene flow between species, seem to have been operative in the Gimån river. The last barrier for complete fusion tends to be a difference in spawning size. The storsik and sandsik with few gillrakers are merging in lake Skåsjön while the planktonsik and aspik were described earlier, involved in the same process in lake Övsjön and lakes within the Hårkan tributary of the Indalsälven river.

## Introgression as an evolutionary agent

Hybrids between fish species are not rare (Hubbs 1955, Schwartz 1972, 1981). If the hybrids are not sterile, then genes may flow from one gene pool into another. This is called introgression and is supposed to be common in plants (Andersson 1948) but rare in animals (Mayr 1963). While

biochemical evidence for introgression in fish accumulates (Verspoor and Hammar 1991), the morphological evidence is still often ambiguous (Smith 1992) due to alternative interpretations. Hybrids were generally thought to be intermediate (Hubbs 1955), due to additive genes, but non-additive inheritance was proved by Simon and Noble (1968) and found in 21 of 34 characters in cyprinid crosses (Ross and Cavender 1981). Thus characters of one parent species may be repressed by those of the other, making cladistic studies inappropriate (Smith 1992, Dowling and DeMarais 1993). Introgression in fish is not only associated with recent human disturbance of their habitats but can occur spontaneously and is proven for pliocene and miocene cyprinids (Smith 1992).

In coregonids, introgression is widespread (Svärdson 1957, 1970, 1979) and has been documented by comparative morphological studies made in nearby lakes and by experiments. Biochemical evidence is sparse, since sympatric coregonid populations tend to have very small genetic differences (Heinonen 1988, Vuorinen 1988, Lyczynski et al. 1995). The prevalent gene flow and convergent selection, by water temperature, on allozymes (Vuorinen et al. 1991, Kirpichnikov 1992) would have this effect. Moreover, differences in quantitative characters – such as gillraker number – are far easier to demonstrate statistically than are the gene frequencies that underlie them (Lewontin 1984).

Additive inheritance is found in coregonids so far as gillraker numbers are concerned. Non-additive inheritance occurs in the position of mouth, which is regarded as important in systematics. Gasowska (1958) studied reciprocal hybrids *C. albula* × *C. lavaretus maraenoides*. Matroclinic similarity was found in the colour of body, fins and pearl organs. All hybrids, however, had a whitefish mouth. This was also found by Svärdsön (1965) using *C. albula* as the mother species. Ferguson et al. (1978) found that the vendace × whitefish hybrids, in the F<sub>3</sub> and subsequent generations, had only the enzyme alleles of the whitefish parent. Prokes and Penaz (1977) made reciprocal crosses of *C. peled* and *C. lavaretus* (not the species so named in this paper). Most characters were intermediate but matroclinic differences appeared and the typical mouth of *peled* disappeared, especially in the progeny from *lavaretus* mothers. Some writers have proposed that the superior mouth of *C. albula* and *C. peled* is a discriminating character for the sub-genus *Leucichthys*. By hybridization, however, this character disappears already in the F<sub>1</sub>-generation.

Svärdsön (1965) discussed the isolating mechanisms between sympatric coregonids at some length. The evidence given in earlier sections of the present paper proves that introgression, on the whole, has progressed only moderately during the postglacial period. Cases showing total swamping do exist and in some cases – especially when man has interfered – introgression may be relatively rapid. The hybrids, very generally speaking, are favoured by hybrid vigour and better growth (Svärdsön 1979), but are selected against by a lower degree of fertility as proved by the high frequency of embryonic chromosome disturbance and less variation in the F<sub>3</sub> than in the F<sub>2</sub> hybrid generations (Svärdsön 1965). Lu and Bernatchez (1998) proved higher embryonic mortality in artificial hybrids between two allopatric whitefish, which live sympatrically in several lakes in Maine or southeastern Quebec.

The tenacity of the shoal, however, seems to be the main obstacle to accelerating introgression. It has recently been found that fish live

in a world characterized by olfaction and gustation (Hara 1994). Taste buds are located on the gillrakers and gillarches. Whitefish have been proved to be conditioned to poisonous cadmium, i.e. to react positively to Cd-contaminated (but familiar) water (McNicol and Scherer 1993). The Arctic char reacts positively to the scent of its own species (Höglund and Åstrand 1973) and avoids water pre-conditioned by the whitefish, which is an important competitor (Höglund et al. 1975). Both Olsén (1985) and Winberg and Olsén (1992) found char reacted to the scent of siblings. The imprinting occurred during the first 15 months of life. The degree of aggression was higher in non-sibling groups of char and the growth rate of the dominating individuals in sibling groups was higher (Olsén and Järvi 1997). The wide-spread recognition of siblings among salmonids has been reviewed by Brown and Brown (1993).

Shoaling enhances the odour response compared to that of individual whitefish (McNicol et al. 1996). The members of the shoal are of equal size, tend to have the same diet and share the same odour-creating metabolites. Specimens of planktophagous whitefish may become 'shoal-trapped' for years, probably when they take larger prey items, i.e. benthic food. They may shoal with, and adapt to the growth rate of, another, benthic species (Svärdsön 1970) and, no doubt, spawn with them. Shoaltrapping is also proved between *C. albula* and *C. trybomi*. Artificially hatched whitefish fry, released by man, may join a shoal of foreign ancestry, like fry or stray fish which are carried downstream from a lake outlet into a lower lake.

Shoaling thus may in some instances favour introgression among sympatric forms, yet in spite of that, be the single most important factor that counter-balances the merging process. Steinmann (1950) stressed the shoaling factor, which he thought could be responsible for sympatric speciation by disruptive selection. However, the main effect must be the opposite, since any new mutant or gene combination is probably trapped within the shoal. The odds cannot be in favour of vendace mutants causing spring spawning or whitefish genes contributing to a new food preference.

The amount of genetic introgression between the five whitefish species in the Baltic region varies according to lake size and local topography. In the fusion process, the ecological traits are the last to disappear, a fact which supports the idea that the spring-spawning vendace must be regarded as a separate species (Svärdson 1988).

Recently, hybrid zones in birds have been studied more intensively (Grant and Grant 1992, 1996, Rohwer and Wood 1998, Gill 1998). There is some evidence that allozymes, mtDNA haplotypes or size-determining genes may penetrate further into the hybrid zone than genes for plumage characters which are involved in assortative matings. Sympatric whitefish populations have no hybrid zones but show different amounts of introgression. Interestingly, some characters, such as mouth shape or head structure in *peled* or vendace, disappear in the first generation and never return in future hybrid generations. Gillraker numbers are much more conservative but when populations have almost merged (as in the lakes Valsjön, Övsjön and Skåsjön) a population difference in diet and growth still exists. Even when growth rates tend to become similar, the diets may be different. The aspsik of lake Parkijaure has evolved closer to the storsik morphologically, but still has a pelagic and not a benthic diet, although it shares the storsik habitat (Bergstrand 1982).

The evidence indicates that, in the merging of two whitefish gene pools, some genes integrate more easily. Those involved in assortative matings are the last to give up. They are the ones most heavily selected for when hybrids are selected against. They are the most species-specific within the genome. Allozymes and mtDNA are not known to influence mating preferences.

European whitefish populations are incipient species, the status of which can only be tested in new sympatric situations. The glacial/interglacial environmental change is brutal, so species flocks of *Coregonus* are small, like the ciscoes in the Great Lakes of America (Todd and Stedman 1988). When the reunion of isolates is less dramatic, e.g. from water level fluctuations in tropical lakes (Johnson et al. 1996), species flocks, like those of the cichlids, may be large (Martens et al. 1994).

## Remarks on systematics and taxonomy

Reticulate evolution, in which morphological species criteria are exchangeable, obviously presents a challenge for cladistic systematics. The phylogenetic species concept (PSC) is based on monophyletic phylogeny. The biological species concept (BSC) stresses the capacity for two populations to exist sympatrically. This concept is mostly used in bird studies, where there is some discussion as to how much gene flow can be tolerated in the contact zone of allopatric populations (Zink and McKittrick 1995). The Linnean or morphological species concept (MSC) is the oldest one and is based strictly on morphology. It is now more or less obsolete.

Neither of these three species concepts can strictly be applied to the European *Coregonus* populations. Their phylogeny is not monophyletic, since introgression is at work. Sympatric co-existence is often true, but not always, since merging of populations may occur.

Coregonids have been treated as polytypic species, where the local forms are all derived from some original colonists (Svärdson 1957, 1979). In this case the morphology of the particular colonist may be locally changed by gene flow, so the strict diagnosis no longer applies. Svärdson (1957) identified the aspsik with many gillrakers as *C. peled*. This view was strongly criticised by Behnke (1972) and others, since the aspsik have neither the head shape nor the gillraker number of the true *peled*. Ironically, the true *peled* was in fact found in lake Storvindeln in 1976 and the aspsik of lake Parkijaure thereby had its phylogenetic origin proved.

A first step towards a new taxonomy of coregonid fish is a knowledge of their origin. While the aspsik in the Baltic region is derived from *C. peled* (not the Siberian form studied by Koljonen et al. 1988), it is also clear that the storsik is conspecific with *C. pidschian*. Morphologically and ecologically there is no real difference.

However, the planktonsik is harder to trace. The Swedish populations, presented in this paper, have 40 gillrakers in lakes Storvindeln and

Parkijaure but fewer, down to 26-27, in other rivers. The arctic cisco, *C. autumnalis*, is anadromous, and large-sized, with some 40-45 gillrakers (Berg 1962). Its distribution westwards stops at the Mezen river (like that of *peled*). The White Sea basin, which was filled by freshwater for some time during the deglaciation process, lies further west. It makes sense, that *C. autumnalis* could have become land-locked and dwarfed in this basin. The Irish *pollan* was identified from its enzymes as *C. autumnalis* by Ferguson et al. (1978). The *pollan* has about 40 gillrakers and a terminal mouth, just like the planktonsik of lakes Storvindeln and Parkijaure.

The sandsik cannot at present be identified with any widespread Russian whitefish. Krogius (1926) described a local population in lake Imandra (Kola peninsula) as *pelagicus/knipowitschi*. It had few gillrakers, was small-sized and sympatric to *pidschian*. No further information on this form is available to the author.

Even if three out of the four members of the northern whitefish quartet can be identified as descendents of *C. peled*, *pidschian* and *autumnalis*, no change towards a new taxonomy is proposed. The proposals given earlier (Svärdson 1957, 1979) have unfortunately added further to the confusion. The time for a new start will not come until more consensus on reticulate evolution exists. Lindsey (1988) proposed recognition of the local 'stock' concept, while Kottelat (1997) was inclined to give all (the Alpine) populations separate names. Himberg and Lehtonen (1995) discussed a new taxonomic system with tri- or even tetranomial names. Their system, however, starts with only three original species in Europe, viz. *C. lavaretus*, *C. albula* and *C. autumnalis pollan*. This means that the entire quartet of whitefish present in northern lakes of the Baltic region is lumped into the anadromous *C. lavaretus*, whereas all five in fact live sympatrically, as biological species, in lake Vänern. The authors also ignore the three biological species of vendace.

The Alpine and British coregonids are probably descendants from pre-Weichselian Baltic forms, isolated in and later dispersed from proglacial lakes. The four populations found in

the Bodensee (lake Constance in Switzerland Wagler 1941), are analogous with those of the northern quartet. According to Bernatchez et al. (1994) the Alpine whitefish have larger genetic distance to the Russian-Siberian species than have the Nordic ones.

The molecular methods so far used have failed to trace hybrids after some few generations (Ferguson et al. 1978, Mamcarz 1992). Mitochondrial DNA from *Salvelinus alpinus* has been found fixed in some *S. fontinalis* populations (Bernatchez et al. 1995). The methods generally rely on cladistic principles viz., similarity suggests common ancestry. When more suitable molecular methods are available (Bernatchez et al. 1996), some calibration tests should be performed on the populations in the lakes Storvindeln-Parkijaure. Specific differences can there be compared with the effects of long-term spontaneous introgression.

## Acknowledgements

My life-long interest in *Coregonus* variation started when I began studying the chromosomes of salmonid fish in the Department of Genetics, Stockholms University, in 1940. I joined the staff of the Institute of Freshwater Research, Drottningholm in 1944, and began a series of field experiments and sampling surveys of the whitefish and vendace populations in Sweden.

Hundreds of people have assisted me in the field over the years, often fishing in the late autumn when the ice is beginning to form and the weather is un hospitable. Some of them, Gösta Molin, the late Elof Halvarsson and Olof Filipsson should be mentioned especially for their most important contributions. Fisheries consultants Birger Ahlmér, Ragne Gydemo and Rickard Öhman also brought most valuable knowledge and material from their districts. Within the institute, another large group have cooperated with me. Birgit Ericsson, Gun Odén, Eva Bergstrand, Monica Bergman, Eva Sers and Olof Enderlein were those most engaged in my recent work.

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# Interactive Asymmetry and Seasonal Niche Shifts in Sympatric Arctic Char (*Salvelinus alpinus*) and Brown Trout (*Salmo trutta*): Evidence from Winter Diet and Accumulation of Radiocesium

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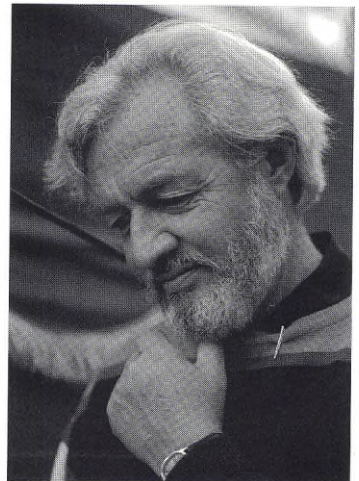
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## Abstract

Dr. Nils-Arvid Nilsson's pioneer work on interactive segregation and resource partitioning in high altitude lakes and reservoirs with sympatric populations of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) is reviewed and extended with dietary surveys elucidating their winter activity. The results, in combination with stomach content analyses from other mountain lakes and reservoirs, with or without introduced new fish food organisms, and supplemented with radio-ecological assessments after the Chernobyl disaster, provide evidence of a displacement in feeding habits when ample winter food resources exist. Whereas Arctic char in November-June feed actively on littoral benthos, such as *Gammarus lacustris* in natural lakes and introduced *Mysis relicta* and *Pallasea quadrispinosa* in reservoirs, brown trout exploits these resources in summer-fall and appear to enter torpor or be quiescent in winter. Reflecting high concentrations of Cs-137 in macro-benthos and low concentrations in zooplankton, an alternating seasonal pattern of radiocesium levels was identified, with Arctic char accumulating Cs-137 during winter and eliminating Cs-137 in summer. Although less pronounced, the opposite processes characterized brown trout feeding on *Gammarus* or *Mysis* during summer. This indicates that Arctic char reoccupies the littoral habitat and its abundant food resources during the frozen season. The mechanisms responsible for interactive segregation in summer seem to be less powerful in winter, apparently because of temperature restriction of the brown trout. The realized niche size of the Arctic char therefore can expand in winter and early spring, and will extend closer to the fundamental niche border, as previously described by Nilsson from allopatric populations of Arctic char.

**Keywords:** Competitive asymmetry, interactive segregation, *Salvelinus alpinus*, *Salmo trutta*, niche shift, temperature, torpor, winter food, *Gammarus lacustris*, *Mysis relicta*, Cesium-137, northern Sweden.



Dr. Nils-Arvid Nilsson at the Drottningholm Institute, August 1983. (Photo: Johan Hammar.)

This paper is dedicated to the memory of Dr. Nils-Arvid Nilsson (1926-90); close friend, colleague and precursor. His classical work on the interactive segregation of Arctic char and brown trout and the re-

lated consequences of water level regulation in Lakes Ankarvattnet and Blåsjön, northern Sweden, has been highly influential on the succeeding work within these important ecological issues.

## Introduction

Gunnar Svärdsen was one of the pioneers in the field of evolutionary ecology and has made landmark contributions to our understanding of concepts such as habitat recognition, interactive habitat segregation, and interspecific dominance among animal populations and in communities (e.g. Svärdsen 1949a, 1949b, 1949c, 1976). Many of these principles of interspecific competition and niche relationships were further elaborated and applied by Nils-Arvid Nilsson using lake dwelling salmonids in high altitude lake ecosystems as illustrative sources for autecological models of resource partitioning and interactive segregation (e.g. Nilsson 1955, 1958, 1960, 1963, 1965, 1967, 1978, 1985, Nilsson and Filipsson 1971). In a parallel research program, Northcote and associates examined similar interactions occurring among equivalent salmonids of western Canada (see Northcote (1995) for a review). Whereas Nilsson focused on the dietary niches and size selective predation, Northcote and colleagues paid more attention to foraging efficiency and visual prey detection.

In head water lakes of northern Scandinavia, when only one species is present, Arctic char (*Salvelinus alpinus* (L.) sp. complex) and brown trout (*Salmo trutta* L.) have roughly similar size-frequency distributions and are both classified as littoral/benthic feeders. In sympatry, the two species segregate as a result of competition for littoral invertebrates during periods of food shortage. Reflecting individual interference, as demonstrated experimentally (Nilsson 1963), brown trout maintain the littoral habitat exploiting its declining summer resources of macro invertebrates (e.g. *Gammarus lacustris*), whereas Arctic char more profitably can utilize the peak summer resource levels of small cladoceran zooplankton in the pelagic food-web. As a consequence of size differences, these competitive interspecific interactions may change into predator-prey relationships with large-sized trout feeding on small-sized char (Nilsson 1964, Aass et al. 1972, Filipsson and Svärdsen 1976, Campbell 1979, Hammar and Filipsson 1988, Aass 1990, L'Abée-Lund et al. 1992a, Greer 1995),

sustaining the segregation and bimodal size distribution (e.g. Hammar 1989, 1998). In synecological terms, however, the species capable of exploiting zooplankton most efficiently, i.e. the Arctic char in high altitude lakes and coregonids in lower systems (Nilsson and Pejler 1973), has been found to dominate the fish community numerically (Svärdsen 1976). Svärdsen suggested these "dominant" populations to be regulated mainly by abiotic factors or intraspecific interactions, while the subordinate populations were controlled more by the interspecific interactions.

The segregation in choice of food and habitat between coexisting Arctic char and brown trout reaches even more extreme levels in regulated lakes, where the environment becomes more stark and "uniform", and where the production of littoral invertebrates, the "prime" source for competition, is severely damaged (Grimås 1961, 1962, Nilsson 1961, 1963, 1964, 1965, 1973). In some reservoirs, the brown trout population has in fact been driven close to extinction, whereas small-sized Arctic char have managed to thrive on the seasonal abundance of zooplankton, as well as profundal chironomid larvae and sphaerid bivalves.

These apparently straightforward mechanisms of interactive segregation among northern salmonids were, however, studied through a narrow seasonal window, namely the ice-free season when higher water temperature and extended daylight prevail. These are environmental conditions assumed to favor brown trout as well as most field biologists. Since Arctic char and brown trout demonstrate major differences in their biogeography and climatic adaptations (see below), the level and direction of interspecific interactions are expected to vary considerably with temperature, and thus between years (Nilsson 1955), with season (Nilsson 1955, 1960, Fürst et al. 1978, 1981, Hegge et al. 1989, Dervo et al. 1991, Langeland et al. 1991), and with latitude and altitude (Schmidt-Nielsen 1939, Curry-Lindahl 1957, Hammar 1987, 1989, Hammar and Filipsson 1988). Hence in a longer perspective with extreme interspecific interactions, we may expect selective changes optimizing resource use (Schutz and Northcote 1972, Svärdsen 1976,

Hume and Northcote 1985, Schluter and McPhail 1992, 1993, Robinson and Wilson 1994), although intraspecific interactions may still favor opportunism, phenotypic flexibility and the potential ability to exploit a wider niche whenever possible. Very few studies, if any, provide comparative information on the winter ecology of these northern salmonids, although investigations of parasites and/or pollutants accumulated during the winter season may offer evidence of feeding activity and the choice of food organisms of these fishes.

The hypothesis that Arctic char, although coexisting with brown trout, during the frozen period exploits littoral resources in lakes with ample diversity of macro-invertebrates will be tested in this paper. The analyses extend Nilsson's studies in Lakes Ankarvattnet and Blåsjön and a series of other lakes and reservoirs with and without introduced new fish food organisms, by examining seasonal diet shifts, above all during the

winter period. This information will be supplemented with radio-ecological markers on pelagic and benthic feeding habits of sympatric Arctic char and brown trout.

## Sites, fish species, and methods

### The study area

Lakes Ankarvattnet ( $64^{\circ}50'13''\text{N}$ ,  $14^{\circ}14'35''\text{E}$ ) and Blåsjön ( $64^{\circ}41'57''\text{N}$ ,  $14^{\circ}12'13''\text{E}$ ) are located in the upper parts of River Faxälven, northern Sweden (Fig. 1, Table 1). Both lakes are deep and oligotrophic, and their catchment areas are mostly barren and alpine. The overall average air temperature recorded in Gäddede (Fig. 1) during 1961-90 was  $1.4^{\circ}\text{C}$  (min:  $-0.7^{\circ}\text{C}$ , max  $3.3^{\circ}\text{C}$ ), with the means for January and July being  $-9.9^{\circ}\text{C}$  and  $12.6^{\circ}\text{C}$ , respectively. The ice-covered season averages mid December to early June. The annual subsurface water temperature in the outlet of Lake Blåsjön ranged between ca

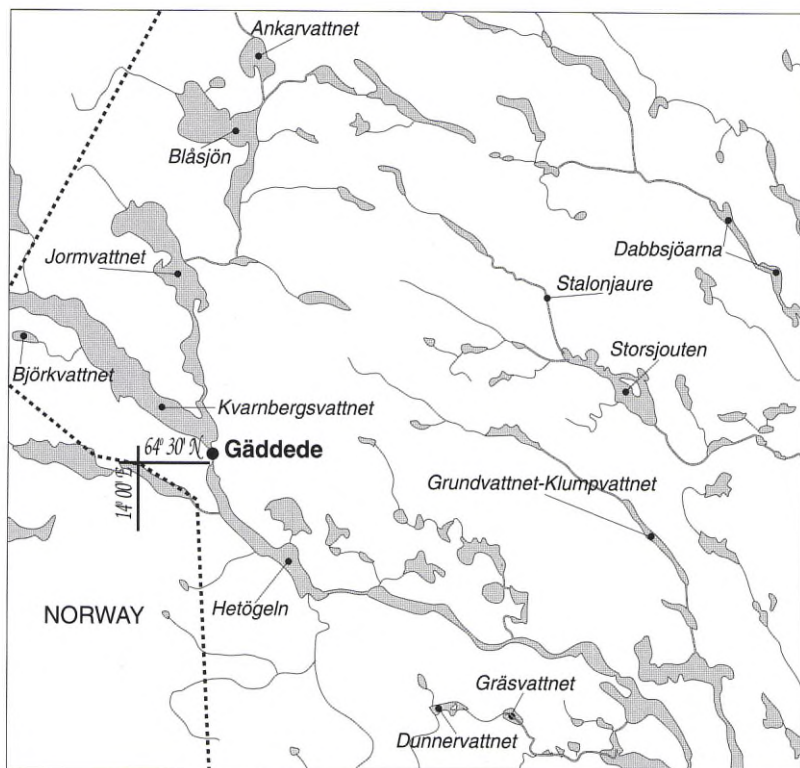


Fig. 1. The tributaries of River Faxälven with the location of Lakes Ankarvattnet and Blåsjön, and a series of other lakes and reservoirs studied for transport mechanisms of radiocesium. (Drawing by Eva Sköld.)

Table 1. Physical, chemical and biological information on the two studied lakes. The higher chemical levels refer to spring samples from April 1988.

	Ankarvattnet	Blåsjön
Altitude (m a.s.l.)	448	423-436
Surface area (km <sup>2</sup> )	9.4	43
Maximum depth (m)	70	145
Catchment area (km <sup>2</sup> )	430	965
Regulation amplitude (m)	-	13.3
Conductivity (mS.m <sup>-1</sup> , 25°C)	(1986-89) 1.62-3.73	2.18-2.73
Total N (mg.l <sup>-1</sup> )	(1989.08) 0.140	0.110
Total P (µg.l <sup>-1</sup> )	(1989.08) 5	6
pH	(1986.10-1989.08) 6.19-7.10	6.60-7.40
Alkalinity (meq.l <sup>-1</sup> )	(1986.10-1989.08) 0.067-0.162	0.108-0.143
Fish fauna	Arctic char brown trout	Arctic char brown trout Europ. minnow*
Introduced new fish-food organisms	- -	<i>Mysis</i> 1964 <i>Pallasea</i> 1964
Deposition of Cs-137 (Bq.m <sup>-2</sup> ) in 1986	34,400	28,100

(\* Unauthorized introduction prior to 1982)

1 and 14°C during 1966-69, when a thermistor at the power station intake was in operation (Fig. 2). The secchi-disc depths average 10-12 m in

both lakes, and the water columns rarely stratify. The smaller and natural Lake Ankarvattnet drains via the river Ankarälven into Lake Blå-

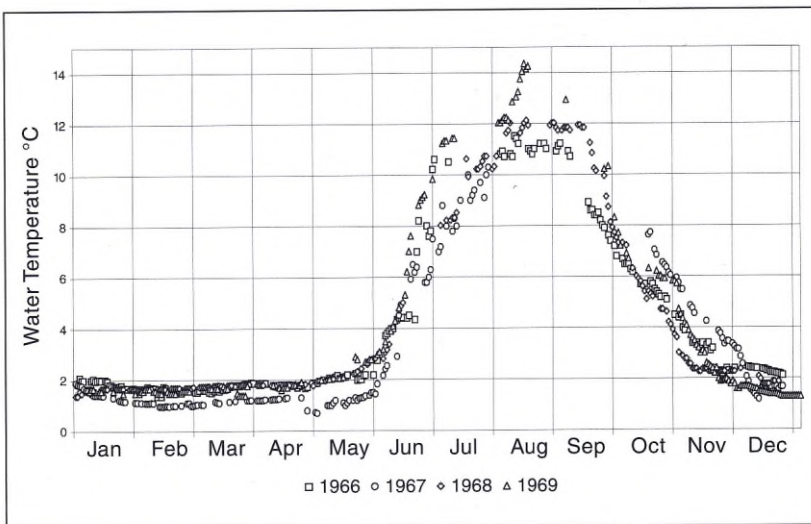


Fig. 2. Subsurface temperature recorded at the power station intake at a depth of ca 0-5 m in the outlet of Lake Blåsjön 1966-69.

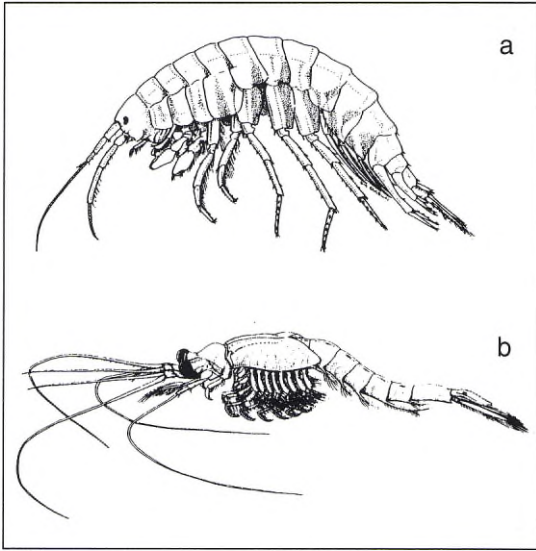


Fig. 3. The freshwater amphipod *Gammarus lacustris* L. (a) and the opossum shrimp, *Mysis relicta* Lovén (b), two macro-crustaceans of significance to winter feeding Arctic char.

(Drawings by Eva Engblom, Limnodata.)

sjön, which has served as a reservoir for hydroelectric purposes since 1949. The water level regulation amplitude was extended in 1958 to its present magnitude of 13 m. In order to compensate for the dramatic loss of the amphipod *Gammarus lacustris* (Fig. 3a) and other important littoral invertebrates following the onset of the regulation (Grimås 1961, 1962, Nilsson 1961, 1963, 1973), two new fish-food organisms, *Mysis relicta* (Fig. 3b) and *Pallasea quadrispinosa*, were experimentally introduced into Lake Blåsjön in 1964 (e.g. Fürst 1981).

The upper parts of River Faxälven (Fig. 1) comprise the alpine area of Scandinavia most heavily affected by the radioactive fallout from Chernobyl in April 26, 1986. The terrestrial deposition over the mountain range north and east of Lakes Ankarvattnet and Blåsjön averaged  $25.4 \pm 7.7$  kBq.m<sup>-2</sup>, with that over Lake Ankarvattnet being one of the highest with 50.0 kBq.m<sup>-2</sup> within its closest range, and a mean of 34.4 kBq.m<sup>-2</sup> within the whole catchment basin. The precipitation in late April came as rain and snow, and the lakes were still frozen by the time of the

accident. The direct total load on Lakes Ankarvattnet and Blåsjön were estimated to 470 and 1,140 GBq Cs-137 respectively, which is 3.2 and 4.2% of the total load of each catchment area (Hammar et al. 1991a). While the uppermost reservoirs with closed dams were found to act as efficient sinks for radiocesium during 1986, the turnover of Cs-137 in natural lakes were faster. An inventory of the total amount of Cs-137 retained in the lake ecosystems revealed the major part to be accumulated in water and surface sediment during 1986, and in sediment almost exclusively in 1987 and later (Hammar et al. 1991a, 1991b).

### Salmonid fauna

In addition to brown trout, Lakes Ankarvattnet and Blåsjön are inhabited by two sympatric taxa of the Arctic char species complex (Nyman et al. 1981). The two populations are highly introgressed, demonstrating a systematic gradient from a semi-littoral, pelagic and fast growing normal form to a deep living dwarf (Fig. 4). Besides a series of different life history characteristics, the genetic criterium for separating the two char taxa has been differences in allele frequencies of the *EST-2\** locus (Nyman 1972, Hammar 1984). In order to shorten the discussion in this paper, the Arctic char is treated as a single species in both lakes.

### Sampling methods

In 1970-71 a substantial program involving merely stomach analyses of Arctic char (150-300 mm,  $N=2,955$ ) and brown trout (150-300 mm,  $N=317$ ) sampled each month from Lake Blåsjön, was carried out in order to highlight the seasonal significance of *Mysis relicta* as new food (Fürst et al. 1978). A parallel sampling program took place during the winters 1969-72 in Lake Ankarvattnet (char 200-350 mm,  $N=529$ , trout 150-300 mm,  $N=24$ ). Specific attention was paid to the food habits during the critical period in March-April, and stomachs from Arctic char (150-300 mm,  $N=1,595$ ), and brown trout when possible (150-300 mm,  $N=134$ ), were collected by "bobbing" from the ice each spring from Lake Blåsjön during 1969-78. In addition, stomachs from Arctic



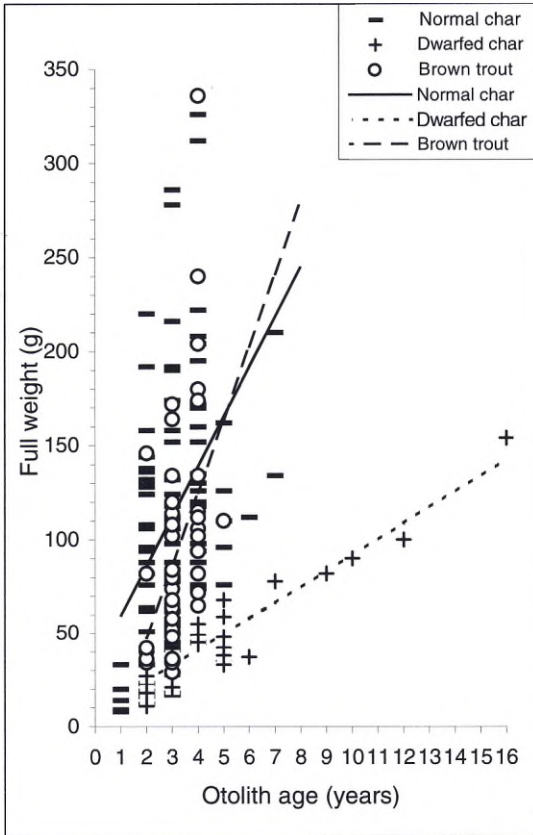


Fig. 4. The weight-age relationships of normal ( $32.83+26.52x$ ,  $r^2=0.12$ ,  $P<0.001$ ) and dwarfed Arctic char ( $7.46+8.45x$ ,  $r^2=0.87$ ,  $P<0.001$ ), and brown trout ( $-29.87+38.73x$ ,  $r^2=0.21$ ,  $P<0.001$ ) collected with multiple mesh-size gillnet sets in Lake Blåsjön, October 1985.

char ( $N=594$ ) caught under the ice in various other natural and regulated lakes with and without introduced new fish food organisms have been examined for comparison.

As an extension of the sampling program performed by Nilsson and his associates in Lake Blåsjön covering the period 1944-66, a continuous testfishing program with standard multiple mesh size gangs of gillnets (16.5-50 mm) set at different stations at the bottom of 1-110 m: s depth, and performed during July-August and September-October, 1967-85, resulted in two long time series of stomach data of Arctic char (summer  $N>1,420$ , fall  $N>2,660$ ) and brown trout

(summer  $N>727$ , fall  $N>701$ ). During 1986-90 another annual sampling program of Arctic char (150-400 mm,  $N=156$ ; 150-350 mm,  $N=182$ ) and brown trout (200-400 mm,  $N=85$ ; 200-400 mm,  $N=92$ ) from both Lakes Ankarvattnet and Blåsjön was performed in order to highlight seasonal differences in the accumulation of radionuclides from the Chernobyl disaster (Hammar et al. 1991a).

For most fish sampled, maximum total length (mm) and full wet weight (g) were recorded, and sex and level of sexual maturation were identified. From 1962 and onwards, otoliths in Arctic char were removed and used for age determination according to criteria and methods given by Nordeng (1961) and Filipsson (1967). Stomachs were usually preserved in formalin, and after a gradual substitution into alcohol were then analyzed under a stereo microscope. Food items were identified, and relative, and occasionally absolute, proportions of various food categories were estimated as volume percent, and in ml. Before 1986 only half-filled and full stomachs were considered for the statistics, and from 1986 the individual stomach content was adjusted to the fullness of the stomach estimated according to a scale of integers, 0-10.

The estimates of diet overlap were based on arithmetic mean values of volume percentages and Schoener's (1970) index, as recommended by Wallace (1981):

$$\alpha = 1 - 0.5 \left( \sum_{i=1}^n |p_{ai} - p_{bi}| \right)^*$$

with a value of 0.0 indicating no overlap, and a value of 1.0 suggesting complete overlap. The index has apparent weaknesses, as it does not include measures of the availability of the food resources, nor any measures of precision (M. Elliott pers comm.). The food categories compared include 8 functional groups: Zooplankton; *Mysis relicta*; *Gammarus lacustris*; *Pallasea quadrispinosa*; Remaining benthic crustaceans, in-

\* $p_{ai}$  is the proportion of food category  $i$  in the diet of Arctic char, and  $p_{bi}$  the proportion of food category  $i$  in the diet of brown trout.

sect larvae, pupae, and mollusks; Surface insects; Fish; and Fish roe. More detailed division of prey categories on the taxonomic level of order did not change the results, except in cases with very few fish analyzed. However, such comparisons have been excluded. Diet data from 1944-59 were recalculated from Nilsson (1955, 1961). In contrast to Nilsson's categories, the semi-benthic cladoceran *Eurycerus lamellatus* was classified as benthos, whereas winged trichopterans, ephemeropterans, tipulids and other aquatic insects were referred to as surface insects. Although extensive ontogenetic shifts in food or habitat use are considered nearly universal in fish (Werner and Gilliam 1984, Werner 1986), no size-specific comparison of diet overlap is given in this paper. The samples of Arctic char and brown trout from each specific period have been collected with identical gear, and are thus considered as roughly comparable in size frequency distribution.

### Analyses of radionuclides

Fish sampled between October 1986 and August 1990 were analyzed for radionuclides. The concentrations of Cs-134 (half-life 2.06 years), Cs-137 (half-life 30.17 years) and K-40 (half-life  $1.25 \times 10^9$  years) were determined by gamma-analysis behind 10 cm of lead protection. The analyses were performed via absolutely calibrated geometries for Ge/GeLi-detectors (Ca 90 cc, 2 keV FWHM at 1.33 MeV), connected to a multi-channel-analyzer with 4,096 channels. The standard deviation for the concentration estimates of the radionuclides was generally below 3%.

Most fish were measured individually, and only muscle tissue was analyzed for radionuclides. However, in 1987 brown trout from Lake Blåsjön, and Arctic char and brown trout from Lake Ankarvattnet were analyzed as size-ordered pooled sub-samples. In 1986-87 freeze-dried tissue was used, whereas fresh tissue was used in 1988-90. The levels of Cs-137 are, however, given as Bq.kg<sup>-1</sup> wet weight unless stated otherwise. In order to convert results in fish given as Bq.kg<sup>-1</sup> wet weight to Bq.kg<sup>-1</sup> dry weight the data should be divided by 0.22.

In addition to Lakes Ankarvattnet and Blåsjön routine sampling for radio-ecological analyses also took place in 5 other comparable and nearby lakes and reservoirs (Lakes Björkvattnet, Dabbsjöarna, Grundvattnet, Stalonjaure, Stor-sjouten, Fig. 1), ranging in size from 1 to 31 km<sup>2</sup>. Besides Arctic char and brown trout, the complete sampling program for radioactive analyses comprised the following components and methods: suspended fine-grained material (sediment traps), surface sediment (1 cm depth, Willner-corer, 2-4 stations per lake), filtered lake water (30 l, 0.45 µm), phytoplankton from filter (0.45 µm), zooplankton (net 0.055-0.060 mm), macro invertebrates such as *Mysis relicta*, *Pallasea quadrispinosa*, *Gammarus lacustris*, mollusks, insect larvae (*Mysis* trawl, amphipod traps, Ekman-grab, hand-net), and prey fish such as minnow (hand-net, gillnet). Surface water samples were also analyzed for standard chemical components.

Based on the fact that no correlations between prey organisms selected from stomach contents, a common method of measuring radioactivity in fish food, and wild specimens collected in the lakes, could be found (Hammar et al. 1991a), the levels of Cs-137 in invertebrates exclusively refer to samples collected alive in the lakes. The diversity of zooplankton species varied with lakes and seasons, but these differences were disregarded with respect to levels of radiocesium in the present study.

General sampling for analyses of radionuclides took place in October 1986, April, August and October 1987, April and August 1988, August 1989 and September 1990. All sampling stations, except for fishing, were oriented towards the outlet areas. Detailed results of these analyses were presented by Hammar et al. (1991a) and will only be referred to here when appropriate.

Besides the samples analyzed in the present study, occasional trout and char from Lakes Ankarvattnet and Blåsjön have also been analyzed for Cs-137 by other institutes in the extensive national monitoring program supervised by the National Food Administration during 1986. Such data and subsequent supplementary records on Cs-137 from 1987-90 have been included in this presentation.

## Results

### Seasonal feeding habits in Lake Ankarvattnet, a natural mountain lake with ample winter food resources

After the dominance of pelagic cladoceran zooplankton (*Daphnia galeata*, *Bythotrephes longimanus*, *Holopedium gibberum*, *Eubosmina longispina*, *Polyphemus pediculus*) in the diet of the Arctic char in Lake Ankarvattnet during August-October, combined with the semibenthic cladoceran *Eurycercus lamellatus* in November, the

littoral *Gammarus lacustris* dominated the stomach content totally during the winter period December-May (Fig. 5a). More than 50 specimens of *Gammarus* were commonly counted in full char stomachs, and occasionally more than 100 individuals. During spring a gradual shift to various littoral insect larvae, especially Plecoptera (*Diura bicaudata*, *Capnia atra*, *Taeniopteryx nebulosa*) but also Trichoptera, Ephemeroptera, Simuliidae, Chironomidae, Tipulidae, Dytiscidae, and mollusks (*Lymnaea* sp.), occurred and reached a maximum level in June. Large proportions of simuliid larvae and the presence of *Hep-*

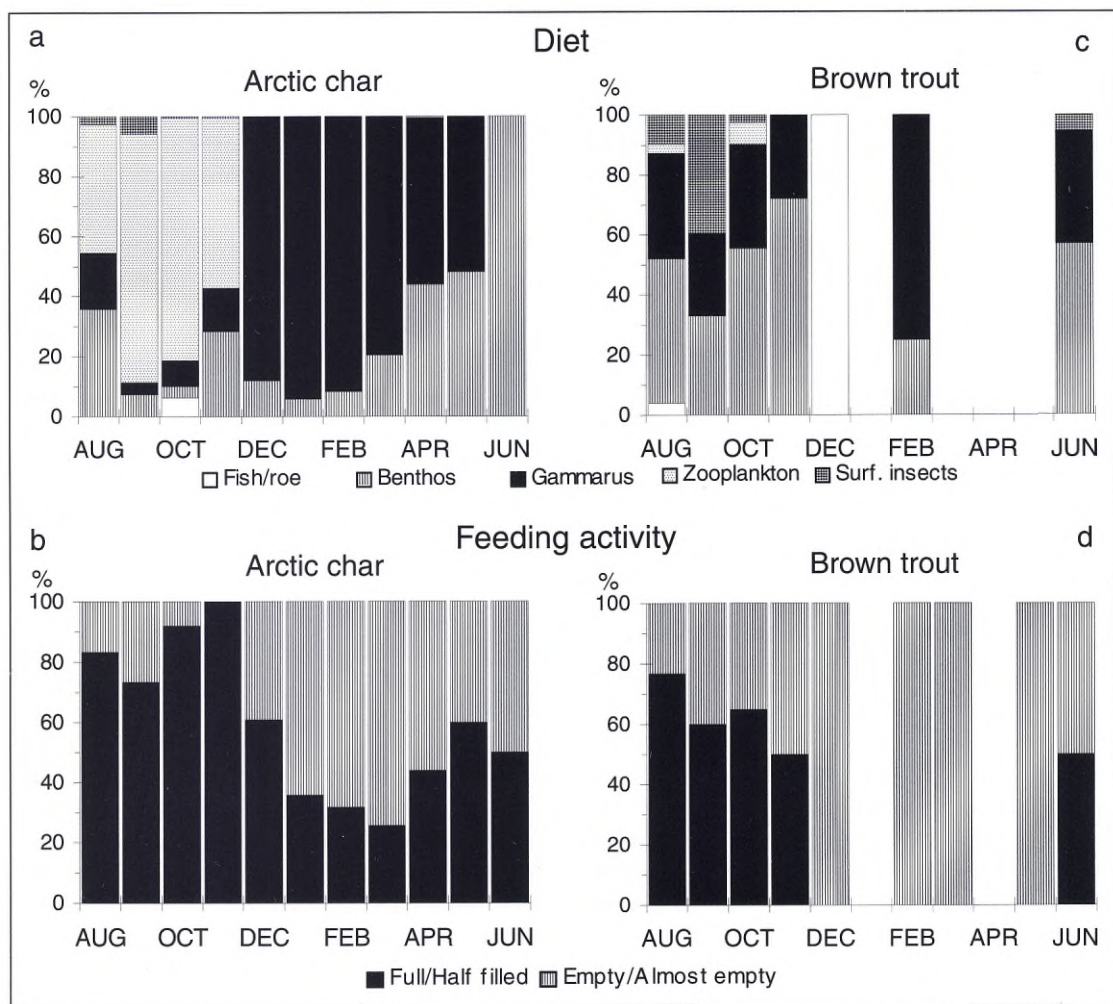


Fig. 5. Seasonal diet composition, and degree of stomach fullness in (a,b) Arctic char ( $N=711$ ) and (c,d) brown trout ( $N=116$ ) collected in Lake Ankarvattnet during 1969-72 and 1986-90.

*tagenia* sp. larvae in char stomachs in April-May suggest that some feeding had taken place close to tributaries or other littoral habitats affected by drift from running water. The feeding activity measured as the degree of fullness in the stomachs analyzed, suggested a gradual decrease from maximum levels in October-November to a minimum in March (Fig. 5b).

Brown trout were basically only caught during June-November (Fig. 5c). During these months the stomach contents comprised mostly various littoral macro-invertebrates e.g. Trichoptera and Plecoptera, *Eurycercus lamellatus*, *Lymnaea* sp., *Gyraulus* sp. and *Gammarus lacustris*. Also winged insects were eaten during August, and particularly in September. The feeding activity measured as fullness of stomachs was highest in August and lowest in November. The few trout stomachs collected and analyzed between December and May were empty or almost empty (Fig. 5d).

Using Schoener's (1970) index of diet overlap (Fig. 6), a large dietary resemblance for Arctic char and brown trout was recorded in late spring and summer, whereas the overlap decreased towards the fall.

### Spring feeding habits of Arctic char in regulated mountain lakes with reduced winter food resources

When comparing the diet and stomach fullness of Arctic char caught from the ice in February-April in a series of natural mountain lakes and reservoirs, with or without introduced *Mysis relicta* and/or *Pallasea quadrispinosa*, the results clearly demonstrate the adverse consequences of absence of suitable winter prey in regulated lakes (Table 2). The majority of char analyzed from natural lakes had either full or half filled stomachs, whereas the majority of char from regulated lakes had empty stomachs. In natural lakes *Gammarus lacustris*, snails and various littoral insect larvae dominated the stomach content, whereas plecopteran and chironomid larvae, sphaerid bivalves and copepods composed the scarce food items found in char stomachs collected in reservoirs.

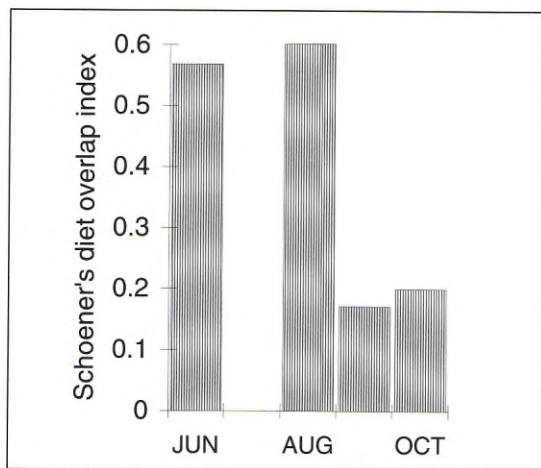


Fig. 6. Seasonal diet overlap between Arctic char and brown trout in Lake Ankarvattnet during 1969-90 ( $N=284$ ).

### Seasonal feeding habits in Lake Blåsjön, a regulated mountain lake with "restored" winter food resources

After having been introduced into Lake Blåsjön, *Mysis relicta* and *Pallasea quadrispinosa* immediately became significant as new semi-benthic fish food organisms for both brown trout and Arctic char. The shift is obvious in a series of stomach analyses of Arctic char collected in March-April 1954-90 (Fig. 7). The proportion of empty and almost empty stomachs has gradually declined, and the actual quantities of food taken during March/April as a result have increased considerably. The stomach analyses from different months in 1970/1971 clearly confirmed the Arctic char (Fig. 8a) to feed actively during the entire winter season. *Mysis relicta* dominated the stomach content between November and May. In June, when the temperature rose and the ice broke up, the char shifted gradually to a diet also including surface insects and cladoceran zooplankton, which then made up the stomach contents until October. The cladocerans were dominated by *Daphnia galeata*, *Bythotrephes longimanus*, *Holopedium gibberum* and *Eubosmina longispina*. The consumed benthic organisms mostly comprised chironomid larvae and *Pisidium* sp., and during early spring plecopteran lar-

Table 2. Winter diet composition (%), and degree of stomach filling (%) in Arctic char collected during February-April from 9 natural and 11 regulated lakes, with or without introduced *Mysis relicta* and/or *Pallasea quadrispinosa*.

Lake	Year	N	MTL (mm)	Surface Zoo-insects plankton	<i>Pallasea</i>	<i>Mysis</i>	<i>Gammarus</i>	Benthos	Fish/roe	Empty and almost empty	Full and half filled	
<b>Natural lakes</b>												
Mullbärsjärn	1963	9	300-350	0.0	0.0	0.0	0.0	100	0.0	77.8	22.2	
Ankarvattnet	1972	232	200-350	0.0	0.0	0.0	74.9	23.9	0.0	63.4	36.6	
Fånsjön	1977	25	92-246	0.0	1.1	0.0	17.7	81.2	0.0	40.0	60.0	
Ö. and V. Rösjön	1986	8	135-320	0.0	0.0	0.0	66.5	33.5	0.0	25.0	75.0	
Rörtjärn	1977	16	153-278	0.0	6.1	0.0	0.0	93.9	0.0	6.3	93.8	
Storrörmyrtjärn	1972	7	240-330	0.0	0.0	0.0	0.0	100	0.0	0.0	100	
Stora Gråsan	1972	7		0.0	2.3	0.0	92.7	5.0	0.0	0.0	100	
<b>Natural lakes with introduced new fish food organisms</b>												
Lidsjön <sup>1</sup>	1980	8	200-410	0.0	0.0	64.8	17.0	18.2	0.0	25.0	75.0	
Björkvattnet <sup>2</sup>	1987	14	166-341	0.0	0.0	77.2	0.0	4.2	0.0	14.3	85.7	
<b>Regulated lakes</b>												
Dabbsjön	1987	8	277-385	0.0	0.0	0.0	0.0	100	0.0	100	0.0	
Stora Mjölkvattnet	1977	91	150-220	0.0	46.2	0.0	0.0	53.9	0.0	97.8	2.2	
Kvarnbergsvattnet	1972	237	150-300	0.0	31.1	0.0	0.6	68.4	0.0	91.1	8.9	
Övre Björkvattnet	1977	12	164-195	0.0	57.9	0.0	0.0	42.1	0.0	83.4	16.6	
<b>Regulated lakes with introduced new fish food organisms</b>												
Riebnes <sup>3</sup>	1980	52	198-470	0.0	0.0	11.1	0.0	0.0	88.9	82.7	17.3	
Kultsjön <sup>4</sup>	1979	10	160-390	0.0	0.0	6.7	0.0	40.0	53.3	70.0	30.0	
Näkten <sup>5</sup>	1979	20	300-350	0.0	0.0	97.7	0.0	2.2	0.1	55.0	45.0	
Torrön <sup>6</sup>	1979	20	188-346	0.0	7.7	78.2	0.0	14.1	0.0	35.0	65.0	
Storsjouten <sup>7</sup>	1978	100	100-300	0.0	0.0	96.7	0.0	3.3	0.0	29.0	71.0	
Kvarnbergsvattnet <sup>8</sup>	1990	12	180-280	0.0	0.0	53.7	0.0	7.9	0.0	25.0	75.0	
Blåsjön <sup>9</sup>	1978	100	150-300	0.0	0.0	78.3	0.0	6.3	0.0	14.0	86.0	
Ajaur <sup>10</sup>	1977	30	240-350	0.0	0.0	92.7	0.0	7.3	0.0	0.0	100	

<sup>1</sup>*Mysis* introduced 1975

<sup>6</sup>*Mysis* introduced 1957+1965

<sup>2</sup>*Mysis* and *Pallasea* introduced 1973

<sup>7</sup>*Mysis* introduced 1970

<sup>3</sup>*Mysis* introduced 1973

<sup>8</sup>*Mysis* and *Pallasea* down stream migration from Lakes Blåsjön, Limingen and/or Björkvattnet

<sup>4</sup>*Mysis* introduced 1972

<sup>9</sup>*Mysis* and *Pallasea* introduced 1964

<sup>5</sup>*Mysis* introduced 1965

<sup>10</sup>*Pallasea* introduced 1971

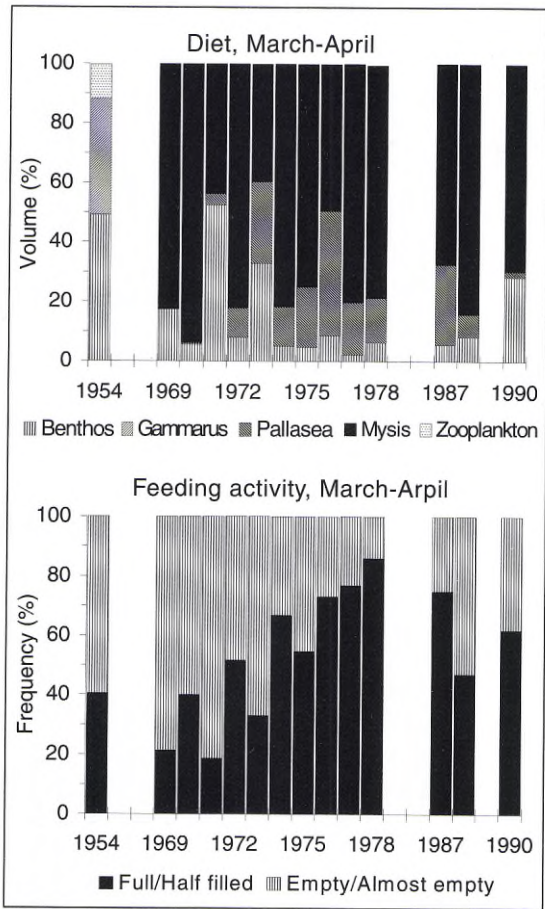


Fig. 7. Spring diet composition, and degree of stomach fullness in Arctic char ( $N=1,595$ ) collected in Lake Blåsjön in March/April during 1954-90.

vae (e.g. *Capnia atra*, *Diura bicaudata*). With the exception of June, the feeding activity expressed as the degree of stomach fullness demonstrated the highest levels, 40-60% full and half-filled stomachs, in May to September, and the lowest values (20-30%) in October to April (Fig. 8b). In terms of absolute stomach contents of an average Arctic char (200-250 mm), the mean individual volume during 8 months in autumn, winter and spring averaged 0.05-0.15 ml and 0.25-0.35 ml of food during the 4 remaining summer months, indicating a significant part of the total annual food intake in Arctic char to occur during the frozen season.

The efforts to collect brown trout in 1970/71 failed during the period November-February. In contrast to the Arctic char, more profundal invertebrates such as chironomid larvae dominated the food choice of brown trout during March-May, whereas *Mysis relicta* made up a significant part of the stomach content later between June and October (Fig. 8c). Surface insects dominated during July-August. The feeding activity rose from low levels in March/April to reach its maximum during September (Fig. 8d). The absolute volume of prey measured in trout stomachs averaged 0.5 ml during ca six months of ice-free water, thus suggesting twice the annual food intake of Arctic char, in half of the year.

Information on the stomach contents of Arctic char collected in 1986-90 supports the earlier findings that the Arctic char indeed feeds actively during the winter. As in 1970/71 the general pattern demonstrates a seasonal feeding shift from cladoceran zooplankton in late summer to *Mysis relicta* and in particular *Pallasea quadrispinosa* as dominating benthic macro crustaceans of significance in December-June, but also including considerable amounts of char eggs during October (Table 3). Brown trout were only sampled in June, August and October, and the stomach contents increased in volume and showed a gradual switch from *Mysis* in June to surface insects in August and *Pallasea* in October (Table 3).

The values of Schoener's (1970) index of diet overlap between Arctic char and brown trout in Lake Blåsjön were found to fluctuate considerably. In recent years the highest levels were recorded in spring, and the lowest in fall. However, differences tended to be smaller within than between years (Fig. 9, Table 3). In a longer perspective the linear trends for the diet overlap in summer ( $r^2=0.18$ ,  $P=0.065$ ) and fall ( $r^2=0.30$ ,  $P=0.029$ ) seem to correlate negatively with the year of sampling. Especially in July/August, for which a reasonable number of years could be compared, the diet overlap index before the impoundment in 1949 was higher than after the introduction of new fish food organisms in 1964 (Wilcoxon two-sample test:  $z=-2.10$ ,  $P=0.036$ ), i.e. the diet overlap between Arctic char and

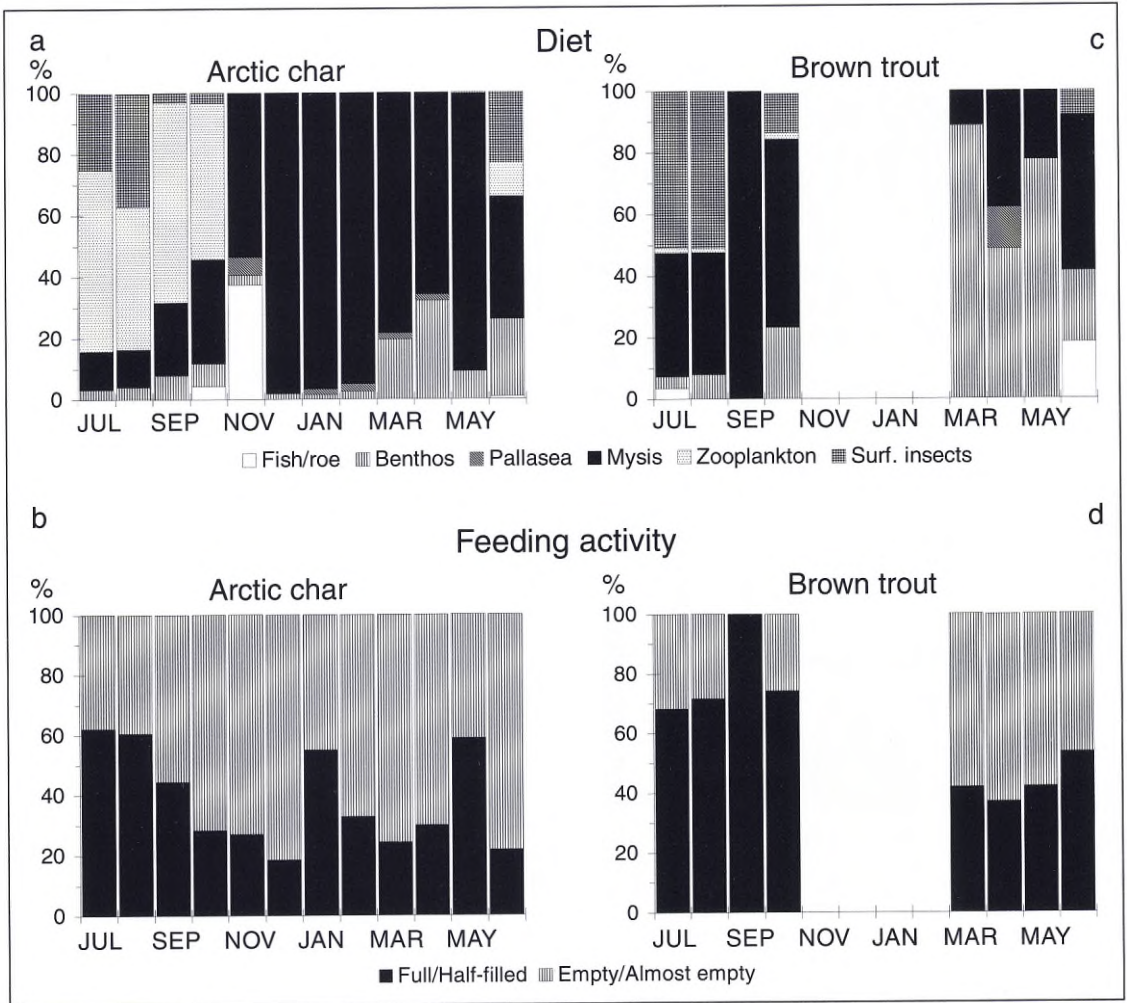


Fig. 8. Seasonal diet composition, and degree of stomach fullness in (a,b) Arctic char (N=2,955) and (c,d) brown trout (N=317) collected in Lake Blåsjön during 1970-1971.

brown trout seems to decline during the open season in Lake Blåsjön.

### Yearly and seasonal variation in levels of Cs-137 in zooplankton and macro-invertebrates

Following the information obtained from stomach analyses, three major groups of invertebrates known to dominate as fish food organisms were examined for concentrations of radionuclides: pelagic zooplankton, amphipods (*Gammarus lacustris*, *Pallasea quadrispinosa*), and *Mysis re-*

*licta*. The earliest record of radioactivity in zooplankton in the area dates from June 29 1986, and was measured in Lake Hetögeltn (Fig. 1), where the levels reached a total of 311 kBq.kg<sup>-1</sup> (dw) with the levels of Cs-137 and Cs-134 being 180 kBq and 91 kBq respectively. By October 1986 the concentration of Cs-137 in zooplankton had decreased to 24.3 kBq.kg<sup>-1</sup> (dw) in Lake Ankarvattnet, and to 7 kBq.kg<sup>-1</sup> (dw) in Lake Blåsjön. The levels then declined rapidly during 1987, and fluctuated around 1,500-4,400 Bq.kg<sup>-1</sup> (dw) during 1989-90 (Table 4). The concentrations of Cs-137 in zooplankton 1987-90 were

Table 3. Seasonal diet composition (volume %) and degree of stomach filling (0-10) in sympatric normal and dwarfed Arctic char, and brown trout collected in Lake Blåsjön during 1986-90.

Month	N	Fill	Surface insects	Zoo-plankton	<i>Pallasea</i>	<i>Mysis</i>	Benthos	Roe	Fish
<b>Normal char</b>									
Feb	7	1.7	0.0	0.0	52.9	38.8	8.3	0.0	0.0
Apr	22	2.2	0.0	0.0	0.0	87.1	12.9	0.0	0.0
May	15	4.1	0.0	0.0	30.9	64.6	4.5	0.0	0.0
Jun	10	7.2	0.7	0.0	67.8	30.7	0.8	0.0	0.0
Aug	45	4.4	2.7	77.8	0.0	19.5	0.1	0.0	0.0
Sep	12	4.8	0.0	100	0.0	0.0	0.0	0.0	0.0
Oct	35	0.9	0.0	13.2	13.0	6.8	18.8	48.2	0.0
Dec	10	1.9	0.0	0.0	1.2	98.7	0.1	0.0	0.0
	<b>156</b>								
<b>Dwarfed char</b>									
Feb	13	3.7	0.0	0.0	52.9	38.8	8.3	0.0	0.0
Apr	32	3.7	0.0	0.0	18.7	63.8	17.5	0.0	0.0
May	18	1.9	0.0	0.0	22.7	60.9	16.4	0.0	0.0
Jun	12	2.5	0.0	0.0	45.8	30.8	23.3	0.0	0.0
Aug	5	4.6	0.0	0.0	5.9	0.0	94.1	0.0	0.0
Sep	3	5.3	0.0	100	0.0	0.0	0.0	0.0	0.0
Oct	38	2.1	0.0	17.1	3.8	7.1	41.0	31.0	0.0
Dec	12	8.3	0.0	0.0	0.4	98.6	0.0	0.0	1.0
	<b>133</b>								
<b>Brown trout</b>									
Jun	10	3.8	0.0	0.0	14.5	63.7	21.8	0.0	0.0
Aug	43	4.6	52.3	9.5	1.6	20.8	5.6	0.0	10.2
Oct	32	5.2	1.2	0.3	75.5	3.2	19.8	0.0	0.1
	<b>85</b>								

positively correlated with the concentrations in unfiltered water ( $r^2=0.13$ ,  $P=0.014$ ,  $N=46$ ), hence indicating a trophic relationship between zooplankton and phytoplankton/particulate matter.

Analyses of the levels of Cs-137 in *Pallasea*, *Gammarus* and *Mysis* during fall 1986 revealed concentrations between 13 and 25 kBq.kg<sup>-1</sup> (dw), with the highest levels recorded in *Gammarus*,

 Table 4. Concentrations of Cs-137 (Bq.kg<sup>-1</sup> dw) in zooplankton, *Gammarus lacustris*, *Mysis relicta* and *Pallasea quadrispinosa* in Lakes Ankarvattnet and Blåsjön during October 1986 to September 1990. (From Hammar et al. 1991a.)

Date	Ankarvattnet		Blåsjön		
	Zooplankton	<i>Gammarus</i>	Zooplankton	<i>Mysis</i>	<i>Pallasea</i>
1986.10	24,300	24,600	7,000	20,900	-
1987.04	25,100	-	5,500	-	-
1987.08	3,400	8,400	5,300	5,800	-
1987.10	4,000	9,000	3,700	11,700	5,300
1988.04	1,400	-	800	-	-
1988.08	5,000	4,100	6,100	4,900	3,000
1989.08	1,500	2,000	2,000	3,900	-
1990.09	2,200	-	4,300	4,600	-



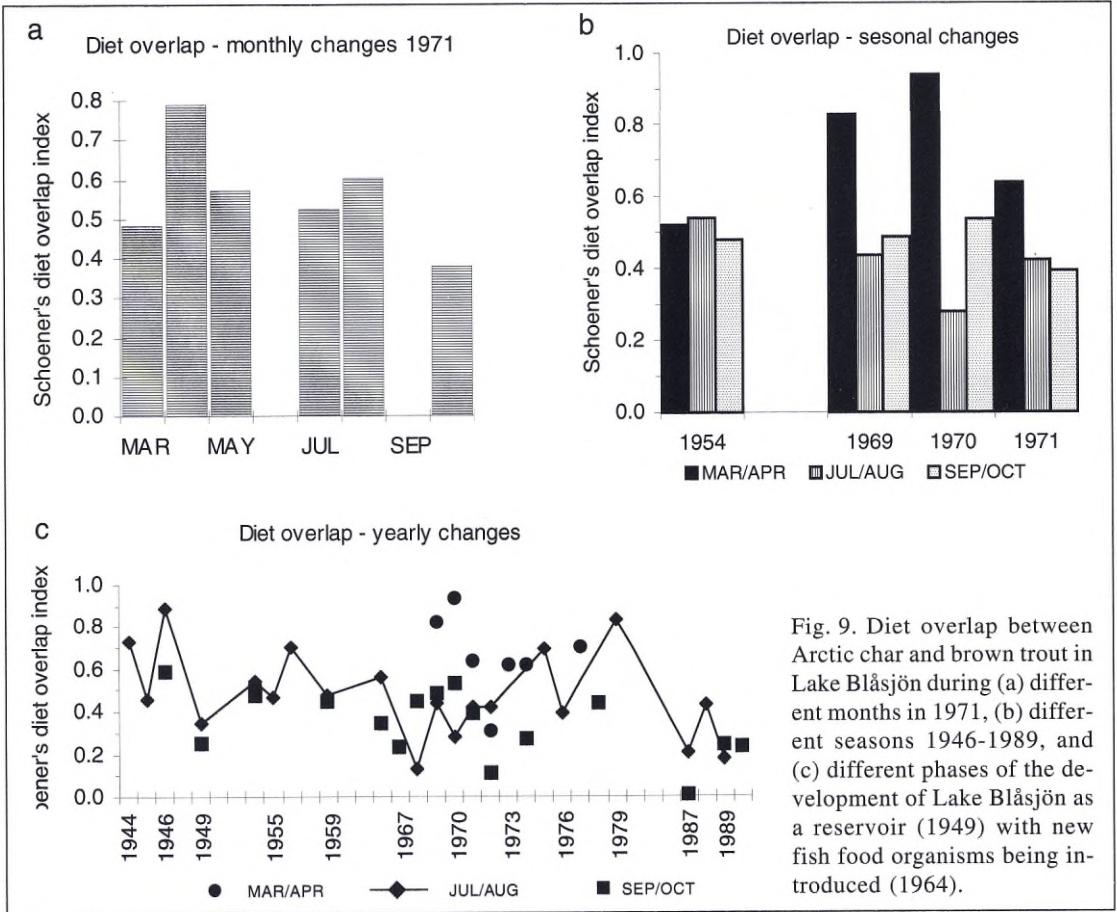


Fig. 9. Diet overlap between Arctic char and brown trout in Lake Blåsjön during (a) different months in 1971, (b) different seasons 1946-1989, and (c) different phases of the development of Lake Blåsjön as a reservoir (1949) with new fish food organisms being introduced (1964).

and the lowest in *Pallasea*. However, during 1987-90 the levels in *Mysis* generally exceeded those in *Gammarus*. The fluctuations of Cs-137 in these macro invertebrates were in general similar to those of zooplankton, although the values were frequently higher (Table 4). The levels of Cs-137 in *Mysis* were approximately 140% higher and in *Gammarus* about 65% higher than in zooplankton. Positive correlations between levels of Cs-137 in *Mysis* and the corresponding concentrations in unfiltered water and suspended matter collected in sediment traps were recorded during 1987-90 (*Mysis* - water:  $r^2=0.34$ ,  $P=0.011$ ,  $N=18$ , *Mysis* - detritus:  $r^2=0.79$ ,  $P=0.003$ ,  $N=8$ ). Covariation between *Mysis* and zooplankton was only demonstrated in one reservoir, Lake Storsjouten, thus indicating a generally closer trophic relationship between *Mysis* and organic parti-

culate matter in the water as well as on the bottom, i.e. detritus, than with zooplankton.

### Yearly and seasonal variation in levels of Cs-137 in salmonids

Samples of Arctic char and brown trout collected from Lake Blåsjön in October 1985 contained very low concentrations of Cs-137 (Arctic char;  $21 \pm 17$  Bq.kg<sup>-1</sup> (ww), brown trout;  $27 \pm 7$  Bq.kg<sup>-1</sup> (ww) (Appendix 2). After the accident, the accumulation of Cs-137 and Cs-134 increased fast and linearly ( $r^2 > 0.85$ ,  $P < 0.005$ ) in both Arctic char and brown trout during the summer and fall of 1986 (Figs. 10-11). In Lake Ankarvatnet the maximum levels in brown trout were recorded by the end of 1986 (mean  $6,970 \pm 1,360$ , max  $9,310$  Bq.kg<sup>-1</sup>) whereas the levels in Arctic char

continued to rise until April 1987 (mean 3,860 Bq.kg<sup>-1</sup>) (Appendix 1). In Lake Blåsjön the highest levels in brown trout were recorded during August 1986 (mean 7,980 Bq.kg<sup>-1</sup>) while the highest levels in Arctic char were measured in spring 1988 (mean 3,960±1,120, max 4,770 Bq.kg<sup>-1</sup>). In dwarfed Arctic char a liable peak level was noted as late as August 1988 (mean 6,130±690, max 6,930 Bq.kg<sup>-1</sup>) (Appendix 2).

The change of the Cs-137 levels in Arctic char ( $r^2=0.51$ ,  $P<0.001$ ) and brown trout ( $r^2=0.46$ ,  $P=0.017$ ) in Lake Blåsjön during 1985-90 matched cubic regression models. After the Cs-137 maxima in 1986-87 the levels declined steadily, although disrupted by a seasonally displaced pattern of Cs-137 elevations in the two species. The most notable changes were seen in Arctic char during winter and in brown trout during summer. Between October 1986 and April 1987 the levels of Cs-137 in Arctic char from Lake Ankarvattnet rose ca 8 Bq.kg<sup>-1</sup> per day, and in Lake Blåsjön ca 12 Bq.kg<sup>-1</sup> per day. During the same period the following winter the levels in-

creased ca 6 Bq.kg<sup>-1</sup> in Lake Ankarvattnet, and ca 10 Bq.kg<sup>-1</sup> per day in Lake Blåsjön. During both winter periods the differences in Cs-137 levels in normal Arctic char were significant (Lake Blåsjön 1986/87:  $P=0.009$ ,  $N=15+3$ , 1987/88:  $P=0.034$ ,  $N=12+8$ , Lake Ankarvattnet 1986/87:  $P=0.009$ ,  $N=16+3$ , 1987/88:  $P=0.018$ ,  $N=3+15$ , Mann-Whitney tests). During the two succeeding summers, 1987 and 1988, the levels declined considerably again. A third winter boost in the levels of Cs-137 in Arctic char from Lake Blåsjön during 1988/89, and to a less extent in Lake Ankarvattnet, was also recorded. Although char were sampled more frequently, the differences recorded during the winter 1989/1990 were not significant. Still a fourth winter boost of ca 3 Bq.day<sup>-1</sup> in Arctic char was recorded between October 1990 and April 1991.

Populations of Arctic char and brown trout feeding on benthos, especially on *Mysis relicta* or *Gammarus lacustris*, had higher levels of Cs-137, whereas populations feeding on zooplankton demonstrated lower levels (Fig. 12). Corre-

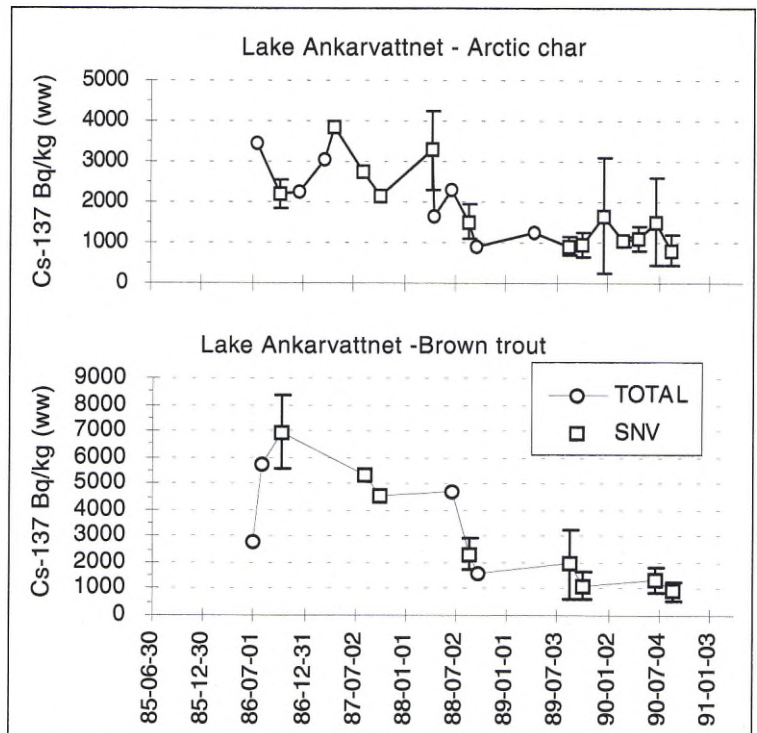


Fig. 10. Arithmetic mean levels and standard deviation of Cs-137 (Bq.kg<sup>-1</sup> ww) in Arctic char and brown trout collected in Lake Ankarvattnet, 1986-90. Values from both external analyses and this study (SNV) are presented.

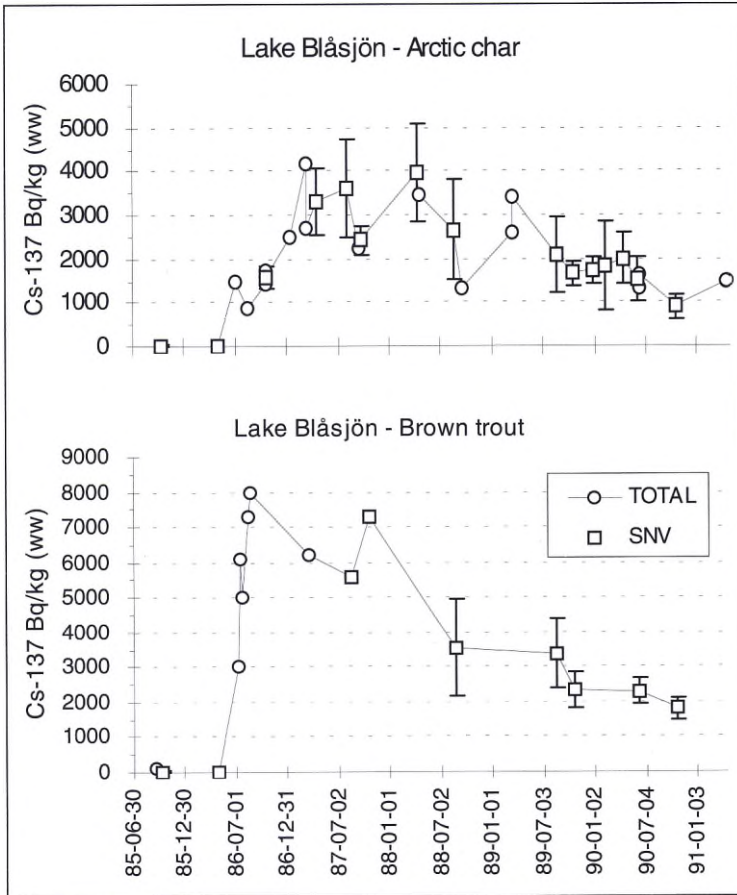


Fig. 11. Arithmetic mean levels and standard deviation of Cs-137 (Bq.kg<sup>-1</sup> ww) in Arctic char and brown trout collected in Lake Blåsjön, 1985-91. Values from both external analyses and this study (SNV) are presented.

lation analyses between the mean levels of Cs-137, adjusted for the differences in deposition of radiocesium in the catchment areas, of different fish populations from different lakes and the corresponding mean proportions of dominating food organisms in the diet, revealed a highly significant pattern for the various seasons in 1986, 1988 and 1989.

## Discussion

### Interactive segregation, light, and temperature

Dietary niche segregation in sympatric species may minimize their diet overlap and thus optimize their use of available food – two components of vital importance when depending on

restricted and highly seasonal resources (Werner 1986). The concept of interactive segregation (Brian 1956) has been considered a phenomenon typical of "young" faunas of closely related species with considerable ecological plasticity, for example, within recently deglaciated areas (Nilsson 1967), and has been considered, partly or completely, to explain partition of habitat and food resources in various salmonid assemblages including species of *Oncorhynchus*, *Salmo* and *Salvelinus* (Lindroth 1955, Nyman 1970, Andrusak and Northcote 1971, Schutz and Northcote 1972, Nilsson and Northcote 1981, Hume and Northcote 1985, Kawanabe et al. 1985, Hammar 1987, Hindar et al. 1988), and *Coregonus* (Nilsson 1958, 1960, Lindström and Nilsson 1962, Svårdson 1979). Few studies, however, have considered how environmental conditions can influ-

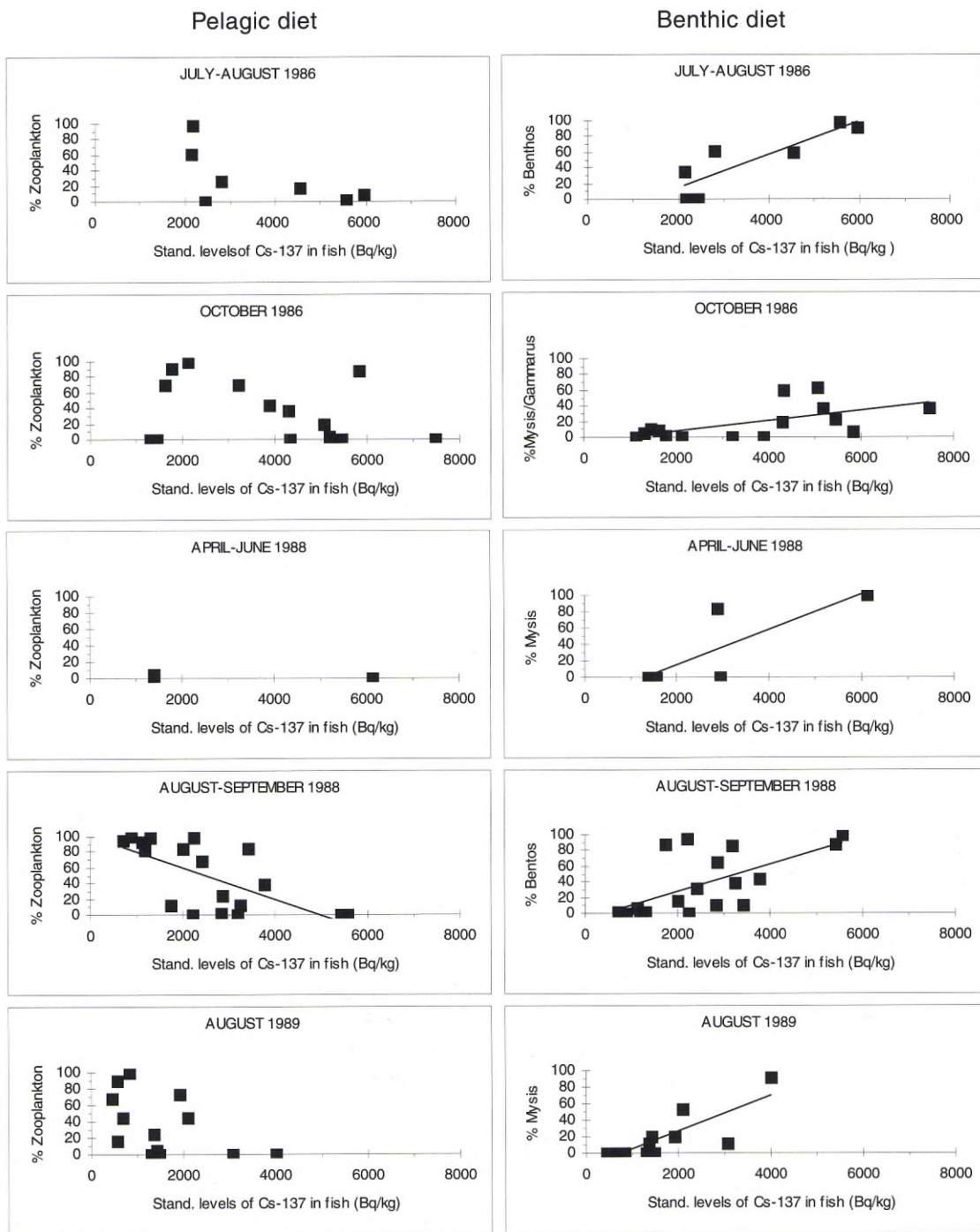


Fig. 12. Correlations between mean levels of Cs-137 adjusted for the local deposition in the catchment basins, and the proportions of benthic and pelagic food items (% volume) in various fish populations, 1986-89. Linear regressions are shown in cases with significant correlation.

ence these interactions, although Larkin (1956) in his early review on competition among fish noted that the outcome of competitive interactions may vary with environmental variables.

Light is one major environmental component mediating segregation of fishes in northern lakes covered by thick ice during long winters. In feeding experiments, Dolly Varden char (*Salvelinus malma*) were described as more successful in capturing chironomid larvae in dim light conditions than cutthroat trout (*Oncorhynchus clarki*) (Schutz and Northcote 1972). The significance of intensity and quality of light in differences of visual prey detection ability of these two North American salmonids was confirmed and further described by Henderson and Northcote (1985). Diel differences in food selection in sympatric planktivorous Arctic char and brown trout in southeast Norway, with char always feeding on zooplankton and trout shifting to more visible prey items such as surface insects and chironomid pupae at night, were also suggested to reflect differences in ability of detection of prey under poor light conditions (Derivo et al. 1991). Thus, char in both North America and Europe seem to be more successful in prey detection under poor light conditions than coexisting trout, and the opposite in bright conditions. This is in complete agreement with the pattern of general adaptations to sub-ice and low light conditions seen in Arctic and Antarctic freshwater organisms. Following the ice-break in summer, photosynthetic efficiency is inhibited, and spring algae are replaced by summer algae occurring at greater depths (Hammar 1989). Although of undeniable importance in explaining seasonal shifts in choice of food and habitat in competing char and trout, however, light has less bearing on the present discussion than temperature.

In his review on salmonids and climate, Power (1990) concluded temperature to be the most likely factor explaining the distribution of salmonid species, and also postulated climate warming to shift the distribution northwards. The influence of temperature on the interspecific interactions in a series of fish species combinations (e.g. Baltz et al. 1982, Skuud 1982, Reeves et al. 1987, Persson 1986, 1988, Bergman 1990) demonstrated that

for every species pair competing in a given environment, one species may be described as a "cold water species" and the other as a "warm water species". Temperature may thus be treated as an ecological resource influencing segregation of fish, with dominant species choosing temperature-defined habitats with conditions closest to its preference temperature (e.g. MacLean and Magnuson 1977, Magnuson et al. 1979).

### Temperature preferences of Arctic char and brown trout

The preferred temperature of brown trout in American studies has been estimated to average 12.2°C, with a diurnal variation between 10.3 and 13.7°C (Reynolds and Casterlin 1979). Early investigations in Britain suggested the temperature of optimum growth in brown trout to average 15-16°C or even as high as 19°C (ref. in Baldwin 1957). The optimum temperature for growth, however, increases with increasing ration size (Elliott 1975b). In a series of elegant experiments by Elliott (1975a), using conditions of maximal food rations, the temperature producing maximal increase of individual weight of English brown trout was estimated as 12.8-13.6°C, while growth was restricted above 20°C and below 4°C.

So far only limited information on the temperature preference, i.e. the temperature at which metabolism is maximized, of Arctic char is available, although the species complex is generally considered to be cold-stenothermic (e.g. Baroudy and Elliott 1994). Using various salmonid species and their intra- as well as intergeneric hybrids in temperature gradient experiments, Peterson et al. (1979) demonstrated that fry of "species" within *Salvelinus* preferred a lower temperature (9.0-11.5°C) than fry of *Salmo* and *Oncorhynchus* (13.0-15.0°C). In gradient experiments including true Arctic char, the char fry chose the lowest temperature, 9.2 (7.7-10.1)°C, among the 13 "species" tested (Peterson et al. 1979). Rearing experiments with Norwegian Arctic char fed to satiation confirmed that growth still occurred at 2.9±0.4°C (Wandsvik and Jobling 1982), although maximal growth was recorded at a temperature as high as 14°C (Jobling 1983). This

verified the temperature interval, 12-16°C, recorded for maximal growth in Lake Windermere char by Swift (1964). Jensen (1985), however, reevaluated the temperatures of maximal growth in Arctic char based on data from a Norwegian lake reservoir, and stated that Arctic char had better growth potential than brown trout at temperatures below 12°C, and vice versa. In experiments during summer months with temperatures reaching above 15°C, the growth of different Swedish Arctic char strains were significantly retarded (Näslund et al. 1990).

Inheritable differences in the adaptations to specific local conditions have been demonstrated experimentally for numerous stocks of both Arctic char and brown trout originating at different latitudes (Rosseland 1975, 1977, Berg and Holm 1989, Jensen 1990, Näslund et al. 1990, 1992), which may explain why results from different studies may differ.

### Seasonal feeding habits and diet overlap in sympatric Arctic char and brown trout in natural and regulated mountain lakes

Although the seasonal segregation in diet and habitat choice of sympatric Arctic char and brown trout in north Scandinavian lakes is well known (e.g. Nilsson 1955, 1960, 1961, 1965), the information available is restricted to the ice-free season. A more complete description of the seasonal dietary shifts of Arctic char inhabiting a natural mountain lake in sympatry with brown trout demonstrates a gradual shift from an almost exclusive diet of planktonic micro-crustaceans (*Daphnia*, *Holopedium*, *Eubosmina*) during summer and fall, to littoral and benthic macro-invertebrates (e.g. *Gammarus*, *Eurycercus* and plecopteran larvae) in late fall, winter and early spring. When actively feeding, the few brown trout caught under the ice showed a similar preference for macro-benthos, although most stomachs examined were empty. During the ice-free season the diet of brown trout varied with littoral, benthic invertebrates (*Gammarus*, *Eurycercus*, mollusks, trichopterans and plecopterans) eaten preferably in early summer and fall, and various winged insects taken at the surface during the late summer.

Using Schoener's (1970) index as a measure of diet overlap, the similarity in diet of Arctic char and brown trout in the present study decreased after a summer level (0.57-0.60) to a lower level (0.17-0.20) in fall. This is in accordance with Nilsson's (1960) findings. When comparing a series of cases of sympatric char and trout, the greatest overlap in diet was recorded in June (38%), when the abundance of various benthic organisms was at a peak, and utilized by both Arctic char and brown trout (Nilsson 1960). Following declining food levels the segregation increased during July, August, and September to attain its maximum in October (overlap 18%), with Arctic char feeding almost exclusively on zooplankton, and brown trout feeding on *Gammarus* and Trichoptera larvae (Nilsson 1960). Nilsson (1955) explained the late summer diet differences as a reflection of the seasonal variations in the availability of various invertebrates, affecting the Arctic char and brown trout in different ways, depending on differences in their behavioral ecology. Nilsson (1955, 1960, 1961, 1965) also showed that food segregation was combined with habitat segregation, with "trout typically dwelling in the upper part of the littoral zone, and char deeper or more pelagical", a general description which numerous later studies have confirmed (e.g. Fürst et al. 1978, 1981, Hammar and Filipsson 1988, Hegge et al. 1989, Forseth et al. 1991, Langeland et al. 1991, L'Abée-Lund et al. 1992b).

The evidence of an extensive diet of littoral macro-benthos in winter and early spring clearly indicates that Arctic char in natural lakes with ample winter prey reoccupies the littoral food resources during the frozen period, which in turn indicates a reestablishment of the littoral habitat occupied by brown trout during periods of competitive interactions in the summer months. The char's utilization of littoral habitats in winter is also confirmed by the distribution of fishermen on the ice. The food and habitat shift of the Arctic char may be a consequence of the brown trout moving down to deeper and warmer water-layers to avoid the declining littoral temperature as suggested by Dahl (1943), or it may simply illustrate the exploitation of an unoccupied feeding

niche not utilized by brown trout entering torpor because of physiological and/or optimal foraging reasons. The proximate cause of the niche shift cannot be read, however, from the above results. The information on the winter ecology of brown trout is still quite limited, and the evidence of quiescence or a torpor-like winter phase is based on sporadic individuals with more or less empty stomachs, although the swollen gut epithelium of such stomachs does seem to indicate reduced food intake.

The niche segregation of coexisting Arctic char and brown trout reaches even more extreme levels in regulated lakes, where the production of littoral invertebrates is severely damaged. The destruction of the littoral zone and the loss of its production of crucial invertebrate prey (Grimås 1961, 1962) eliminate the fundamental resource allowing seasonal diet overlap of Arctic char and brown trout, as well as changing the structure of the populations as well as the fish community towards "dominance" of small-sized Arctic char. Nilsson (1961, 1964) demonstrated a gradual decline of the proportions of benthic invertebrates in the diet of brown trout and Arctic char as a major effect of the water-level regulation in Lake Blåsjön. In addition to a sharpened segregation in summer, with the brown trout seriously affected, the Arctic char also lost its prime winter prey, as seen in a number of reservoirs (Table 2). The benthic taxa most severely affected by water level regulation are *Gammarus lacustris*, littoral mollusks (e.g. *Lymnaea* sp., *Planorbis* sp.) and various insects (e.g. large trichopterans). Less than 6-7 years after the impoundment of Lake Blåsjön, *Gammarus lacustris* in char and trout stomachs had become very rare (Nilsson 1961).

The two introduced crustaceans, *Mysis relicta* and *Pallasea quadrispinosa*, seem to have replaced the lost amphipod *Gammarus lacustris* as the significant spring-summer-fall food resource for brown trout and fall-winter-spring food resource for Arctic char in Lake Blåsjön, and also influenced their diet overlap during summer and fall. Especially the trajectory of the diet overlap in July/August during 1944-89 (Fig. 9) suggests a succession of major ecological events in the dynamics of interspecific interactions between

Arctic char and brown trout because of (a) water level regulation and thus the elimination of littoral benthos during 1944-68, (b) the introduction of new fish food organisms and thus the partial compensation of lost benthos in 1968-79, and finally (c) the impoverished zooplankton community caused by selective predation by *Mysis relicta* in 1979-90. In contrast, the introduced macro-crustaceans in Lake Blåsjön also seem to increase the diet overlap during spring, and the two salmonids seem to show differences in their seasonal preferences (Fig. 8, Table 3). The values of diet overlap between benthic Arctic char and brown trout reported by Hegge et al. (1989) from a Norwegian reservoir without new fish-food organisms were also low, and again demonstrating extensive seasonal fluctuations. The lowest value was recorded in June (0.02), the highest in July (0.41), while levels of food overlap in August to October were intermediate (0.14, 0.11, 0.24). The large number of empty stomachs in June (55%,  $N=355$ ) may be caused by the major rise in temperature and break up of ice, by the successive food and habitat switch, and/or by the successive change in the selectivity of the gear, from an active method with hook and line to a passive one with gillnet, where the gear may be left for more than one night in the water. The opposite changes may explain the low number of empty stomachs recorded in January (29%,  $N=304$ ).

The increased proportion of Arctic char with full stomachs in lakes with introduced *Mysis* and *Pallasea* in early spring suggests an increased feeding activity during the frozen season. In experiments with sockeye salmon (*Oncorhynchus nerka*), Brett and Higgs (1970) suggested that metabolic compensation in low temperature was greater in amount of food consumed than the rate of digestion. The increased growth rate recorded in Arctic char after the *Mysis* introduction (Fürst et al. 1978) may in fact be the result of a combined effect of improved feeding conditions during winter and a declining population size. The fact that otoliths from Arctic char caught in lake reservoirs with introduced new fish food organisms tend to be more difficult to age supports such a conclusion.

### Seasonal variation in levels of Cs-137 in Arctic char and brown trout

The brown trout in the present area demonstrated almost always higher levels of Cs-137 than the Arctic char ( $Cs-137_{(trout)} = 872 + 1.08 \times Cs-137_{(char)}$ ,  $r^2 = 0.52$ ,  $P < 0.001$ ,  $N = 50$  observations of pairs of arithmetic means). Similar differences between char and trout were recorded in Norway and the English Lake District (e.g. Ugedal and Blakar 1990, Elliott et al. 1993). Ugedal et al. (1988), and later Forseth et al. (1991), estimated brown trout in a Norwegian lake to consume 4.5 and 6.2 times more food per day than the sympatric Arctic char in June and July 1987, a major difference in food uptake which was concluded to partly explain the differences in levels of Cs-137 among the two species. In September and October, the difference in uptake rate between the species was only 1.3-1.5. No rations were presented for the winter and spring seasons. The significance of the quality of the diet in explaining differences in cesium levels between species should, however, not be neglected. In fact, Hammar et al. (1991a) demonstrated that the diet of Arctic char and brown trout in oligotrophic lakes with similar chemical characteristics were more important for the explanation of the differences in levels of Cs-137 in individual fish than size, age and growth rate. The concentration of Cs-137 in the dominating prey organism and the size or turn-over rate of the lake were the major components explaining the levels of Cs-137 in Arctic char and brown trout from different lakes.

Seasonal variations in levels of Cs-137 illustrate seasonal variations in the rates of accumulation and excretion, two processes which increase with increasing temperature in fish (Bryan et al. 1966, Häsänen et al. 1967, 1968, Ugedal et al. 1992). Trends of increasing concentrations of Cs-137 in low temperature conditions should thus occur in fish during periods of reduced growth, extensive intake of contaminated food, and/or during periods of combined active feeding and prolonged biological half-life. The observed regularity of accumulation of radiocesium during winter and the opposite process during summer in Arctic char, with significant accumulation in

brown trout only observed during summer periods, indicates major seasonal species differences. These are known to involve 1) differences in feeding rate and prey choice, 2) changed growth rates and/or other physiological processes at low water temperature, and 3) reproduction costs and compensatory feeding after spawning. However, other explanations such as 4) differences in catching methods may also add to the observed process.

When assimilation exceeds respiration in winter the levels of Cs-137 are expected to increase, and vice versa. Decreases in water (and body) temperatures generally lead to decreased rates of various physiological processes. The ecological half-life of Cs-137 has furthermore been shown to increase with decreasing temperature (e.g. Häsänen et al. 1968). In experimental conditions with brown trout fed with a solution of Cs-134, Ugedal et al. (1992) estimated the elimination rate in four different size groups of trout in four different water temperatures. Besides increasing with decreasing water temperature, the biological half-life decreased with decreasing body weight. Using their equation,

$$T_b = 290 \times W^{0.176} \times e^{-0.106 t}$$

where  $W$  is weight in grams, and  $t$  is temperature in °C, the biological half-life of an average 250 g brown trout may vary between 190 and 620 days in Lake Blåsjön, assuming the temperature range to be ca 2-13°C. Since the ecological half-life of Cs-137 in Arctic char apparently is longer in summer as well as in winter (Hammar et al. 1991a), because of the char's general choice of habitats with lower temperature than brown trout, these circumstances may in fact cause an increase in Cs-137 levels, which may partly explain a seasonal difference in the accumulation/excretion rates of char and trout. It would, however, not be restricted specifically to Arctic char in Lakes Ankarvattnet and Blåsjön. Apparently, a lower winter elimination rate of Cs-137 is associated with an extensive intake of Cs-137.

The spawning process of both species, which peaks in September-October (dwarfed char may spawn until January), represents a period of major loss of stored energy. Females loose considerable quantities of energy in producing eggs, and



both sexes suffer from major losses of energy during the physical spawning act itself. In small-sized landlocked Arctic char the gonad weight of a mature female may reach about 15% of full body weight (Hammar unpubl.). Analyses of the amount of Cs-137 in roe from mature Arctic char collected in Lake Blåsjön in October 1986 and October 1990 revealed the levels to be 23-45% and 20-28%, respectively, of the burden measured in pooled muscle tissue and roe. Parallel measurements of eggs from brown trout collected in August 1986 in a Norwegian lake gave 45%, which was three times higher than in the trout milt (Brittain 1988). The spawning process thus could cause a minor decline in the total burden of Cs-137 in late fall of both Arctic char and brown trout. However, also an increase in levels of Cs-137 in muscle tissue could be expected in both species due to a concentration factor. Obviously such a pattern of temporary changing levels in late fall should not be restricted specifically to Arctic char in Lakes Ankarvattnet and Blåsjön.

After spawning in September-October, Arctic char and brown trout both need to refill their energy reserves for the winter. A major loss of energy in late fall may jeopardize the survival of a spent fish during the coming winter. Brown trout and in particular Arctic char, however, are known to continue feeding actively in late fall. In fact, char eggs seem to be a major food resource for Arctic char during October-November (Figs. 5 and 8). In contrast to brown trout, the stomach analyses of Arctic char in Lake Ankarvattnet and Blåsjön clearly showed that Arctic char actively feed all winter, and that *Gammarus lacustris*, *Mysis relicta* and *Pallasea quadrispinosa* dominated the diet under the ice. The levels of Cs-137 in these three crustaceans were previously pointed out as very high, and populations feeding on these prey demonstrated the highest levels of Cs-137. Consequently winter consumption of heavily contaminated benthos must be a significant explanation to the significant winter rise of Cs-137 in Arctic char. This was also the conclusion by Lønvik and Koksvik (1990), who recorded a seasonal spike in May-June 1987 to ca 150% of the radiocesium levels

of salmonid fish measured during February-August 1987 in the Norwegian Lake Vekteren, just west of Lake Ankarvattnet. The lake, in which *Mysis relicta* has been introduced, contains Arctic char and brown trout, although the species were not kept separate in the analyses. Lønvik and Koksvik (1990) assumed the diet of benthic organisms (feeding on detritus) to explain the increase during April-May, and the diet of zooplankton to explain the decreasing levels during June-August. In contrast, Brittain (1988) and Forseth et al. (1991) recorded consistently declining levels of Cs-137 in brown trout and Arctic char during the winters 1986/87, 1987/88 and 1988/89 in two other Norwegian lakes. Although *Gammarus* was recorded, only brown trout is present in the first lake, and neither char nor trout seem to feed on *Gammarus* in the second lake, thus illustrating the significance of reduced winter activity in trout and the lack of benthic winter prey to char for depletion of Cs-137 levels under the ice.

Southern, warmer lakes may confirm these assumptions. In Tennessee, USA, Kolehmainen (1972) described seasonal fluctuations of Cs-137 in bluegill (*Lepomis macrochirus*) and six other sympatric species, demonstrating higher levels in winter and lower levels in summer. The variation in the fish tissue was parallel with the variation in levels of Cs-137 in the stomach content. In a later paper Kolehmainen (1974) extended the relationship to include temperature dependent processes such as growth and feeding rate as well. In southern Sweden, Carlsson and Lidén (1978) described seasonal variations in winter active northern pike (*Esox lucius*). The reappearing peaks of Cs-137 in early spring were explained by reduced excretion because of low temperatures.

The sampling differences with gillnetting in summer and angling from the ice in winter may add a factor contributing to differences in the composition of fish analyzed. Whereas gillnetting selects for large sized and fast growing fish, "bobbing" from the ice tends to select for smaller and more slow growing individuals (Filipsson and Svärdson 1976). In Lake Ankarvattnet the difference in median length values of Arctic char

collected with gillnets and by angling was highly significant (Mann-Whitney,  $P < 0.001$ ,  $N = 63 + 98$ ). Higher concentrations of Cs-137 have typically been recorded in Arctic char with slow growth (Hannerz 1968, Hammar et al. 1991a), and was recently also demonstrated for  $\Sigma$ PCB and p, p-DDE (dominating DDT-compound) in Lake Blåsjön (Hammar et al. 1993). An increased proportion of slow growing char in winter catches may thus cause the seasonal variation described. However, among the Arctic char collected in Lake Blåsjön during winter and spring, dwarfs and normal char were kept separate, and both groups demonstrated the same seasonal increase.

### Seasonal consumption rates in Arctic char and brown trout

Consumption and hence growth at low temperatures depend heavily on the rate of gastric evacuation (Windell 1978). To what extent does winter consumption in Arctic char contribute to its annual energy budget? Evans (1988a) concluded the amount of Cs-137 accumulated in fish to depend on 1) feeding intensity, 2) the concentration of Cs-137 in the diet, and 3) the assimilation efficiency for intestinal absorption. At least 90%, probably more, of the cesium levels in fish originate from the food (for references see Evans 1988b). Hewett and Jefferies (1976, 1978) estimated 57% of the digested Cs-137 to be allocated in muscle tissue of brown trout when fed experimentally with polychaetes of known radioactivity. The amount of radiocesium digested from the food, however, varies with the prey (Kevern 1966, Pentreath and Jefferies 1971, Kolehmainen 1972, 1974). Fish feeding on zooplankton or fish have been concluded to absorb Cs-137 more completely from its prey than fish feeding on benthic invertebrates.

With the presented information on diel net accumulation of Cs-137 during periods of increasing levels in Arctic char and brown trout, the retention rate calculated using the biological half-life at different temperatures according to the equation derived for brown trout by Ugedal et al. (1992), the assessed mean concentrations of Cs-137 in major prey organisms for the vari-

ous periods, and assuming the levels of Cs-137 in the muscle to comprise 40-80% uptake rate from the prey, the daily food rations may be calculated. In order to reduce the complications of seasonal shifts in food organisms, Lake Blåsjön has been used as an example, with Arctic char feeding on zooplankton during July-October and *Mysis* during November-June, whereas brown trout feed on *Mysis* diet all year around (Table 5). The estimated daily rations depend very much on the accuracy of the estimates of concentrations of Cs-137 in the various prey, with underestimated cesium levels in *Mysis* and zooplankton producing overestimated rations in the fish. Dilution of Cs-137 due to growth has been ignored.

A seasonal curve of estimated daily rations of brown trout matches closely the temperature curve of Lake Blåsjön. With an absorption level ranging between 70-80% the summer values of 2-6 mg (dw) per g (ww) fish in June-September are in good agreement with those presented by Elliott (1975b) as daily maintenance rations for trout, although much lower than the figures presented by Forseth et al. (1991). These were more comparable with the daily maximum rations presented for brown trout by Elliott (1975a). The June-September rations calculated for Arctic char, however, seem to represent even higher levels of absorption than 80% when adjusted to figures such as 1.1-2.7 mg (dw) per g (ww) fish presented by Amundsen and Klemetsen (1988) and Forseth et al. (1991). A similar disagreement with the parameters affecting the uptake of Cs-137 in Arctic char was recorded by Nordlinder et al. (1993) when modelling the turnover of radiocesium in these two salmonid species in Lakes Ankarvatnet and Storsjøuten. Also in that study the equation for the biological half-life of brown trout derived by Ugedal et al. (1992) was used for Arctic char. Assuming a high level (80%) of absorption of Cs-137 in Arctic char, the winter rations of 0.5-1.9 mg (dw) per g (ww) fish support the findings of an extensive feeding activity also under the ice (Table 5).

In spite of the winter temperature the Arctic char is able to feed actively all winter, given there is suitable winter prey resources, such as larger

Table 5. Estimated daily accumulation and retention rates of Cs-137, and daily rations of food for 100 g brown trout and Arctic char collected in Lake Blåsjön 1986-90. Diel net accumulation of Cs-137 was calculated from a series of periods of increasing levels in Arctic char and brown trout. Elimination rates for different mean temperatures were estimated using the biological half-life equation derived for brown trout by Ugedal et al. (1992). The figures given assume the fish have eaten *Mysis relicta* and/or zooplankton with given concentrations of Cs-137, and that the levels of Cs-137 assimilation ranges between 40 and 80%. The seasonal change in food organisms is simplified with Arctic char feeding on zooplankton during July-October, and *Mysis* during November-June, whereas the brown trout is feeding on *Mysis* at all occasions.

Period	Mean Temp. °C	Accum Bq.day <sup>-1</sup> (dw)	T <sub>1/2b</sub> days	Excret. Bq.day <sup>-1</sup> (dw)	Mysis Bq.kg <sup>-1</sup> (dw)	Zooplankton Bq.kg <sup>-1</sup> (dw)	Daily rations at different absorption levels				
							40% (mg (dw)	50% (dw)	60% (dw)	70% (ww)	80% (ww)
<b>Brown trout</b>											
860406-860725	5.7	25.1	357	3.2	40,000	-	3.9	3.1	2.6	2.2	1.9
860725-860815	12.0	49.4	183	9.0	30,000	-	10.7	8.6	7.1	6.1	5.4
860815-870315	4.4	-2.3	409	3.4	20,900	-	0.3	0.2	0.2	0.2	0.1
870315-870813	5.1	-1.7	380	3.4	5,800	-	1.5	1.2	1.0	0.9	0.8
870813-871016	9.4	11.8	118	6.9	11,700	-	8.7	7.0	5.8	5.0	4.4
<b>Arctic char</b>											
860426-860817	6.6	3.1	324	0.6	30,000	10,000	1.0	0.8	0.7	0.6	0.5
860817-861018	9.4	5.7	241	1.5	-	7,000	5.7	4.5	3.8	3.2	2.8
861018-870115	2.9	4.7	480	1.2	16,000	-	2.0	1.6	1.3	1.2	1.0
870115-870315	1.5	1.4	556	1.1	15,000	-	0.9	0.7	0.6	0.5	0.5
870315-870419	1.6	7.9	551	1.4	13,500	-	3.8	3.0	2.5	2.2	1.9
870419-870802	5.1	1.3	380	2.2	5,800	-	3.3	2.6	2.2	1.9	1.6
870922-880412	3.0	3.5	475	1.9	11,700	-	2.5	2.0	1.7	1.4	1.3
891016-891230	3.1	0.3	470	0.8	3,900	-	1.6	1.3	1.1	0.9	0.8
891230-900208	1.6	1.3	551	0.8	3,900	-	2.9	2.3	1.9	1.7	1.4
900208-900417	1.5	1.1	556	0.8	3,900	-	2.7	2.2	1.8	1.6	1.4

insect larvae, mollusks, *Gammarus lacustris*, *Mysis relicta* and *Pallasea quadrispinosa*. This raises a series of questions. Does an increased abundance of littoral or sub-littoral macro-invertebrates such as *Mysis* and *Pallasea* in time escalate the feeding activity also of brown trout in Lake Blåsjön and other reservoirs, and thus maintains the trout's dominant character in conflict situations also under the ice. Metabolic compensation for low seasonal temperatures has been discussed for fish by various authors (e.g. Brett and Higgs 1970, Windell 1978, Kolok 1991). With more time spent in deeper and warmer water in winter, brown trout may in fact adapt to the restored food resources in reservoirs with introduced new fish food organisms also in winter.

The length of the winter period differs between years and thus influences the dynamics of inter-specific resource partitioning. Do brown trout affect the abundance or diversity of available littoral macro-benthos for winter feeding Arctic char, or the opposite? Will an extended summer period postpone or restrict the success of winter feeding Arctic char in the littoral habitat, and will an extended winter period with a prolonged winter exploitation of macro-benthos by Arctic char postpone or decrease the chances for an early feeding start of sympatric brown trout in spring. These scenarios no doubt depend on the temperature preferences expressed by different taxa of Arctic char, brown trout and other species involved. The environmental conditions in some

Atlantic regions with sympatric char-trout populations, such as the Hebrides, Orkneys, Shetlands and the Scottish Highlands, where the lakes face short and mild winters and thus rarely freeze, seem to offer the Arctic char populations an extremely vulnerable sanctuary from further interspecific interactions.

## Conclusions

From information on feeding behavior during the cold winter months and data demonstrating increased rates of accumulation of radionuclides via contaminated benthic food organisms, it is possible to conclude that Arctic char in Lakes Ankarvattnet and Blåsjön feed actively all year around and switch from pelagic zooplankton between July and October to littoral macro-benthos during November-June. In the natural Lake Ankarvattnet the littoral amphipod *Gammarus lacustris* dominates the winter diet of Arctic char, whereas the introduced *Mysis relicta* and *Pallasea quadrispinosa* dominate the winter diet of Arctic char in the regulated Lake Blåsjön. Brown trout which exploit these littoral food resources only during May-November appear to be quiescent or in torpor between December and April when the temperature is below 2°C. The littoral prey choice may be taken as evidence of a seasonal shift in the direction and dominance of the interspecific interactions between Arctic char and brown trout. The absence of diet data for trout in winter is a weakness. However, the decrease in Cs-137 levels during the winter strongly suggests that practically no feeding occurs.

The factors promoting interactive segregation between Arctic char and brown trout in sympatric conditions seem to be reduced to a minimum in winter, probably because of the low temperature. If its major competitor suffers from reduced activity when temperature is low, the Arctic char will enjoy a temporary seasonal release during winter, which allows it to survive closer to its southern species border, which is defined by interspecific interactions. The winter period thus provides a refuge necessary for long term survival of the char in situations close to competitive exclusion. In conclusion, the realized niche of the Arctic char expands seasonally and ap-

proaches the fundamental niche border. Regular niche shifts no doubt contribute to the maintenance of these interactive processes rather than leading to extreme specialization of either or both species. Apparently the ecological conditions have favored opportunism, dietary flexibility and a potential of the Arctic char species complex to exploit a relatively wide food niche during past glaciations and interglaciations.

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Appendix 1. Concentrations of Cs-137, Cs-134 and K-40 (Bq.kg<sup>-1</sup> ww) in brown trout and Arctic char collected in Lake Ankarvattnet during July 1986 to August 1990. Samples analyzed individually (Ind) or as pooled (Pool) fish have been identified. (From Hammar et al. 1991a.)

Date	N	Length (mm)	Weight (g)	Cs-137	SD	Cs-134	K-40	I/P
<b>Brown trout</b>								
1986.07.01				2,783				Pool
1986.07.28	6			5,739				Pool
1986.10.06	14	314	300	6,967	1,362	3,230	137	Ind
1987.08.06	3	271	215	5,344	-	1,903	182	Pool
1987.09.26	11	302	281	4,548	-	1,564	153	Pool
1988.06				4,720				Pool
1988.08.17	15	280	246	2,340	595	583	194	Ind
1989.08.15	15	300	294	1,966	1,300	325	171	Ind
1988.09				1,590				Pool
1989.10.05	10	266	206	1,149	500	202	190	Ind
1990.06.19	10	319	332	1,360	486	208	180	Ind
1990.08.20	10	265	197	918	338	124	165	Ind
<b>Arctic char</b>								
1986.07				3,432				Pool
1986.10.06	15	282	210	2,183	350	1,013	140	Ind
1986.12				2,260				Pool
1987.03				3,070				Pool
1987.04.23	25	195	66	3,863	-	1,604	161	Pool
1987.08.06	14	284	214	2,734	-	1,031	174	Pool
1987.10.01	13	323	431	2,146	-	722	195	Pool
1988.04.06	15	217	82	3,281	957	913	159	Ind
1988.04				1,660				Pool
1988.09				880				Pool
1988.08.17	15	308	285	1,517	432	348	161	Ind
1988.09				880				Pool
1989.04				1,270				Pool
1989.08.15	15	301	247	917	220	155	179	Ind
1989.10.05	10	266	166	946	306	170	149	Ind
1989.12.15	7	245	121	1,664	1,431	279	196	Ind
1990.02.28	6	229	91	1,032	122	156	196	Ind
1990.04.24	10	252	118	1,088	305	166	155	Ind
1990.05.31	5	356	397	-	-	-	-	-
1990.06.24	6	314	282	1,523	1,079	222	168	Ind
1990.08.16	10	272	194	824	382	112	148	Ind

Appendix 2. Concentrations of Cs-137, Cs-134 and K-40 (Bq.kg<sup>-1</sup> ww) in brown trout, normal and dwarfed Arctic char collected in Lake Blåsjön during October 1985 to April 1991. Samples analyzed individually (Ind) or as pooled (Pool) fish have been identified. (From Hammar et al. 1991a.)

Date	N	Length (mm)	Weight (g)	Cs-137	SD	Cs-134	K-40	I/P
<b>Brown trout</b>								
1985.10.12	4	291	-	27	7	0	102	Ind
1986.07.09	5			3,000				Pool
1986.07				6,070				Pool
1986.07.25	7			4,989				Pool
1986.08				7,270				Pool
1986.08				7,981				Pool
1987.03				6,190				Pool
1987.08.13	13	246	151	5,609	-	2,159	128	Pool
1987.10.16	12	289	275	7,264	-	2,437	212	Pool
1988.08.18	15	276	231	3,553	1,414	920	165	Ind
1989.08.15	15	325	345	3,375	991	595	166	Ind
1989.10.17	10	297	269	2,363	513	428	165	Ind
1990.06.04	10	302	268	2,297	376	334	146	Ind
1990.10.21	10	290	255	1,800	310	233	140	Ind
<b>Normal Arctic char</b>								
1985.10.12	3	258	-	21	17	1	135	Ind
1986.07.05	6			1,500				Pool
1986.08.17				881				Pool
1986.10				1,410				Pool
1986.10				1,720				Pool
1986.10.19	15	232	129	1,580	234	735	134	Ind
1987.01				2,500				Pool
1987.03				4,180				Pool
1987.03				2,680				Pool
1987.04.19	3	238	123	3,291	768	1,328	138	Ind
1987.08.02	15	241	128	3,595	1,112	1,263	168	Ind
1987.09				2,200				Pool
1987.09.22	12	248	162	2,417	352	815	150	Ind
1988.04.12	17	218	96	3,960	1,117	1,154	240	Ind
1988.04				3,480				Pool
1988.08.18	15	260	194	2,668	1,121	676	165	Ind
1988.09				1,330				Pool
1989.03				2,580				Pool
1989.03				3,420				Pool
1989.08.22	15	287	264	2,094	873	371	162	Ind
1989.10.16	10	259	168	1,670	286	301	175	Ind
1989.12.30	10	262	170	1,718	305	256	262	Ind
1990.02.08	7	255	158	1,832	1,012	279	165	Ind
1990.04.17	9	244	119	1,998	598	274	151	Ind
1990.05.29	15	292	245	-	-	-	-	-
1990.06.04	10	300	240	1,514	507	217	129	Ind
1990.06				1,300				Pool
1990.06				1,620				Pool
1990.10.21	10	266	176	904	273	118	138	Ind
1991.04				1,470				Pool

## Appendix 2. cont.

Date	N	Length (mm)	Weight (g)	Cs-137	SD	Cs-134	K-40	I/P
<b>Dwarfed Arctic char</b>								
1986.10.18	15	197	72	1,430	735	652	147	Ind
1987.04.19	3	196	64	3,450	520	1,390	230	Ind
1987.08.02	1	212	80	5,982	-	1,887	142	Ind
1987.09.22	3	238	149	3,007	1,257	1,049	196	Ind
1988.08.18	4	185	55	6,128	692	1,572	178	Ind
1989.10.16	11	195	70	3,085	1,221	549	199	Ind
1989.12.30	12	198	66	3,394	859	539	188	Ind
1990.02.08	13	208	81	3,384	1,039	494	248	Ind
1990.04.17	12	187	53	3,337	927	495	186	Ind
1990.05.29	18	212	83	-	-	-	-	-
1990.06.05	12	214	73	2,553	922	367	199	Ind
1990.10.21	12	206	76	2,024	1,436	263	162	Ind

# The Pattern of Atlantic Salmon Smolt Migration in the Varzuga River (White Sea Basin)

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## Abstract

The rate of Atlantic salmon smolt migration in the Varzuga River was correlated with the water temperature and water level. These correlations had a 2-3-day lag in warm and moderate years and a 5-day lag in cold years. The migration took place through the last three weeks of June and very beginning of July, starting at 8.5-13 °C, peaking at temperatures >13 °C, and usually terminating at 15-22 °C. In the years when the period of increase of temperature is long or when there are short periods of decreased water temperature, the migratory run is highly compressed. The migration rate may be affected by insolation, through water temperature. The peak migration by day usually occurs between 6 and 8 p.m., but in cold years between 4 and 6 p.m. Short-term increases of water level may inhibit the smolt run.

Keywords: Atlantic salmon, smolt migration, physical triggers, lag.

## Introduction

There are a lot of investigations concerning the problems of Atlantic salmon smolt migration in different rivers (Hansen and Jonsson 1985, Hansen et al. 1989, Hesthagen and Garnås 1986, Hvidsten and Hansen 1989, Jonsson and Ruud-Hansen 1985, Thorpe et al. 1994, Thorpe and Moor, 1996, Thorpe and Morgan 1978, Österdahl 1969). Of special interest is the study of migration in the northern rivers (Jensen et al. 1989, 1997, Erkinaro et al. 1997). In order to get a more complete view of the life of the Atlantic salmon we need to know more about those populations.

In the North of Russia (rivers of the White and Barents Sea Basins) the migration of Atlantic salmon (*Salmo salar* L.) smolts, takes place in the spring/summer period. Its duration is usually no longer than a month, with 3-7 days of burst-

like run (Melnikova 1970, Bakshtanskiy et al. 1976, Yermolayev 1980, 1988, Kazakov and Protopopov 1988, Kuzmin and Smirnov 1982). Specific geographical and hydrological characters seem to be responsible for the special pattern of environmental control, for the timing of smolting, and for the rate of smolt migration (number of migrants per unit time). Water flow and water temperature stimulate downstream fish migration and they appear to trigger the behaviour in the rivers (Österdahl 1969, Solomon 1978, Jonsson 1991, Saksgård et al. 1992). Migration occurs in spring during rising temperatures at different times of year in different river systems, and at differing latitudes (Thorpe et al. 1994). Since any Atlantic salmon population is unique in these characteristics, its migration pattern should be investigated separately in every river (Ruggles 1980).

The goal of the present paper was to give a comprehensive picture of the smolt run, and the influence of environmental conditions on it, in the Varzuga River. These environmental conditions may vary yearly and, to a greater extent, daily. The Atlantic salmon stock of the Varzuga River is the largest in the North of Russia and it is largely responsible for the success of the fisheries in this region (Kazakov et al. 1992). In addition, it differs in some of its biological aspects from the populations of the adjacent rivers (Draganov et al. 1990, Kazakov 1994).

## Materials and methods

The 254 km Varzuga River (67°N) flows from the Kola Peninsula into the White Sea (Fig. 1), with no significant impact. The most part of the river is situated beyond the North Pole Area. The greater part of its main channel and tributaries represents suitable habitats for Atlantic salmon. The total area of the salmon spawning grounds in the river is 12.5 km<sup>2</sup> (Kazakov et al. 1992), and during the last decades the spawning stock has remained stable at about 60,000-70,000 individuals.

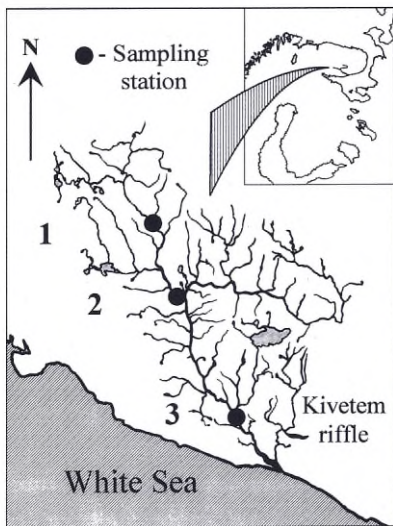


Fig. 1. The map of the Varzuga River and study area. The location of the fish counting fence is marked with a square figure. 1, 2, 3 - the stations of underwater investigation.

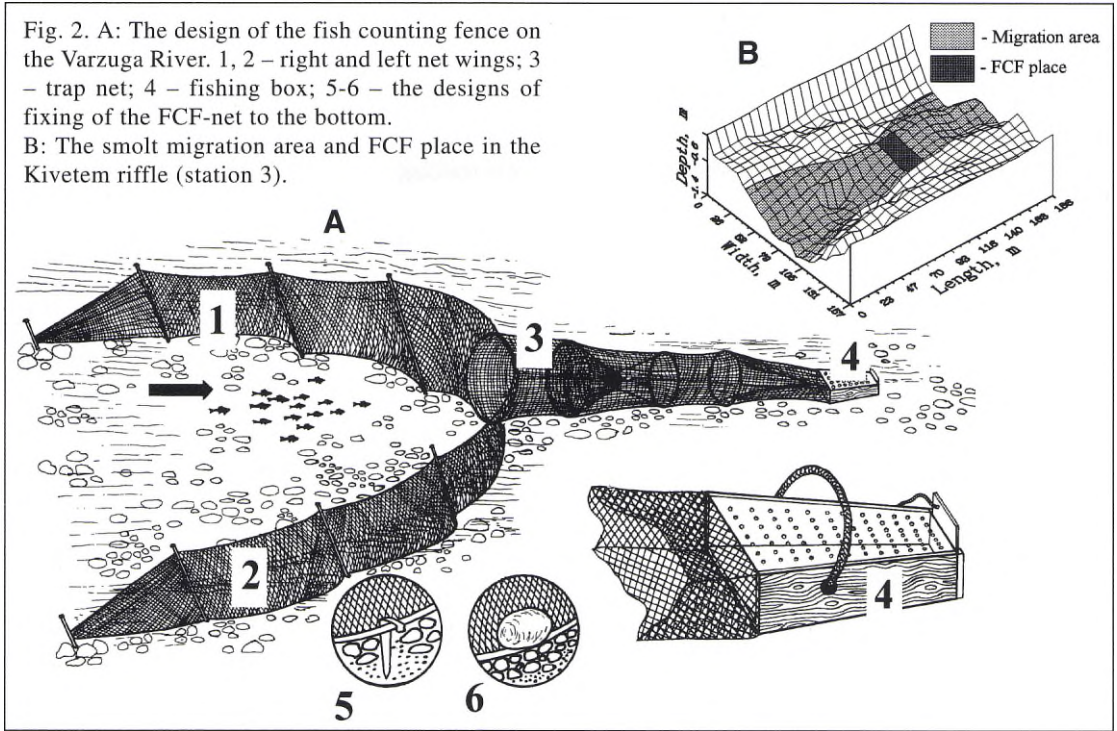
The ages of the smolts in the Varzuga River are found to be 2+ – 4+. The most part (70-85%) are 3+ smolts. There are 17 fish species (families: Salmonidae, Thymalidae, Esoxidae, Cyprinidae, Gadidae, Gasterosteidae, Percidae, Pleuronectidae and Petromysonidae) inhabiting the River Varzuga.

The present survey was carried out in 1988-1990 and in 1993-1995. The runs were estimated at a fish counting fence (FCF) on the Kivetem riffle, where the channel was 185 m wide, at about 28 km upstream from the mouth (Fig. 1, station 3). The fence with its wings was 8-12 m long, with a mesh size of 10 mm knot-to-knot. It was fixed at a depth of 0.3-0.7 m in the narrow place of smolt migration way, being moved off the bank during low water to retain this depth (Fig. 2A, B). The efficiency of FCF is stable yearly and equal to 5-7%.

The migrants were recorded throughout the day: they were removed every two hours, counted and returned to the river downstream of the fence. Insolation rate, temperature and water level were recorded at the same time. Hydrometeorological data were obtained from the observation post in the village of Varzuga. The insolation rate was not recorded in 1993 because of technical problems. The data were analysed statistically by means of time series analysis, dispersion and regression analysis, using BMDP. From these analyses a range of environmental factors was determined at which the number of migrating smolts was within 5% of the maximum value (Larher 1976).

## Results

From underwater investigations made at three separate stations on the Varzuga River (Fig. 1) it was found that smolt migration began simultaneously throughout the river. The beginning of migration coincided with the end of the spring flood and with the rapid rise in water temperature, water got heated from 4-5 °C to 12-13 °C during 1-2 weeks of June. At a critical value of 8.5-13 °C the parr and smolts appeared from winter shelters at the same time when single smolts



migrated. Then shoals formed, which promoted the more rapid migration to the river mouth. From the time series analysis the rate of migration indices were correlated with the water temperature in a given year, with a two-day lag (Table 1). In other words, the abundance of migrants decreased one or two days after the water temperature had risen.

Over the 6-year period the duration of the smolt migration in the Varzuga River averaged 21 days (range 16-26 days). The earliest occurred on 4 June in 1989, and the latest – on 17 June in 1990. The last smolts arrived between 29 June to 5 July. An annual average of 3,172 smolts was trapped (range 1,002 (1993) – 4,490 (1994)) (Table 2). About 70% were taken between 17-24 June, which coincided with water temperature increase from 13 to 17 °C (Fig. 3). In 3 of the 6 years, the maximal catch was observed on 23 June.

Table 1. Cross-correlations (CCR) between the number of smolts and various environmental variables (water temperature, water level). Cross-correlation for a negative lag indicates a relationship between the fish catch and environmental parameters that number of days earlier. Only significant correlations are presented.

Year	CCR			
	Water temperature		Water level	
	lag	r	lag	r
1988	-2	0.85	-2	0.62
1989	-3	0.56	-3	0.46
1990	-5	0.50	-5	0.60
1993	0	0.52		–
1994		–		–
1995	-4	0.64	-3	0.72

Table 2. Migration conditions: degree-day sums from May 1 to the start of migration, and from 1 May to the end of migration; and number of smolts trapped in different years.

Parameter	Year					
	1988	1989	1990	1993	1994	1995
Start	16.06	04.06	17.06	14.06	13.06	08.06
Degree-day sum	261.3	264.9	300.8	248.6	225.5	236.4
Termination	05.07	29.06	02.07	03.07	03.07	28.06
Degree-day sum	620.6	695.5	527.8	494.2	526.7	631.2
Duration, days	20	26	16	20	21	21
Number of smolts	3880	2892	3449	1002	4490	3320

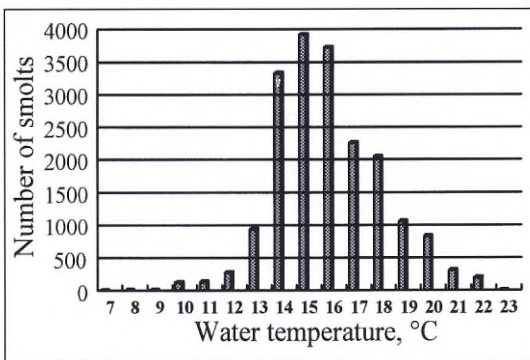


Fig. 3. The total number of smolt descending at different water temperatures in the Varzuga River during 1988-90 and 1993-95 ( $n=19,033$ ).

### Water temperature and the migration pattern

In 1988 the smolt migration occurred at gradually increasing water temperatures, reaching 10 °C in mid-June and 13 °C after 16 June. Over the next 5 days, 65% of the total run were taken. Thereafter and until the beginning of July, the migration rate decreased gradually (Fig. 4a). The last smolt was trapped on 5 July at a water temperature of 20 °C. The peak run of smolts occurred on 17 June at 13.7 °C, when 948 were trapped, comprising 24% of all the migrants for that year.

In 1989 (Fig. 4b) the first migrants occurred at 12-13 °C and 40% of that year catch were trapped between 6-11 June when the temperature was increasing from 14 to 18 °C. From 12-13 June the temperature fell to 11.5 °C and the catch fell to nearly zero. Subsequently, it became warm

again, and the catch increased until 19 June (16.5 °C) and then declined to the end of June (22 °C). Most smolts (79%) were trapped at temperatures from 14-19 °C: the peak catch was on 8 June (15%) at 18.2 °C.

In 1990 the first small catch was taken at 8.5 °C on 16 June (Fig. 4c), but then from 22-27 June, after the temperature reached 13 °C, 89% of the years catch were taken, 37% on 23 June at 16.2 °C. Thereafter the catch declined to zero by 2 July.

In 1993 the temperature increased rapidly to 14.5 °C on 5 June, but then gradually fell to 7.1 °C on 13 June. No smolts were trapped until 14 June (8.7 °C), later on the temperature was steadily rising to 14 °C on 18 June. It was stabilised at that level until 27 June. During this interval 90% of that year catch were taken (Fig. 4d) The burst-like migration occurred from 20-25 June, when 75% of smolts were taken at a mean water temperature of 14.6 °C. As in 1992, maximum catch (32%) was taken on 23 June at 14.6 °C.

In 1994 the first 10-20 smolts were caught between 13-18 June at temperatures between 13 and 14 °C (Fig. 4e). The catch grew markedly on 19-20 June (24%) at temperatures 13.5-14.0 °C, but then fell to almost nothing on 21 June when the temperature slightly lowered to 13 °C. Then 61% of the year catch was taken over 22-23 June at 14.0-14.7 °C, before the fall to zero on 24 June when the temperature fell to 12.3 °C. As the temperature rose again after 25 June the catch also increased by 27 June and then declined to zero by early July. In 1994 the majority (87%) were caught between 19 and 23 June at temperatures from 13.5-14.7 °C.

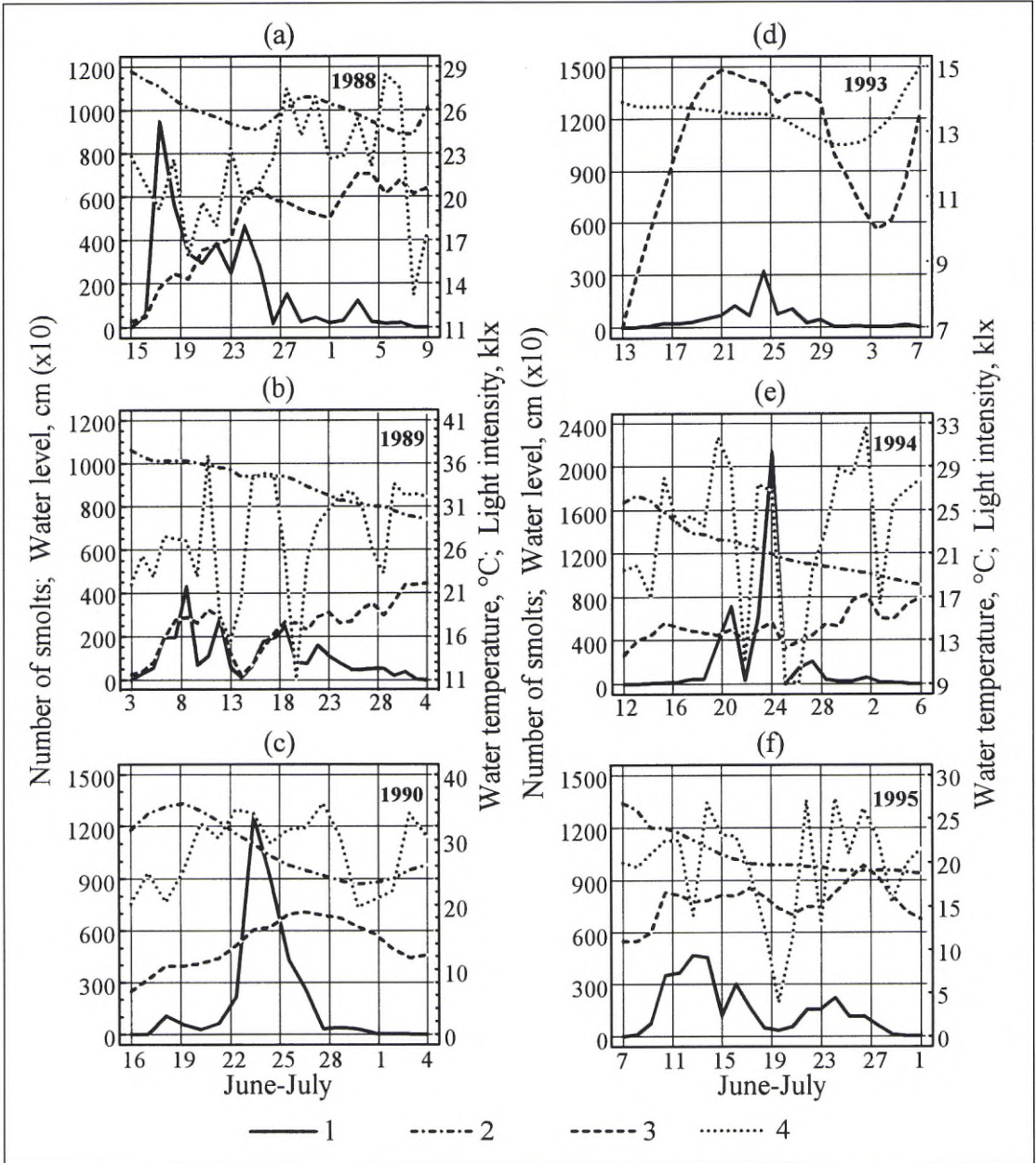


Fig. 4 a-f. The influence of water temperature, insolation rate, and water level on the smolt migration pattern in Atlantic salmon in the Varzuga River (1980-90 and 1993-95). Labels: 1 – number of smolts; 2 – water level, cm; 3 – water temperature, °C; 4 – light intensity, klx.

The year of 1995 was similar to 1989 as for the environmental factors affecting the smolt migration (Fig. 4f and 4b). The trap catches started on 8 June after the water temperature had reached

11°C, and became heaviest over 10-13 June (50%), at temperatures reaching 16 °C. Thereafter the catches decreased relatively smoothly finishing by 29 June.



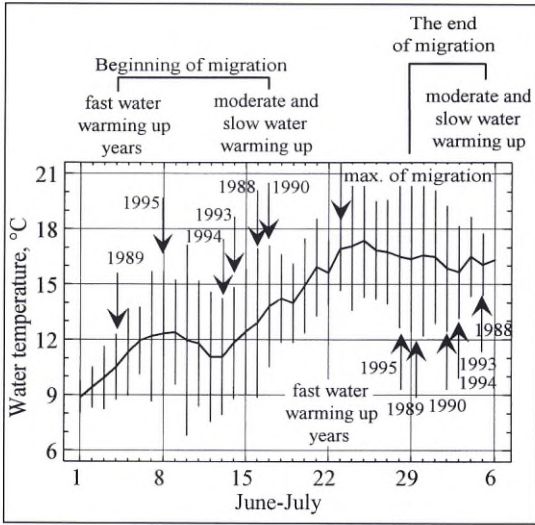


Fig. 5. The mean temperatures ( $\pm$ SD) during smolt migration in the Varzuga River (1988-90 and 1993-95).

The migration rate was correlated with the water temperature with a 2-4-days lag in 1988, 1989 and 1995. In 1990 there was a late cold spring and the lag increased to 5 days. The migration rate was correlated with the water temperature with no time lag in 1993 and there was no significant correlation in 1994 (Table 1).

We conclude that the water temperature has a stable tendency to warm up during the first week in June and then the smolt migration began in the fast water warming up in 1989 and 1995 (Fig. 5). Later on, from 9 to 12 June, the temperature usually decreased, which resulted in more intensive heating, to 11-16 °C, from 13 to 22-23 June. During this increase smolt migration began in 1988, 1990, 1993 and 1994, reaching the peak on 23 June. After 22-23 June the water temperature tended to stabilise and the smolt migration decreased.

Throughout the six years migration rate was not correlated with the very unstable insolation rate (Fig. 6).

### Water level and migration pattern

The dynamics of water level had some fluctuations but on the whole the smolt migration took place under a gradually lowering water level during the years of investigation (Fig. 4a-f). The mi-

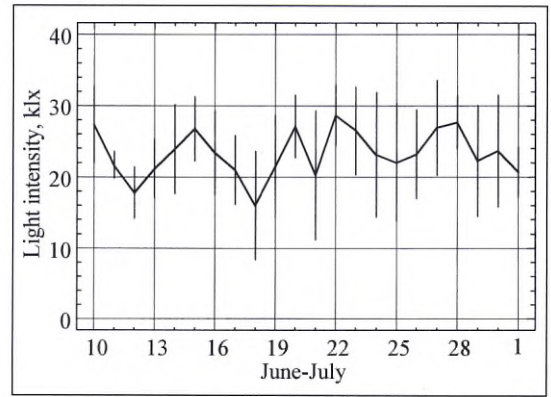


Fig. 6. The mean light intensities ( $\pm$ SD) near water surface during smolt migration in the Varzuga River.

gration rate values were correlated with the water level and lagged 2-3 days in 1988, 1989 and 1995 (Table 1). In 1990 the lag was 5 days, possibly due to unusually low temperatures. There were no significant correlations with water levels in 1993 and 1994.

During the whole period of investigation (Fig. 7) the water level decreased during the first week of June. Just at that moment the migration began in 1989 and 1995. Then the water level stabilised from 8 to 12 June and was falling steadily

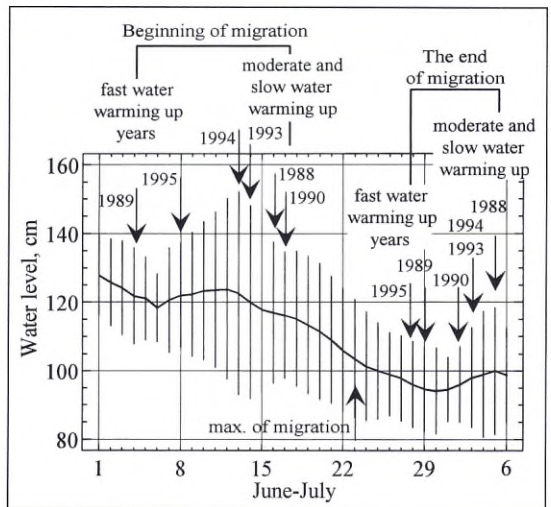


Fig. 7. The mean water levels ( $\pm$ SD) during smolt migration in the Varzuga River (1988-90 and 1993-95).

between 13 and 29 June. In moderate and slow water warm-up periods of 1988, 1990, 1993, 1994, the migration began on 13, 14, 16 and 17

June, respectively. After 29-30 June, the water level had increased due to rainfall, and the migration ceased.

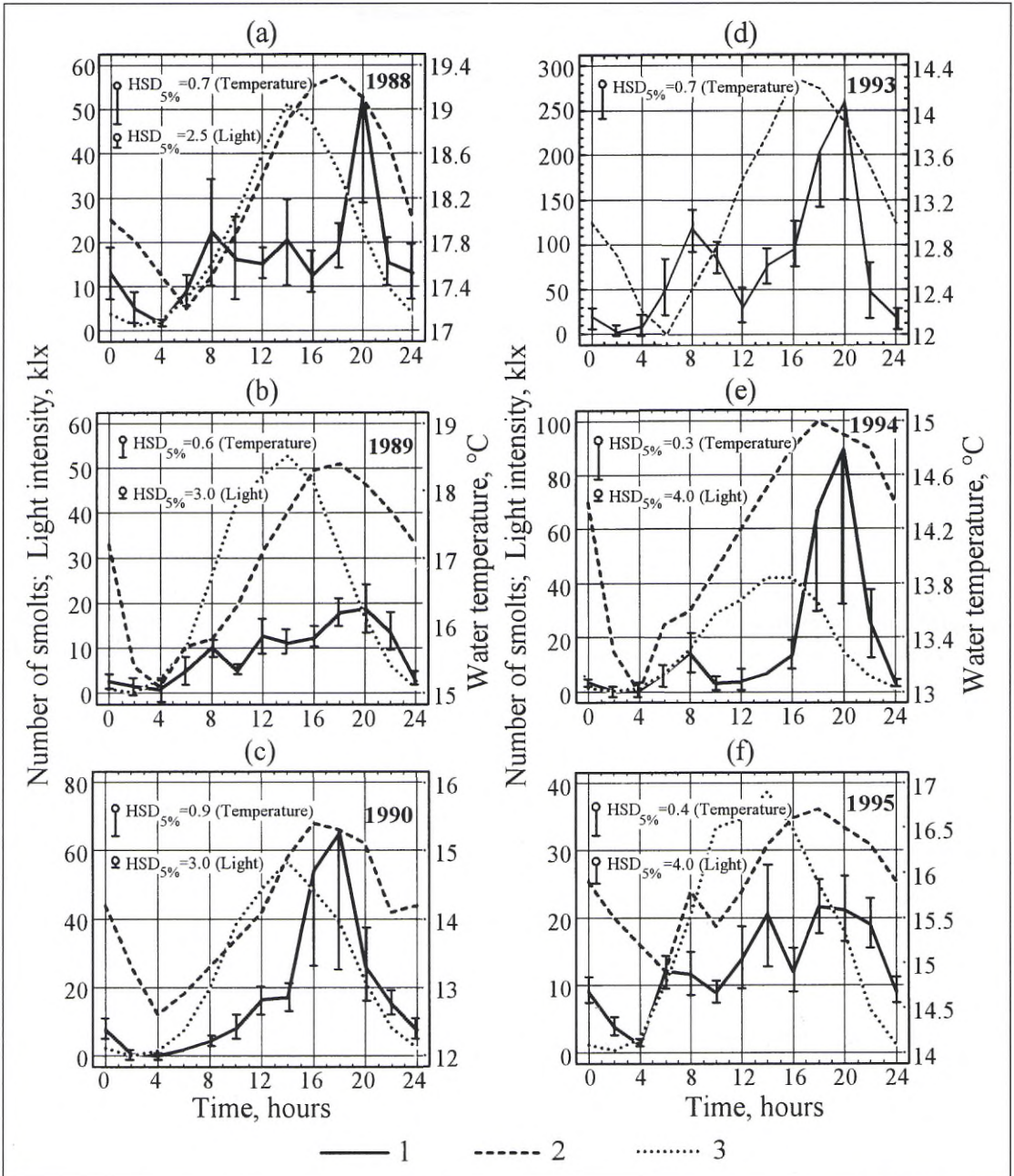


Fig. 8 a-f. The influence of insolation rate and water temperature on the daily smolt migration pattern (1988-90 and 1994-95). Labels: 1 – number of smolts; 2 – water temperature, °C; 3 – light intensity, klx.

Table 3. Cross-correlations (CCR) between daily number of smolts and daily values of insolation rate and water temperature. Cross-correlation for a negative lag indicates a relationship between the fish catch and environmental parameters that number of hours earlier. Only significant correlations are presented.

Year	CCR			
	Daily water temperature		Daily insolation rate	
	lag	<i>r</i>	lag	<i>r</i>
1988	0	0.50	–	–
1989	0	0.81	-2	0.60
1990		–	-2	0.75
1993	0	0.75	no data	
1994	0	0.64	-2	0.73
1995	0	0.73	-1	0.59

### Daily fluctuations in migration

The smolt migration usually peaked at 8 p.m., but there were lots of variation (Fig. 8a-f). In 1993 and 1994 there were two clear peaks, one in the morning and one in the evening and in 1995 there no clear peaks were found. The migration rate was well-correlated in time with the daily water temperature in all years and had 1-2 hour

lags behind insolation in 1989, 1990, 1994 and 1995 (Table 3). There was no significant correlation with the insolation rate in 1988.

### Factor areas of maximal migration

The data obtained during this research allowed to make regression equations (models) concerning the dependence of the smolt maximal migration rate on the environmental factors (Table 4 and 5). While making the regression equations with the inclusion of 95%-area of smolt maximal migration on "water temperature" – "water level" scale for the whole period of migration, and "water temperature" – "light intensity" scale for day migration, lags have been taken into consideration. The smolt maximal migration rate areas were found to be non-constant in size and about the axes (Fig. 9 and 10).

The time series analysis has shown that an increase in migration rate can have a prolonged, 2-5 days, response (lag) on the environmental impact. So, in 1988, the migration reached its maximum in 2 days after the water temperature raised up to 10-14 °C and the water level lowered from 117 to 112 cm; in 1989 – in 3 days, after it became 11-13 °C warm, the water level dropped

Table 4. Equations describing the influence of water temperature (*T*) and water level (*H*) on the smolt migration rate (*N*) in the Varzuga River. In 1993 and 1994 no reliable equations could be calculated.

Year	Equation	<i>R</i> <sup>2</sup>	SE
1988	$N = -23960.0 + 13159.08 * T - 1275.22 * T^2 + 50.90 * T^3 - 0.74 * T^4 - 468.79 * H + 1.78 * H^2 + 5.96 * H^3$	0.59	154.78
1989	$N = -32645.83 + 7970.37 * T - 766.62 * T^2 + 32.19 * T^3 - 0.50 * T^4 + 47.34 * H - 0.24 * H^2$	0.45	73.77
1990	$N = -60427.56 + 67.83 * T - 2.77 * T^2 + 1751.45 * H - 16.91 * H^2 + 0.05 * H^3$	0.78	163.14
1995	$N = 14024.77 - 1105.68 * T + 17.39 * T^2 - 100.37 * H + 0.13 * H^2 + 5.0 * T * H$	0.61	93.34

Table 5. Equations describing the influence of water temperature (*T*) and insolation rate (*E*) on the daily smolt migration rate (*ND*) in the Varzuga River. In 1993 no reliable equations could be calculated.

Year	Equation	<i>R</i> <sup>2</sup>	SE
1988	$ND = 420.72 - 54.75 * T + 1.77 * T^2 - 0.32 * E + 0.22 * E^2 - 0.01 * E^3 + 0.0001 * E^4$	0.50	9.42
1989	$ND = -863.31 + 108.84 * T - 3.42 * T^2 - 6.73 * E - 0.025 * E^2 + 0.47 * T * E$	0.74	3.14
1990	$ND = 181.32 - 24.33 * T + 0.81 * T^2 - 9.82 * E - 0.02 * E^2 + 0.77 * T * E$	0.71	11.36
1994	$ND = -11120.0 + 1659.71 * T - 61.89 * T^2 - 127.69 * E - 0.25 * E^2 + 9.56 * T * E$	0.88	10.10
1995	$ND = 2455.36 - 317.02 * T + 10.25 * T^2 + 3.44 * E - 0.018 * E^2 - 0.16 * T * E$	0.59	4.29

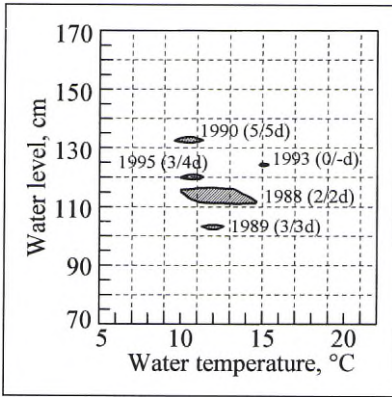


Fig. 9. Location of the Atlantic salmon smolt maximal migration in factor space: “water temperature” and “water level”. Corresponding lag values are given in brackets.

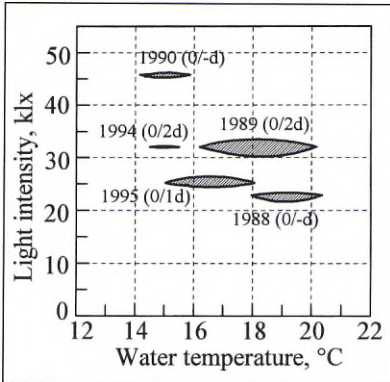


Fig. 10. Location of the Atlantic salmon smolt maximal migration in factor space: “water temperature” and “light intensity”. Corresponding lag values are given in brackets.

from 105 to 99 cm. In 1990, due to a prolonged and cool summer, the maximum values shifted towards lower temperatures (9.8-11.2 °C) at higher water level (130-135 cm). That year showed a 5-day maximum intensive migration lag. In 1995, the migration rate reached its maximum in 3-4 days after the water temperature had become warmer, from 10.0 to 11.2 °C and its level lowered from 122 to 118 cm.

As there was no adequate correlation detected between the migration rate and water level in 1993, we could not obtain a reliable regression

equation. Therefore, the areas of high migration rate were determined directly from experimental data. That year, the maximal migration rate fell on a small range of water temperatures from 14.0 to 15.0 °C, and on a stable water level of 125 cm. In 1994, the areas of maximal migration rate were impossible to define as reliable correlation between the migration rate and water temperature and water level was not found. The max. migration rate values were found to shift greatly towards the high values of water level (from 99 to 135 cm). The range of temperatures within the area of maxima was from 9.8 to 15.0 °C depending on the lag (Fig. 9).

The analysis of the location of maximal day migration rate values in «water temperature» and «light intensity» scales has shown that insolation values varied much less than those of water temperature (Fig. 10). The growth of migration rate, or its decrease during the day lagged 1-2 hs behind insolation, and strictly followed fluctuations in temperature.

The broadest ranges of temperature, covered with maximum-migration areas were derived for 1988, 1989, and 1995 years of observation. In 1988 the maximum-migration area covered the range of water temperatures from 18.0 to 20.1 °C, at the insolation rate of 21-24 klx, in 1989 – 16.2-20.1 °C and 30-34 klx, in 1995 – 15.2-18.0 °C and 23-27 klx. In 1990 and 1994 the maximum-migration areas appeared to be shifted towards the lower temperatures – from 14.0 to 16.0 °C and from 14.5 to 15.5 °C, respectively, – and at rather high insolation rate in 1990 (44-46 klx), and the lower one in 1994 (32-33 klx). For four from five years of the observation period, the derived maximum-migration areas covered the temperature range from 14.0 to 20.0 °C, and the insolation-rate range from 21 to 34 klx. In 1990, rather a cold year, the maximum-migration field appeared to be shifted towards the higher values of the insolation rate – 44-46 klx.

## Discussion

In Karelia, Arkhangelsk Region and the Kola Peninsula, the migration of Atlantic salmon smolts from the rivers usually starts late in May

and proceeds through June, sometimes it terminates in the very beginning of July. According to some publications, it is triggered after the water temperature exceeds some definite value, i.e. 7-8 °C – the Salatsa river, the Baltic Sea basin; 10.2-14.3 °C – the Porja River, the White Sea basin; 7.9-17.6 °C – the Soyana River, the White Sea basin; 10.0-12.0 °C – the Schuya River, the Onega Lake basin. But the smolt migration generally peaks at water temperatures exceeding 12 °C (Mitans 1968, 1975, Yakovenko 1974, Bakshtanskiy et al. 1976, Yermolayev 1980). Start of migration depends on the latitude. Smolt descent begins at temperature 3-5 °C and ceases at 10-12 °C in the Scottish, English (51-57°N), and Norwegian (63°N) rivers (Thorpe et al. 1994, Jensen et al. 1997). Smolts migrate at temperature 8-10 °C in the rivers of Sweden (62°N), Norway (59-70°N), Finland (70°N) (Österdahl 1969, Hansen and Jonsson 1985, Thorpe et al. 1994, Jensen et al. 1997, Erkinaro et al. 1997).

In our study the migration started when the water temperatures were between 8.5 and 13.0 °C. At these temperatures the smolts appeared on the line river bed from their winter shelters (under stones) and were distributed actively throughout the riffles of the Varzuga River, so smolt migration began simultaneously throughout the river. The migration rate strongly increased at water temperatures >13 °C, so that the main run occurred between 14-15 °C. In the Varzuga River the migration did not start until the very beginning of June. This river has a lot of shallow riffles 0.4-0.9 m deep and a low lake/river ratio (<3%). Riffles can work as quite an effective heat exchanger at the water/atmosphere margin (Smirnov 1979), quickly providing an equilibrium between water and air temperatures. We suggest that this could cause the smolt migration peaks in late June in the Varzuga River.

Some authors have suggested that Atlantic salmon smolt migration is triggered not by some temperature threshold but by the rate of the water warming during the spring/summer period (Bakshtanskiy et al. 1976, Nesterov 1985, Nesterov et al. 1985). If the total sum of degree-days to the beginning of migration is taken as an index of this rate of warming, then we found no

evidence that this was related to the start of migration, or to its duration (Table 2) – a 20-day migration period could have occurred over 359 degree-days (1988), or over 245.6 degree-days (1993). However, Jonsson and Ruud-Hansen (1985) studied the migration in the Imsa River (59°N) and concluded that the migration was not triggered by water temperature or a specific number of degree-days during spring.

A short-term decrease in water temperature may inhibit migration as noted in Latvian rivers by Mitans (1967). This happened in the Varzuga River when the water temperature dropped below 13 °C, but the migration resumed quite intensively when the temperature rose again above 13 °C, but lasted for only 2-3 days.

Migration rate in the Varzuga was not correlated with insolation rates but was affected by them indirectly, *via* the water temperature. The changes in temperature in the Varzuga as in other Russian Arctic rivers depend greatly on the insolation (in its turn being dependent on cloud conditions), and on the duration of Arctic (cold) and Atlantic (warm) windy periods.

As the water temperature grew over 13 °C, the migration rate was likely to peak. Further temperature increases did not significantly affect migrant numbers as most smolts had already migrated. We suggest that when migration was interrupted by a short-term fall in temperature a large number of fishes smolted simultaneously and migrated together as soon as the temperature grew again above 13 °C. Then the trap took up to 500 smolts per hour. It seems likely that short-term falls in temperature intensified the whole migration process to 2-5 days with the peaks in the evening. If during an increase the water temperature levels out, this does not make the migration period longer but changes its pattern. The water temperature correlated with the migration rate with a having lag of about 2-5 days (depending on cold and warm years). Thus so, the fall in water temperature usually promoted migration 2-5 days later. The same correlation but with lower lag was found for the Teno River in Finland (Erkinaro et al. 1997). The underwater investigation has shown that the smolts aggregated in the areas where they met the temp-

erature fall. Then the subsequent temperature increase promoted the run of a larger number of migrants. In warmer years (1988-89), the temperature falls were weak and were rather short-time, so the migration lag (the compression effect) was 2-3 days long. In colder years, as in the long cold spring of 1990, the migration process was interrupted, and the compression effect grew to 5 days.

It is noteworthy that in the Arctic rivers the migration usually takes place during the day when water temperatures exceed 12 °C (Yakovenko 1977, Bakshanskiy et al. 1980, this paper). In contrast, in the Baltic rivers Atlantic salmon smolts migrate mostly at night, though during the peak period they may migrate during the day also (Mitans 1975). In the Schuya River (Lake Onega basin), closer to the Arctic than the Baltic rivers, salmon smolts migrate mostly at night (Yermolayev 1980). In Scotland, England (51-57°N) and in central Norway (63°N) the smolt migration takes place mostly at night (Thorpe et al. 1994, Thorpe and Moore 1996, Jensen et al. 1997) and at more northerly rivers in Sweden, Norway and Finland it occurs mostly at temperatures 8-12 °C (Jensen et al. 1997, Erkinaro et al. 1997). The authors suppose that at temperatures >13.6 °C the migration becomes progressively more diurnal. In the Varzuga River there is no smolt migration at temperatures <8.5-12 °C and the whole migration is diurnal. But in the River Alta located in the northern part of Norway (70°N) smolt descent occurred in the day and in the night (Jensen et al. 1997).

The insolation rate and water temperature were strongly correlated with the smolt migration rate throughout 24 hours. The water temperature simultaneously influences the daily smolt migration, but the insolation rate has a 1-2 hours lag. There were several regular diel increases and decreases in the migration rate curve. With the use of the dispersion analysis, the main peaks in the daily migration were found to occur in the evening at 18:00-20:00 but in the cold 1990, the daily peak occurred two hours earlier, at 16:00-18:00. This was probably due to a slight warming up during the day, and a rapid cooling after 18:00.

In the Varzuga River the smolt migration starts with the end of the spring flood (May-early June). By this time, the river drains snow-melt water from the marshes which occupies a significant part of its basin. They release river water slowly, so that the level and flow gradually decreases. This, together with the gradually increasing water temperature, creates favourable conditions for the smolt migration. But a short period of rain with accompanying cloudiness and reduced insolation rate can lower the water temperature and retard the smolt migration. Strong increase in the water level and accompanying shift in climatic conditions is likely to stop the migration, which happened in 1990 and 1994. This disagreed with other reports where heavy rainfall and increasing water level intensified the migration (Mitans 1968, 1975, Jakovenko 1974, Bakshanskiy et al. 1976, Erkinaro et al. 1997). It was also pointed out that smolt descent was initiated by the increase in spring flood (Hesthagen and Garnås 1986).

Underwater observations and experimental FCF have shown that the migration of individual smolts starts simultaneously at all riffles. But the shoal formation begins first at lower riffles where the smolts amount is larger, and later goes on at higher riffles. Social behavior of individual smolts might be an important trigger ensuring a coordinated migration (Jensen et al. 1997). In some days, this process takes place at most riffles, and then one can observe a "peak" of smolt migration in shoals in the "upper-lower riffle" direction. This took from 4, in 1995, to 6 days in 1989 and 1993 (Fig. 11). However, smolts from upstream riffles seem to initiate the descent of smolts further downstream (Hvidsten et al. 1995). Most productive riffles and rolls are located at a 130-km area, from the Polisarka tributary (the channel width is 15-20 m) to the Kivetem riffle (the channel width is 180-200 m) where the FCF were installed. The smolt migration rate in the river does not exceed 3-4 km per hour, and the time of active migration was no longer than 10 hours a day. Therefore, the smolts have to overcome the distance of 30-40 km a day. Accounting that longer time, a third plus, is needed for

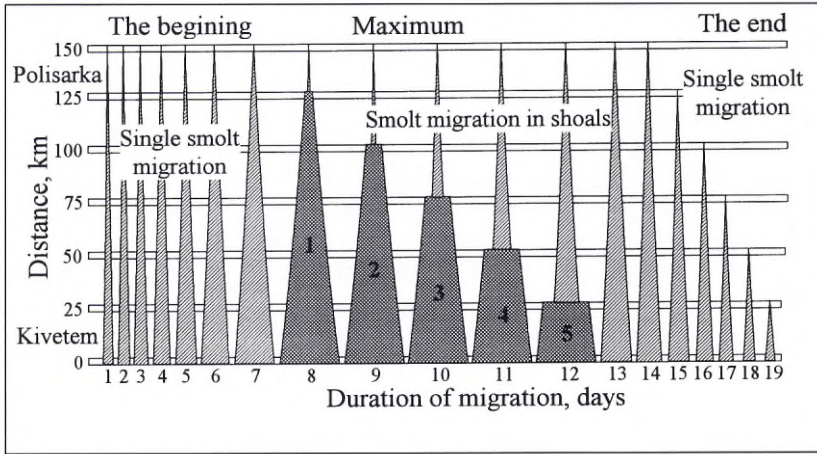


Fig. 11. Scheme of smolt migration in the Varzuga River.

the shoal to get over the riffles, the factual rate could be higher than 20-30 km a day under favorable conditions.

Consequently, the smolt shoals cross the distance from upper to lower riffles for 5 days, and on the fifth day the migration becomes maximal at the Kivetem riffle. Later, it becomes less intensive and the process ceases first at upper, lower-size, riffles. Prolonged migration dates are likely to be connected with uneven ripening of presmolts. But 40-89% of smolts migrates during a 4-7 day peak.

It is not clear by now why the migration in Arctic rivers takes place during only the day. It may be connected with anti-predator behaviour of smolts (Bakshtanskiy et al. 1976, 1983, Jensen et al. 1997) and protection from pike ensured by silver color (Thorpe et al. 1994). Probably such kind of behaviour is typical for smolts in small rivers with a lot of pikes and burbot. At white night period predators can feed active by during 24-hour period in smolt migration areas. But in the Varzuga River smolt migration area and habitat area of predators are not overlapped. Thus, predators do not influence significantly the migration behaviour of smolts in this river. From the other point of view diurnal migration is the advantage for sight-feeding (Thorpe et al. 1994). We believe that with increase of latitude the complex influence of environmental factors (water discharge, light intensity, water temperature,

moon phases and others) decreases and the temperature becomes the main trigger of smolt descent. It is known that smolts move in the night when temperature is lower than 8 °C and in the day at higher temperatures (Fraser et al. 1993).

The results of model studies show that the temperature scale during the beginning of migration fell on the temperature scale during the maximal intensity smolt migration in 1989, 1990 and 1995; they were calculated with regard to the lag (Fig. 12). In a warm year, the migration peak can be expected in 2 days after its beginning, in a moderately warm year – in 3 days, and in a cold year – already in 5 days. It is important that temperature and water level remained more or less stable; sharp fluctuations occurred due to heavy

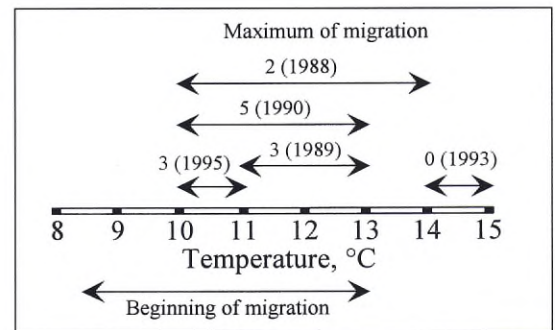


Fig. 12. Temperature ranges of the migration beginning (experimental data) and the migration maximum (model data) in the Varzuga River.

rains in 1993 which led to a shift in migration maximal values.

In conclusion it may be said, that the presented study is a result of 6-year investigation of mechanisms, regulating the rate of smolt migration in Atlantic salmon, its dependence on the effect of the set of environmental factors, and the pattern of control, set by these factors upon the migration rate. Using the methods of multicomponent statistics with some elements of modelling, we managed to clear up some aspects of the effect, produced by the habitat factors on the migration process.

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# Sea Water Temperatures at Atlantic Salmon Smolt Entrance

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## Abstract

Analysis of timing of Atlantic salmon, *Salmo salar*, smolt migration in five Norwegian rivers revealed delayed descent with increasing latitude. The time of smolt entrance into the sea was four to six weeks earlier in the season for the southern rivers than for northern rivers included in the present study. The results show a close correlation with the sea water temperatures outside the rivers and the timing of smolt migration. Peak smolt migration in all the rivers studied takes place when sea water temperatures reach 8 °C in spring and early summer. There is normally no simple connection between river water temperatures and sea water temperatures in temperate areas. Salmon smolts in the river, therefore "do not know" the temperature and feeding conditions at sea when leaving the river. The present study shows that proximate factors such as water flow and water temperature in the rivers triggered smolt migration differently in the different salmon populations studied. The results suggest that timing of smolt migration is population-specific, and adapted to meet optimal osmotic and feeding conditions at sea outside the native river.

Keywords: descent, latitude, *Salmo salar*, smolt sea entrance.

## Introduction

Body morphology, number and size of eggs, individual growth rate, timing of different salmon stocks at return from the sea and homing precision have been shown to be heritable (Riddell et al. 1981, Heggberget et al. 1986, Saunders 1986, Refstie 1987, Hansen and Jonsson 1991). Atlantic salmon stock characteristics differ in most stages of their life histories (Thorpe 1989), but some threshold values seem to exist (Elson 1957). Salmon parr which reach 10 cm in the autumn are normally able to descend to the sea the following spring (Elson 1957). They leave the river within a short period in spring (Larsson 1977). Survival is reported to be very low for smolts leaving the river outside the normal smolt migration period for that river (Larsson 1977; Hansen and Jonsson 1989). Smolts arriving seawater are hypotonic compared to saline water and dehydration is prevented by osmoregulation.

Marine survival of salmon smolts is generally very low, and population fluctuations are driven by factors in both fresh water and in the marine environment (Thorne and Ames 1987, Friedland et al. 1993). The significance of river conditions and the marine environment during smolt migration and early postsmolt period for survival of wild salmon is poorly known. The present study, therefore aims to analyse the timing of smolt migration in relation to both river conditions (water flow and water temperature) and marine conditions (water temperature and feeding conditions) in the period of smolt migration.

## Methods

Timing of Atlantic salmon smolt descent was studied in the rivers Imsa, Orkla, Saltdalselva, Halselva and Altaelva, at latitudes 59-70°N, Norway (Fig. 1, Table 1). In the rivers Imsa and Halselva, the total smolt run was recorded by Wolf traps (Wolf, 1951). The traps were operated



Fig. 1. Map of the Norwegian coast indicating the locations of the Rivers Imsa, Orkla, Saltdalselva, Halselva and Altaelva. The position of the stations where sea water temperatures were recorded is also shown.

all year round. In the rivers Orkla, Saltdalselva and Alta, relative catches were achieved by using net traps during the smolt run (Tyler and Wright 1974). The date for smolt descent was defined as the day each year when 50% of the smolts had descended (Table 2). Numbers of years sampled varied from 6 to 20 years (Table 2). Since data for several years from each river

were available, we used the median value of 50% yearly cumulative descent to represent the date for smolt descent all years. The smolts were caught at different positions from the rivers' outlets and the sea, but the time the smolts spend from the trap to the sea is well within the annual variation of smolt descent and, therefore should not affect our conclusions.

Table 1. Location of the outlet of the rivers to the sea, distance from the smolt trap to the outlet of the river (km) and mean annual water discharge ( $\text{m}^3\text{s}^{-1}$ ).

River	Location	Trap position	Water discharge
Halselva	70° 3' N 22° 57' E	0.1	5
Altaelva	69° 58' N 23° 25' E	10	77
Saltdalselva	67° 6' N 15° 25' E	17	55
Orkla	63° 19' N 9° 50' E	41	64
Imsa	58° 55' N 5° 58' E	0.1	5

Table 2. Median date as well as earliest and latest date of 50% smolt descent in the rivers. Number of years studied in each river is also given.

River	Date of 50% descent			Number of years analysed
	Median	Earliest	Latest	
Halselva	21 Jun	13 Jun	30 Jun	9
Altaelva	25 Jun	17 Jun	11 Jul	7
Saltdalselva	5 Jun	23 May	19 Jun	6
Orkla	19 May	8 May	3 Jun	14
Imsa	15 May	7 May	25 May	20

Sea water temperatures were measured in the period 1936 through 1970 (Sætre 1973). The temperatures were recorded in the surface layer at 4 m depth by coastal liners along the Norwegian coast (Fig. 1). The temperatures are given as average water temperature for 10 day periods through the year. In total there are 22 different recording stations along the Norwegian coast (Sætre 1973). We selected the temperature station closest to the respective rivers to represent the temperature experienced by the smolts.

## Results

Salmon smolts descend Norwegian rivers later in northern compared to southern regions (Table 1 and 2). Time of smolt migration differed by about six weeks from Imsa (59°N) to Altaelva (70°N).

Water temperatures in the rivers studied during the period of smolt descent varied between 3 and 15 °C (Fig. 2). There was no correlation between river temperatures during smolt migration and latitude. The mean water temperature during

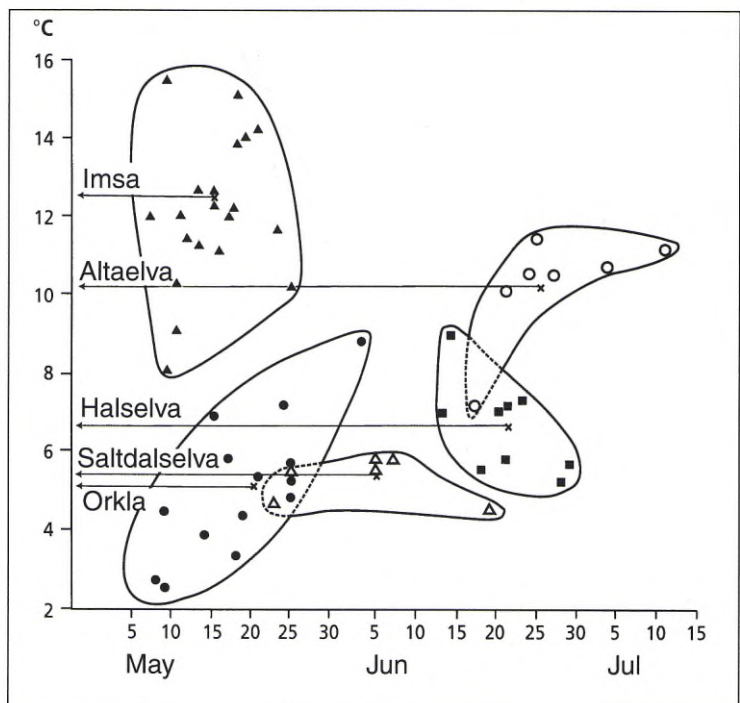


Fig. 2. Mean water temperature in the Rivers Imsa, Orkla, Saltdalselva, Halselva and Altaelva at the date of yearly median smolt migration.

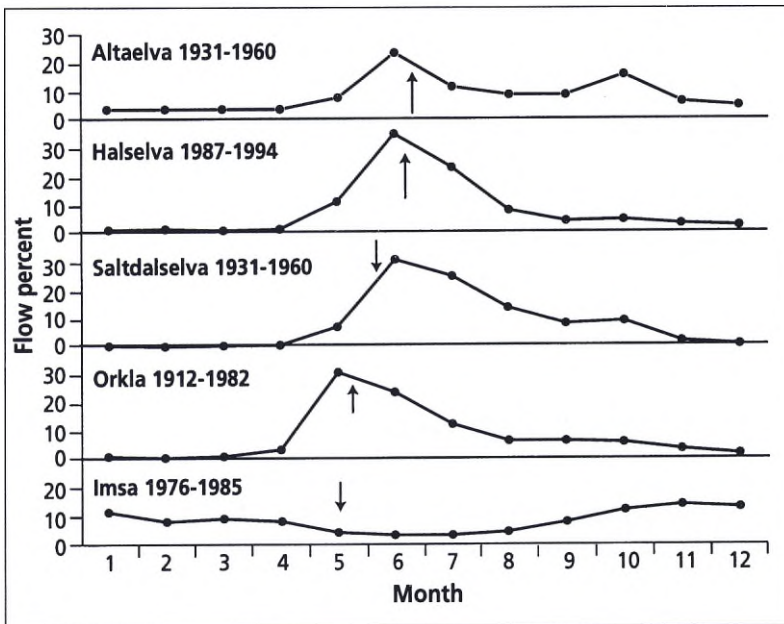


Fig. 3. Water discharge through the year in the rivers Imsa, Orkla, Saltdalselva, Halselva and Altaelva. Arrows indicate the date of median smolt migration.

smolt descent in the River Alta (70°N) was 11 °C, while the respective temperatures in the River Imsa (59°N) was 12 °C. Mean water temperature in the River Orkla (63°N) during smolt migration was 5 °C. These results show that water temperature trigger smolt migration differently in the different salmon populations studied.

Water flow during smolt migration also varied considerably in the rivers studied (Fig. 3). In the Rivers Imsa and Alta the spring peak runoff was finished or nearly finished at the time of smolt descent. Smolt descent in the Rivers Orkla, Saltdalselva and Halselva occurred during spring peak water discharge. As for water temperature, there was no correlation between variations in water flow and the latitude of the rivers studied, and the data show that smolt migration takes place at both high and low water flow, both before and after spring peak runoff.

The timing of smolt migration between years varied by about three weeks in the individual rivers studied (Fig. 4). The latitudinal variation in timing of smolt migration between rivers were similar in the years studied. There is a strong latitudinal correlation in sea water temperatures in May-July along the Norwegian coast. At the beginning of May, sea water temperatures off River

Imsa reach 8 °C, while sea water temperature off River Alta at that time is only about 3 °C. By the end of July, sea water temperatures outside Alta reach 8 °C. Thus, timing of the smolt migration in all rivers studied was closely matched to the time when sea water temperatures outside the respective rivers reach about 8 °C (Fig. 5).

## Discussion

The results from the present study show that the timing of smolt migration in 5 geographically widespread Atlantic salmon populations along the Norwegian coast is closely correlated to the seawater temperatures of about 8 °C in the coastal waters outside the rivers. The main physical factors in fresh water triggering smolt migration are water flow and water temperature. In the present study, smolts migrated under varying conditions concerning water flow and water temperature, indicating that the triggering system is population specific. However, there was a strong correlation between timing of smolt migration and sea water temperature, indicating that water temperatures in coastal areas outside the rivers represent the governing factor for timing of smolt migration.

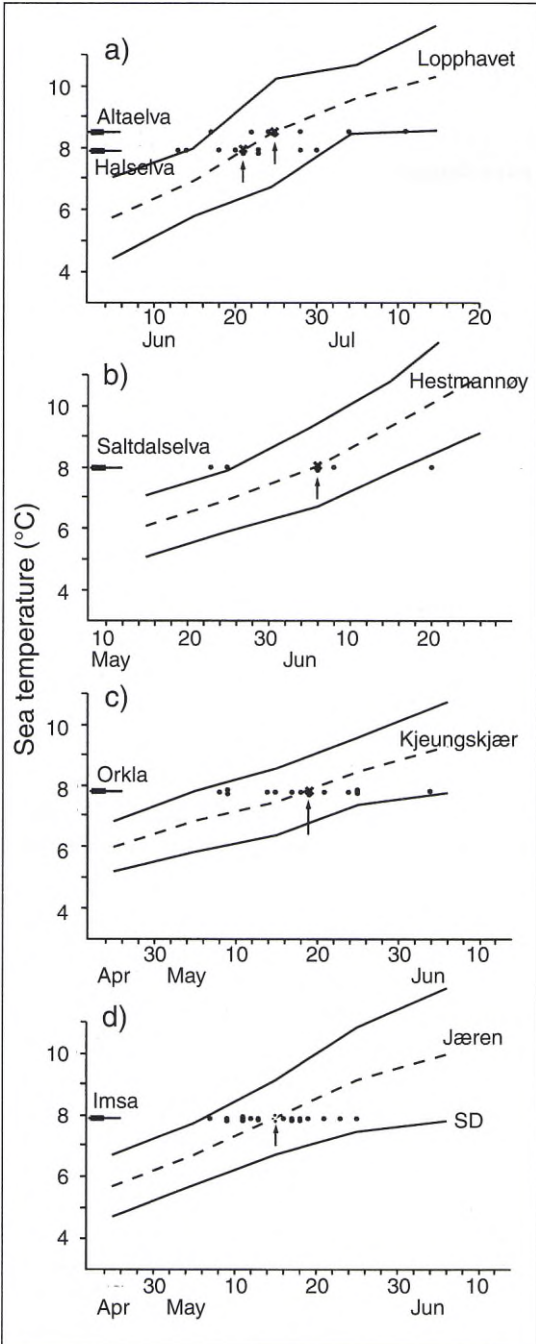


Fig. 4. Yearly date of 50 % cumulative descent of Atlantic salmon smolts in; **a)** Halselva (1987–95) and Altaelva (1989–95), **b)** Saltdalselva (1990–95), **c)** Orkla (1980–95, except for 1981 and 1989), **d)** Imsa (1976–95). Dotted lines represent mean sea water temperature and line is SD for the period 1936–70.

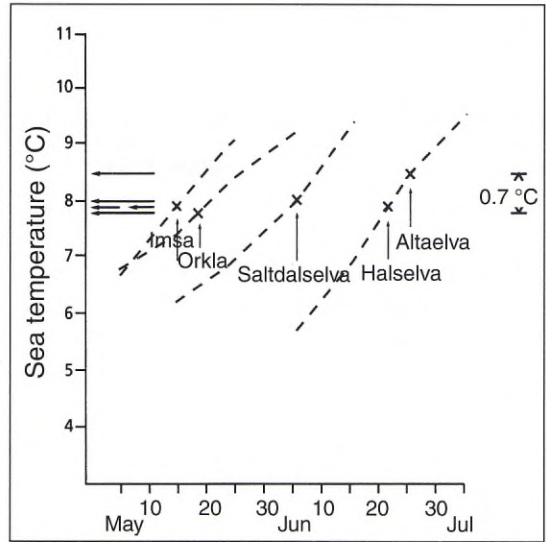


Fig. 5. Sea water temperature (dotted line) during smolt migration from the Rivers Imsa, Orkla, Saltdalselva and Altaelva. The sea temperature at the date of median smolt migration is indicated by a cross.

Several studies report timing of smolt migration from other rivers within the distributional area of Atlantic salmon. In River Lussa, Scotland (55°N) peak smolt migration occurs at the end of April and the beginning of May at seawater temperatures of 8 °C (Turell and Slesser 1992, Greenstreet et al. 1993). In salmon rivers situated in the north of Iceland (River Nepsa, 65 °N) the smolt migration is one month later compared to Icelandic southern rivers (Ulfarsa and Ellidar rivers at 64°N) (Antonsson et al. 1995). Arctic sea temperatures in the north, and warm Atlantic water in the south appear to explain this difference (Antonsson et al. 1995). Smolts entering sea hit seawater of about 8.5 (8.3–8.7) °C when migrating from these rivers located at 64 and 65°N in Iceland (Icelandic Metreologic Office, 1984–92). Emigration of smolts takes place later in the season in Eastern North American rivers than at similar latitudes in Europe. These differences are probably due to the cold Irminger Polar Current in North America and the warm Gulf Current in Europe. At 45°N (Big Salmon River and Miramichi River in North America) median date of (50% cumulative descent) smolt migration occur

1 June, which is about one month later than at the same latitude in Europe. At 60°N, (Ungava Bay) smolt migration takes place in July (Forsythe 1967, 1968, Power 1969, Jessop 1975), which is more than one month later than at similar latitudes in Europe.

Anadromy in salmonids increase individual fitness by utilising better feeding conditions in the sea than in fresh water (Gross, 1987). Early migrating smolts are subjected to predation pressure, osmotic stress and variable food conditions in the fjord and the sea. Late migrating smolts may miss the spring plankton bloom described for several marine waters (Parson and Lalli 1988). Predation in the estuary during the migration period can be extremely high (Larsson 1985, Hvidsten and Lund 1988, Greenstreet et al. 1993). Osmotic pressure will be a problem for fully developed smolts at sea water temperatures lower than 6-7 °C (Sigholdt and Finstad 1990). Small sized fish may be less well adapted to sea water than large fish (Hoar 1976), and osmotic stress is particularly pronounced at low sea temperatures (Knutsson and Grav 1976, Finstad et al. 1988). Favourable temperatures for feeding and growth of postsmolt salmon seem to be in the range of 4-12 °C (Saunders 1986), but little is known about temperature requirements during the early postsmolt phase of Atlantic salmon. Feeding conditions in the fjords may vary in quality and quantity from year to year (Levings et al. 1994, Hvidsten et al. 1995b).

Smolt migration from the rivers is regulated by ultimate and proximate triggers (Jonsson and Ruud-Hansen, 1985; Hvidsten et al. 1995a). The best known ultimate trigger is day length, which probably provides the date thresholds for start and finish of the smolt run (Wagner 1974, Hoar 1988). Proximate triggers might be water discharge, water temperature, precipitation, moon phases, cloudiness, wind, relative changes in the variables and combinations of several of these and other factors (Ruggles 1980). Water temperature and water flow levels differ considerably among salmon rivers. Particular values, variation and possible interactions among these physical parameters seem to act as triggers (Jonsson and Ruud-Hansen 1985). In addition, social interac-

tions among descending smolts may stimulate the migration of the smolts situated downstream (Hvidsten et al. 1995a).

Sea water and river temperatures often differ in the spring. Smolts obviously have no knowledge of the sea water temperatures when they initiate migration. The annual cycle of sea temperatures outside the respective rivers have been experienced by generations of salmon. Due to increased mortality for individuals of salmon entering sea at periods of suboptimal marine conditions, a strong selection pressure for the individuals entering sea at optimal temperatures is expected. Sea and river temperatures are increasing during smolt migration in the spring, but are independent, as discharge is regulated by snow-melt in most northern rivers.

Our results show that wild smolts in most years meet temperatures close to 8 °C when entering the sea outside the coast. In North American Arctic Atlantic salmon rivers, where temperatures in the estuaries are extremely low in spring and summer, the proportion of freshwater resident salmon increase. The low temperatures (<1.0 °C) in Ungava Bay, Canada, are probably responsible for the development of two anadromous life history strategies (Power 1969, Robitaille et al. 1984). One strategy involves migration only as far as the river estuary, with the salmon reaching only 30 cm adult body length, while the other involves migration farther out into the sea, with the salmon achieving "normal" body size. Another way of compensating problems connected to low sea water temperatures in the estuaries of northeastern Canadian rivers, is the increased body size of smolts leaving these rivers. The smolts in Ungava Bay are extremely large ( $\geq 18$  cm) (Power 1969, Lee and Power 1976) compared to the smolts along the Norwegian coast (11-15 cm) (Jensen and Johnsen 1986).

Passive and direct displacement of smolts out from the river and estuary are reported (Fried et al. 1978, McCleave 1978). Residency of smolts in the estuary are normally not found in Atlantic salmon, probably due to predation which might be very high (Piggins 1959, Hvidsten and Møkkelgjerd 1987, Kålås et al. 1993).

In Atlantic salmon, a population-specific system of proximate triggers for optimal timing of

smolt migration seems to have evolved over the last 10,000 years. The recent increase in farming of Atlantic salmon has resulted in high numbers of escapees in most of the Norwegian salmon rivers. Proportions of 50% farmed salmon in spawning stocks of native Atlantic salmon are frequently observed, and maximum proportions of farmed salmon exceed 80% (Gausen and Moen, 1991; Lund et al. 1996). Farmed salmon are ecologically and genetic different from wild salmon and have been selected for fast growth and late maturation. Immigration of high numbers of spawning farmed salmon into wild salmon populations may erode population-specific adaptations in wild salmon. If the timing of smolt migration becomes altered, we expect an increased mortality of Atlantic salmon from Norwegian rivers in the future.

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# The Effects of Temperature, Temperature Shift and Temperature Fluctuation on Daily Feed Intake, Growth and Proximate Composition of Underyearling Lake Inari Arctic Charr (*Salvelinus alpinus* (L.))

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## Abstract

Twelve groups of underyearling Arctic charr were acclimated to 11.0 °C, and following acclimation groups were then either held at 11 °C, or temperature was shifted upwards to 14.4 °C, to 17.7 °C, or to 14.3 °C with a daily temperature fluctuation of  $\pm 1$  °C. Fish were fed in excess during the experiment. The temperature shift *per se* did not seem to cause any time related changes in growth pattern because the growth-temperature curve had a similar form during the different periods following the temperature change. Consequently it is suggested that the charr may have recovered rapidly from the small single temperature changes leading to minimal influences on growth. Growth was most rapid amongst fish held at 14.4 °C, and thermal fluctuation ( $\pm 1$  °C) around 14.3 °C had little influence on either feed intake or growth. There were no statistically significant differences in proximate composition among groups held at different temperatures, but energy concentration was found to increase with increasing fish size and was negatively correlated with percentage moisture.

Keywords: Feed intake, growth, thermal regimes, Arctic charr

## Introduction

The influences of temperature on growth and metabolism of fish have been much studied (Fry 1971, Brett and Groves 1979, Cossins and Bowler 1987), and studies conducted on Arctic charr have examined thermal influences on feed intake, growth and respiration (Swift 1964, Holeton 1973, Jobling et al. 1993). The basic thermal relationships appear to be consistent with those of other salmonids, but the influence of supra-optimal temperatures on the feeding and growth of charr has not been investigated in detail (Jobling et al. 1993).

Most studies of thermal influences on feed intake and growth have been performed on fish held at constant temperatures, and the acute ef-

fects of temperature shifts, and responses to fluctuating temperatures, have been examined less thoroughly. Thermal changes influence both standard metabolic rate and routine activity, and when temperatures are shifted upwards metabolic rate may overshoot before returning to a lower value as the fish acclimate to the new conditions (Alderdice 1976, Cossins and Bowler 1987, Evans 1990). It is unclear how feed intake and growth may be influenced by such temperature changes, although this could have implications for aquaculture because temperatures are rarely constant in rearing units. Further, there is evidence that thermal fluctuations may affect feed intake and growth of fish (Hokanson et al. 1977, Spigarelli et al. 1982, Jobling 1997).

The current study was carried out to examine the influences of temperature shifts, and thermal fluctuations of small amplitude, on feed intake, growth and proximate composition of under-yearling Lake Inari Arctic charr held at temperatures assumed to be close to the thermal optimum for growth.

## Material and methods

Eyed eggs, obtained from broodstock of Lake Inari Arctic charr held at the Sarmijärvi Aquaculture Station (68.5°N, 28.4°E), were brought to Laukaa Aquaculture and Fisheries Research Station of Finnish Game and Fisheries Research Institute (FGFRI) (62.5°N, 25.5°E) in March 1995. Eggs were incubated, and following hatch the fish were reared, under standard culture conditions of FGFRI, at 4 m<sup>2</sup> tanks, at the density of

5,000 individuals per tank, at ambient water temperature (3–15 °C) and fed appropriate dry feeds by automatic feeders. On 5 September 1995 the fish ( $n=2,360$ ) for use in the experiment were transferred to the test facility, and 363 fish ( $>3$  g) were marked with PIT-tags (passive integrated transmitters), injected into the body cavity under tricaine sulphonate, MS-222 (0.15 g l<sup>-1</sup>) anaesthetisation. At this time ambient water temperature was approximately 11.0 °C.

The fish were divided among twelve plastic (67 l) tanks on 2 October 1995. Each tank contained both marked ( $n=24-40$ ) and unmarked ( $n=150-200$ ) fish. Average wet weight at this time was 6.2 g. Eight tanks held 180 and four tanks held 230 individuals. Water temperature in all tanks was held at 11.0 °C (with 95% CL of  $\pm 0.06$ ) for a further 22 days (Fig. 1).

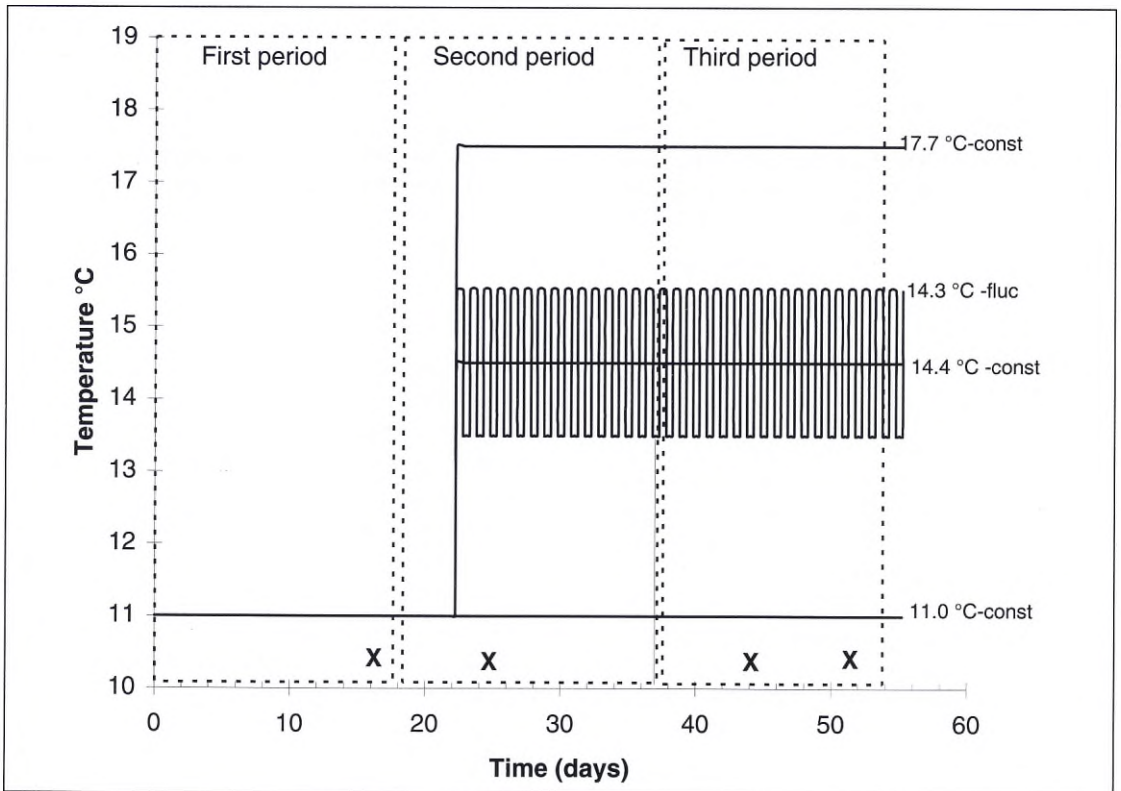


Fig. 1. Schematic illustration of the experimental design. The times of daily feed intake measurements are marked with X (duration two days). The fish were weighed on days 0, 17–18, 37–38 and 52–53.

After 22 days, constant temperature treatments were established at 11.0 °C (11.0 °C<sub>const</sub>), 14.4 °C (14.4 °C<sub>const</sub>) and 17.7 °C (17.7 °C<sub>const</sub>) (with 95% CL of ±0.06 °C). A fourth treatment group was subjected to a diel fluctuating temperature: a daily mean 14.3 °C with daily fluctuation of ±1 °C (14.3 °C<sub>fluc</sub>) (Fig. 1). Oxygen saturation was maintained over 65%, and water flow rates were adjusted to 1.5-3.0 l min<sup>-1</sup>. A 12L:12D photoperiod was established and was synchronized with temperature fluctuation in the 14.3 °C<sub>fluc</sub> treatment so that the high temperature phase (15.3-15.6 °C) was during daylight (06:00-18:00) and the cold temperature phase (13.2-13.5 °C) was during the dark part of the photoperiodic cycle (18:00-06:00).

The fish were fed with commercial salmon feed (Tess Nutra G, 2.0 mm: 44.5% protein, 25.7% lipid, 10.4% carbohydrate, 8.3% water and energy content 22.7 kJ g<sup>-1</sup>) in excess using belt feeders. Feeding started at 06:00, simultaneously with 'lights on', and lasted for four hours.

Feed intake was measured four times by X-radiography using an adaptation of the method first described by Talbot and Higgins (1983). The first measurement was made before the temperatures were changed (days 17-18) and the second measurement was made three to four days after temperatures were changed (days 25-26). The last two feed intake measurements were made 21-22 days after temperature change (days 44-45) and at the end of the experiment (days 52-53), respectively (Fig. 1).

Diets used for feed intake measurements were prepared from the standard feed by incorporation of X-ray dense ballotini (size 10, Jencons Ltd., Leighton Buzzard). Standard curves were determined for each portion of marked diet by X-raying known weights of marked feed and counting the numbers of ballotinis present. The coefficients of determination of regressions were 0.990-0.996 and the 95% confidence limits for accuracy of individual feed intake estimates were ±6%.

On days that feed intake was to be measured, the standard feed was replaced by feed containing ballotini and procedures for feed intake meas-

urements started immediately after termination of the daily feeding period. Samples of 30-60 fish per tank were anaesthetized (MS-222, 0.15 g l<sup>-1</sup>), X-rayed, (Siemens Nanodor X-ray machine; Agfa Structurix D7 film) and then weighed individually to the nearest 0.1 g. All fish were weighed before transfer to the experimental tanks (day=0) and 17-18, 37-38 and 52-53 days thereafter in order to study periodic changes in growth (Fig. 1).

Proximate body composition of fish was analyzed for samples (10 fish per sample) taken from each tank prior to the temperature change, and at the end of second and third periods. Proximate body composition analyses were performed as described earlier on Koskela et al. (1997).

## Data analysis

Specific growth rate ( $G$ ) was monitored for the PIT-tagged fish within each tank, and  $G$  was also calculated using the tank mean weight of unmarked individuals. Calculation was done similarly as Jobling 1983.  $G$ -estimates were corrected for size-effects as described by Saether et al. (1996). The responses to temperature change were examined by considering changes in size-adjusted  $G$ s during the different periods of the study:

$$G_{tc} = G_{2nd} - G_{1st} \text{ and} \\ G_{acc} = G_{3rd} - G_{2nd}$$

Where  $G_{1st}$ ,  $G_{2nd}$  and  $G_{3rd}$  are the size-adjusted growth rates of the fish during 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> periods, respectively (Fig. 1).  $G_{tc}$  indicated the direct impact of a temperature change on growth and  $G_{acc}$  indicated the periodical changes after temperature change.

The effects of temperature on  $G_{tc}$  and  $G_{acc}$  were tested using ANCOVA models. In the models temperature was a factor and the influence of tank was nested within temperature treatments. There were some small differences in fish size deviation between unmarked and marked fishes within a tank so studentized deviation from mean size within a tank was used as a covariate in both

growth and feed intake tests. This was calculated as:

$$W_d = (W_s - W_m) / sd_w$$

Where  $W_d$  is the studentized deviation of sampled fish from the tank mean,  $W_s$  is the wet weight of sampled fish,  $W_m$  is the tank mean weight and  $sd_w$  is the within tank standard deviation of wet weight.

The effect of temperature on daily feed intake was tested separately for each of the four measurement dates (Fig. 1) using an ANCOVA-model similar to that used for the  $G$  analyses. Size corrections were performed according to Saether et al. (1996). In both  $G$  and feed intake analyses the pairwise comparisons were made as contrasts using nested tank mean square as an error term. The statistical significance limit for pairwise comparisons was  $P < 0.05$ . Statistical analyses were performed using SYSTAT -6.01 statistical software (SPSS Inc., USA). Results are given as mean,  $\pm$ SE.

## Results

### Feed intake

Prior to the temperature change daily feed intake did not differ among treatment groups ( $1.02\% \text{ d}^{-1}$ ,  $\pm 0.05$ ). A direct impact of temperature change was seen 3-4 days after the temperature change when feed intake was lower at  $17.7 \text{ }^\circ\text{C}_{\text{const}}$  ( $0.80\% \text{ d}^{-1}$ ,  $\pm 0.06$ ) and at  $11 \text{ }^\circ\text{C}_{\text{const}}$  ( $0.86\% \text{ d}^{-1}$ ,  $\pm 0.07$ ) than at  $14.4 \text{ }^\circ\text{C}_{\text{const}}$  ( $1.20\% \text{ d}^{-1}$ ,  $\pm 0.05$ ) ( $P < 0.05$ ). Feed intake of the charr held at  $11.0 \text{ }^\circ\text{C}_{\text{const}}$  did not differ from that of the fish exposed to  $17.7 \text{ }^\circ\text{C}_{\text{const}}$  ( $P > 0.05$ ).

Feed intake increased in all groups between feed intake measurements two and three, and there were no statistically significant differences among treatments at the third feed intake measurement ( $P > 0.96$ ) taken 21-22 days after temperature change ( $1.50\% \text{ d}^{-1}$ ,  $\pm 0.10$ ). Temperature was however, found to have a marked effect on feed intake at the last measurement ( $P < 0.001$ ). At this time feed intake was highest in the fish held at  $11.0 \text{ }^\circ\text{C}_{\text{const}}$  ( $1.71\% \text{ d}^{-1}$ ,  $\pm 0.05$ ) and  $14.4$

$^\circ\text{C}_{\text{const}}$  ( $1.83\% \text{ d}^{-1}$ ,  $\pm 0.05$ ) and was lowest at  $17.7 \text{ }^\circ\text{C}_{\text{const}}$  ( $0.57\% \text{ d}^{-1}$ ,  $\pm 0.04$ ). The changes in feed intake at  $17.7 \text{ }^\circ\text{C}_{\text{const}}$  after temperature change were all statistically highly significant ( $P < 0.0001$ ). The proportion of non-feeders were low ( $< 10\%$ ) in all cases and there were no statistically significant differences among treatments.

Under conditions of fluctuating conditions feed intake was similar 3-4 days after the temperature change to that recorded at  $14.4 \text{ }^\circ\text{C}_{\text{const}}$ . Later in the experiment, however, there was a tendency for feed intake to be lower under fluctuating temperature conditions but differences were not statistically significant ( $P > 0.05$ ).

Studentized size deviation of individuals from the mean size within a tank had a significant influence on daily feed intake. The covariate ( $W_d$ ) was statistically significant ( $P < 0.01$ ) on all four measurement dates with a positive slope within the range 0.26-0.63. Feed intake did not differ between marked and unmarked fish ( $P > 0.05$ ).

### Growth

Treatment differences in growth observed using the data for the PIT-tagged fish were consistent with those seen when tank mean data for of unmarked fish were used in analyses. Size-adjusted specific growth rate did not differ among groups during the first period ( $1.67\% \text{ d}^{-1}$ ,  $\pm 0.25$ ), when all fish were held at  $11.0 \text{ }^\circ\text{C}$ . Following the temperature change there was a significant increase in growth rates in the groups exposed to  $14.4 \text{ }^\circ\text{C}_{\text{const}}$  and  $14.3 \text{ }^\circ\text{C}_{\text{fluc}}$  ( $4.08\% \text{ d}^{-1}$ ,  $\pm 0.20$ ). There was, however, also an increase in  $G$  amongst the fish held at  $11.0 \text{ }^\circ\text{C}$  ( $3.35\% \text{ d}^{-1}$ ,  $\pm 0.27$ ). But the direct impact of temperature change ( $G_{\text{tc}}$ ) was significantly larger in fish exposed to  $14.4 \text{ }^\circ\text{C}_{\text{const}}$  and  $14.3 \text{ }^\circ\text{C}_{\text{fluc}}$  than in fish held at  $11.0 \text{ }^\circ\text{C}$  ( $P < 0.05$ ). On the contrary the temperature change to  $17.7 \text{ }^\circ\text{C}_{\text{const}}$  resulted a  $G_{\text{tc}}$  that was lower than in the fish held at  $11.0 \text{ }^\circ\text{C}$  ( $P < 0.001$ ).

The size-adjusted  $G$  of the unmarked fish increased with time in groups exposed to constant temperature, but the relative effect of temperature on  $G$  remained similar despite this overall increase in  $G$  (Fig. 2). The optimum temperature for growth can be estimated from the tempera-

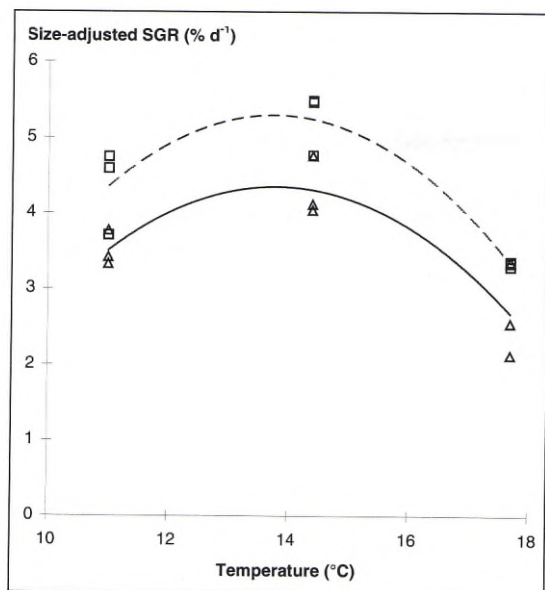


Fig. 2. Influence of temperature on size-adjusted specific growth rates ( $G$ ) of Lake Inari Arctic charr over two periods following temperature change from 11.0 °C. Symbols: squares indicate  $G$ -estimates for the second period and triangles indicate  $G$  estimates for the third period of the experiment. Lines indicate second degree polynomial fits; second period (solid line):  $G = -0.125T^2 + 3.445T - 18.388$ ,  $r^2 = 0.85$  and third period:  $G = -0.109T^2 + 2.996T - 16.298$ ,  $r^2 = 0.77$ .

ture-growth rate functions (Fig. 2). The estimates were almost identical for the second and third period: 13.74 and 13.78 °C, respectively. The further  $G$  changes of the PIT-tagged individuals showed a similar pattern and no statistically significant temperature effects on  $G_{acc}$  were found ( $P > 0.05$ ). There was, however, a non-significant decrease in growth of the fish exposed to fluctuating temperature (14.3 °C<sub>fluc</sub>) during the third period, which produces negative  $G_{acc}$  in that treatment group.

### Proximate composition

There were no statistical differences in proximate composition among treatments neither before the temperature change nor at the end of the experiment. Relative lipid and energy contents increased slightly during the course of the experi-

ment, from 9.5% to 10.5% of wet weight and from 7.4 kJ g<sup>-1</sup> to 7.8 kJ g<sup>-1</sup>, respectively. Simultaneously moisture percentage showed a decline from 72.3% to 71.4% of wet weight. Protein content showed no time dependency and was averaging 15.5% of wet weight.

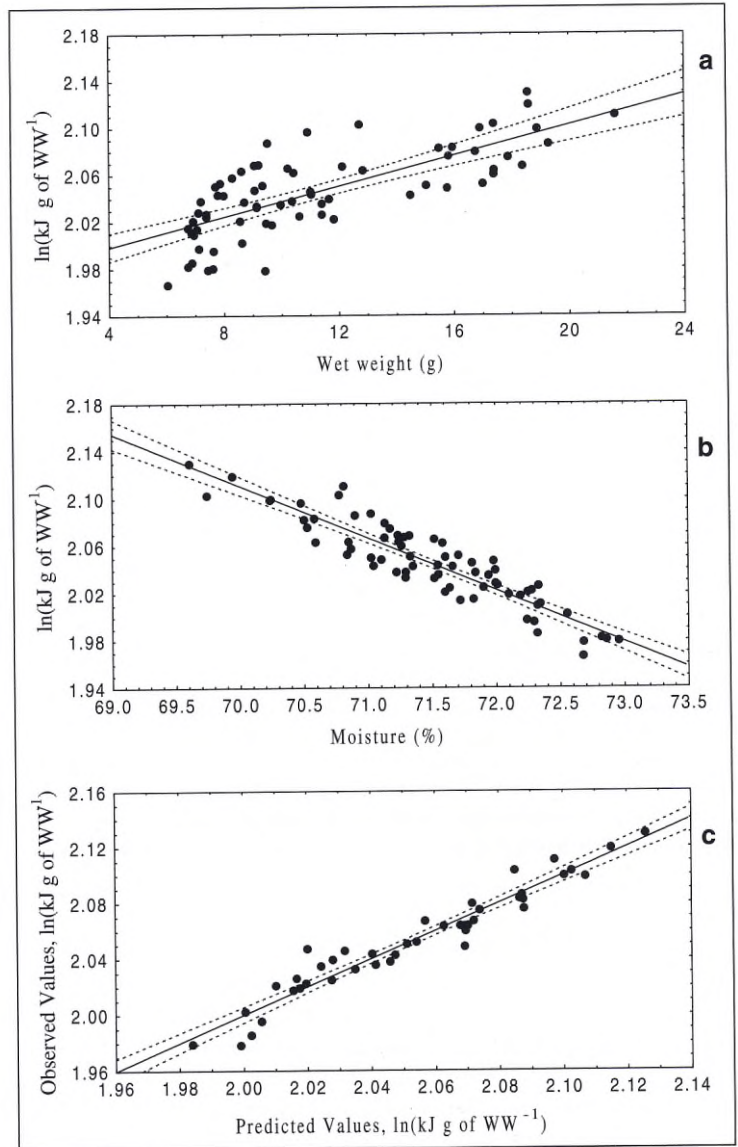
Irrespective of the thermal regime to which the fish were exposed there were significant positive correlations between energy, lipid content and mean wet weight within a sample ( $r = 0.78$  and  $r = 0.72$ , respectively;  $P < 0.001$ ). The slopes of regressions were similar for each temperature regime and the intercepts did not differ from each other. There was a highly significant correlation between fish wet weight and log energy concentration ( $P < 0.0001$ ) (Fig. 3a), whereas percentage moisture had a negative correlation with body size ( $r = -0.62$ ,  $P < 0.001$ ), and percentage protein was only weakly correlated with body size ( $r = -0.26$ ,  $P < 0.04$ ). Percentage moisture and energy concentration were negatively correlated (Fig. 3b). Body weight and moisture were used to estimate log energy concentration, and it was found that 90% of the variation in energy concentration could be explained by wet weight and percentage moisture (Fig. 3c).

### Discussion

The optimum temperature for growth of Arctic charr is reported to be within the range 12–15 °C (Swift 1964, Jobling et al. 1993). In the present experiment there were only small differences in feed intake and growth between 11.0 and 14.4 °C, suggesting this temperature range spans the optimum. The estimate of optimum temperature for growth was 13.7–13.8 °C (Fig. 2). Daily feed intake and growth were lower at supra-optimal temperature. Similar losses of appetite and growth at temperatures above the optimum have been observed in other salmonids (Brett et al. 1969, Elliott 1975, 1982).

The temperature shift from 11.0 °C to higher temperatures did not seem, *per se*, to have any marked effects because the form of the temperature-growth rate curve was similar over the two periods following the temperature change. This may indicate that thermal acclimation occurs rap-

Fig. 3a, b and c. The relationships between mean wet weight (g) and percentage moisture and energy concentration of underyearling Lake Inari Arctic charr. **a)** relationship between body weight and energy concentration:  $\ln(\text{energy concentration}) (\text{kJ g}^{-1}) = 0.0065W + 1.973$ ,  $r^2 = 0.54$ ,  $P < 0.0001$ ,  $n = 69$ ; **b)** relationship between percentage moisture and energy concentration:  $\ln(\text{Energy concentration}) (\text{kJ g}^{-1}) = -0.044\text{Moisture} (\%) + 5.189$ ,  $r^2 = 0.84$ ,  $P < 0.0001$ ,  $n = 69$ , and **c)** the predicted and observed energy concentration, when energy concentration was predicted from body weight and percentage moisture:  $\ln(\text{Energy concentration}) (\text{kJ g}^{-1}) = 0.0026W - 0.0355\text{Moisture} + 4.55$ ,  $P < 0.0001$ ,  $r^2 = 0.90$ ,  $n = 69$ .



idly when temperatures are shifted upwards, and that relatively small single temperature changes have negligible consequences for the temperature-growth relationship. These contentions seem to be supported by the findings of Evans (1990) who reported that acclimation of rainbow trout, *Oncorhynchus mykiss* (Walbaum), was completed within four days following a 10 °C shift. The temperature change did not seem to increase proportions of non-feeders 3-4 days after the tem-

perature change, which is also suggestive of a reasonably rapid acclimation.

The daily feed intake showed interaction with measurement day. When temperature was shifted to a supra-optimal temperature, feed intake 3-4 days after the temperature change was almost the same as in fish held at 11.0 °C. Feed intake was increased 21-22 days after the temperature change, but at the end of experiment feed intake was clearly suppressed. Loss of appetite and a

decline in growth are symptoms of chronic stress (Rice 1990), and the suppression of feed intake at the end of the experiment could be interpreted as an indication of this. Thus at supra-optimal temperatures the acute and chronic responses may differ, resulting in time-related feed intake and growth responses at temperatures above the thermal optimum for growth.

Although small amplitude temperature fluctuation was not found to have a significant influence on feed intake and growth there was a trend towards reduced feed intake and poorer growth under the fluctuating regime than at 14.4 °C<sub>const</sub>. In several earlier studies temperature fluctuations have been found to have significant effects on growth, but the amplitudes of fluctuations tested have been larger than those used in the present study (Hokanson et al. 1977, Spigarelli et al. 1982, Vondracek et al. 1989). This may, in part, explain the apparent lack of influence of temperature fluctuation in this study. Further the influences of temperature fluctuation on feed intake and growth are expected to be reduced if fluctuations occur around a mean temperature that is close to the optimum (Jobling 1997).

The growth of underyearling Lake Inari charr seemed to be lower than that of Hammerfest strain of equal size (Jobling et al. 1993). This may indicate that there are strain differences in growth potential because thermal responses of the two strains appear to be similar. In other words, fish of the two strains appear to have similar temperature tolerances (Lyytikäinen et al. 1997) and growth optima, so the growth differences do not seem to be the result of shifts in the rate-temperature curves along the thermal axis (Jobling 1997). However, confirmation of this would only be obtained by rearing fish of the two strains under identical conditions.

Temperature did not seem to have any direct influence on proximate composition of the fish in the present experiment. The results are consistent with the suggestions made by Shearer (1994) that the proximate composition of fish is largely determined by fish size if nutritional conditions are adequate. A non-destructive biometric method has been developed for estimation of

fat levels of Atlantic salmon, *Salmo salar* L., (Simpson et al. 1992) and body weight has been used in the estimation of various components of proximate composition in other species (Wolynetz and Sibbald 1990). Work on teleost fish indicates that body size and moisture can be used to estimate proximate composition (Brett et al. 1969, Elliott 1975, Weatherley and Gill 1983, Shearer 1994), and we were able to develop a predictive model for the estimation of energy concentration of underyearling Arctic charr using these two variables (Fig. 3c).

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# Domestication Genetically Alters the Anti-Predator Behaviour of Anadromous Brown Trout (*Salmo trutta*) - a Dummy Predator Experiment

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## Abstract

Domesticated, anadromous brown trout juveniles have been reported to be more prone to take risks in order to obtain food than juveniles from a wild strain. This study looked at changes in the actual response to an attacking predator of juvenile sea trout due to domestication. The progeny of wild and sea-ranched sea trout were reared in hatcheries under identical conditions for one year. When exposed to a model predator, domesticated juveniles were more likely to swim or sink to the bottom and to keep still (freeze) than wild juveniles, which more often escaped by panic swimming. No difference was found in escape distance. The results support the view that the hatchery environment selects for risk-taking individuals.

Keywords: Domestication, anti-predator behaviour, dummy-experiment, sea-trout.

## Introduction

An anti-predator behaviour is selectively favoured when the individual optimises the trade-off between the cost of performing the behaviour (e.g., in terms of reduced growth) and the gain in terms of increased probability of escaping the predator (Ydenberg and Dill 1986, Bennett and Houston 1989, Leonardsson 1991). The decision role for such a trade-off could be genetically controlled (e.g. Magurran 1990, Johnsson and Abrahams 1991), but a learning process may also be involved (e.g. Dill 1974, Järvi and Uglem 1993).

In a hatchery environment, 'risky' phenotypes may be favoured as the predation pressure is relaxed and rapid growth favoured in comparison with natural conditions (Kohane and Parsons 1989, Swain and Riddell 1990, Johnsson and

Abrahams 1991). Indeed, Johnsson et al. (1996) observed that domesticated anadromous brown trout (*Salmo trutta* L.) parr visited patches with a predator in order to obtain food more frequently than parr from a wild strain. Although several studies have shown that domestication alters the risk-sensitive foraging decision, it is unknown how domestication alters the behavioural response to an attacking predator.

When salmon (*Salmo salar* L.) and trout juveniles become aware of a predator they may perform a number of behaviours, such as avoiding the predator before it attacks, or they may respond to an attacking predator by swimming away in panic (flight behaviour) or by swimming (alternatively sinking) to the bottom and remaining motionless there (freezing, see Jakobsson and Järvi 1976, Järvi and Uglem 1993). Domesticated salmonid juveniles take more risks to obtain food

and they should therefore be expected to choose a lower-intensity reaction to an attacking predator and exhibit shorter escape distances than wild juveniles. In this study, we tested these assumptions on juvenile anadromous brown trout by presenting a mobile dummy predator simulating a predator attack to individual fish in a standardized situation.

## Materials and methods

### Experimental fish

The fish used were the offspring of either sea-ranched or wild anadromous brown trout originating from the River Dalälven (central Sweden). The sea-ranched strain has been subjected for five generations to artificial breeding to the smolt stage and then released into the River Dalälven. This strain was identified by missing left pectoral fins, which were removed from all smolts released. The wild strain consisted of naturally spawning fish with the left pectoral fin intact (see Petersson and Järvi (1995) and Petersson et al. (1996) for a more detailed description of the two stocks). A genetic analysis of the ND-1 gene on the mitochondria (mtDNA-analysis) has revealed that the two strains differ significantly (Dr. T. Öst, Salmon Research Institute, Älvkarleby, Sweden, pers. comm.). The sea-ranched strain has been shown to be domesticated in various traits such as growth pattern (Petersson and Järvi 1995, Petersson et al. 1996), risk-proneness (Johnsson et al. 1996), stress tolerance (Olivier Lepage and Svante Winberg pers. comm.) and reproductive behaviour (Petersson and Järvi 1997). The experimental fish from the two strains were artificially bred for one year (1+) at the National Board of Fisheries Research Station at Älvkarleby before the experiment commenced.

The domesticated and wild juveniles originated from mixing the eggs and sperm from two females and two males, and three females and three males respectively. In addition, one group of wild juveniles and two sibling groups of domesticated juveniles originated from the spawning of one male and one female, making a total of 14 parental fish. The fish were reared under

standard conditions in river water of ambient temperature and were fed dry pellets at a ration of about four per cent of body weight per day (satiation diet). Juveniles of the domesticated and wild strains were reared in five and seven tanks respectively, and the experimental fish were sampled from these tanks. Total body length of the experimental fish was 8.0 to 14.5 cm, with no significant differences between the two categories of juveniles (domesticated:  $\bar{X}$ =10.9 cm,  $SD \pm 1.32$ ; wild:  $\bar{X}$ =10.3 cm,  $SD \pm 0.98$ ; Kruskal-Wallis ANOVA,  $H=1.2$ ;  $P=0.3$ ).

### Experimental procedure

The experiments were conducted in September-October 1992 at the Institute of Freshwater Research, Laboratory for the Study of Stream Water Ecology at Älvkarleby, Sweden, in two identical test arenas (Fig. 1). Individual test fish were gently introduced into a compartment (test chamber) at one end of the arena, and allowed to acclimate for 20 min. The predator dummy (an approximately 30 cm long model with large mouth and eyes and dark dorsal side representing a general predator) was placed at the other end of the arena behind plastic strips, which made the dummy invisible to the juvenile. A transparent glass wall with small holes (allowing a flow of water into the test chamber) separated the test chamber and the 'dummy compartment'. The current speed was 4-8 cm/s in the dummy compartment. Water temperature was 7.6-7.7 °C and three 60 W bulbs illuminated each arena.

When the juvenile after acclimation swam against the current at the glass wall and remained within the white marked zone (Fig. 1), the dummy was released and accelerated towards the juvenile at a maximum speed of about 100  $\text{cm s}^{-1}$  (5 video frames per predator length). The dummy stopped when it hit the glass wall, which exposed the fish to a pressure wave through the holes in the glass wall, in addition to sound stimuli and visual stimuli. After the 'attack', the model was returned to its original position within 10 s. A video camera was placed over the test arena, and the approaching dummy and the behaviour of the juvenile were recorded for later analyses.

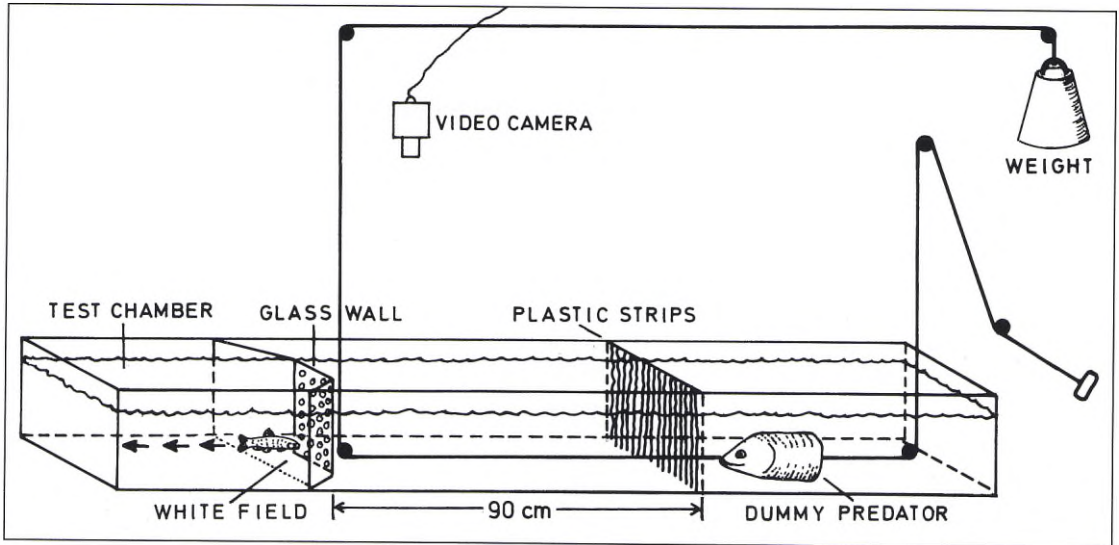


Fig. 1. The test-arena. When the test fish was swimming against the current within the white field in the test chamber the dummy predator was released and attacked from behind the plastic strips.

No fish was kept in the chamber for more than 2.5 h, after which all trials were terminated. Each individual was exposed to as many as 20 attacks, but as all juveniles did not remain in the specified position in the test chamber 20 times during the 2.5 h trial the fish were not all exposed to the same number of simulated attacks (range: 3-20 exposures). The mean number of exposures did not differ between domesticated and wild juveniles (wild: 15.9, domesticated: 16.2). In order to include all experimental fish, the following analysis is based only on the first three attacks. Two domesticated and two wild juveniles were tested each day with the order of testing and arena varying between days. A total of 21 domesticated and 21 wild juveniles were tested.

### Behavioural analyses and statistical treatments

The videotapes were analysed for anti-predator behaviour and escape distance to the attacking dummy. One of the following alternative behaviour patterns were recorded:

1. 'Escape-reaction': The fish turned and swam away from the attacking dummy with a burst of speed.

2. 'Freezing': The fish swam or sank directly to the bottom and stayed there motionless.
3. 'No-reaction': The fish showed no visible response to the attacking dummy or swam slowly away.

The estimated probability ( $Pr$ ) of a given juvenile responding with a certain behaviour to the attacking predator dummy was calculated as the proportion of exposures in which the individual exhibited one of the three responses. The mean estimated probability ( $Pr_j$ ) of responding with a certain behaviour  $j$  to an attack in the two categories of juveniles was compared ( $H_0$ :  $(Pr_j)_{Domesticated} = (Pr_j)_{Wild}$ ). The escape distance (the distance to the glass partition the dummy reached before the juvenile escaped) was recorded to the nearest cm ( $H_0$ :  $\bar{X}_{Domesticated} = \bar{X}_{Wild}$ ).

### Results

The response to predator attacks varied from no reaction to intense escape reactions. An ANOVA Repeated Measurement test showed no change in escape distance in the course of the three attacks and no difference between the test arenas

Table 1. The mean escape distance analysed using ANOVA Repeated Measurement. Summary of effects for track, strain and repeated measurement of escape distance.

Effect	DF	F	P level
Track	1:28	0.10	0.75
Strain	1:28	0.03	0.86
Repeated measurement	2:56	0.60	0.55
Track X Strain	1:28	0.21	0.65
Track X Repeated measurement	2:56	1.03	0.37
Strain X Repeated measurement	2:56	1.59	0.21
Track X Strain X Repeated measurement	2:56	0.04	0.96

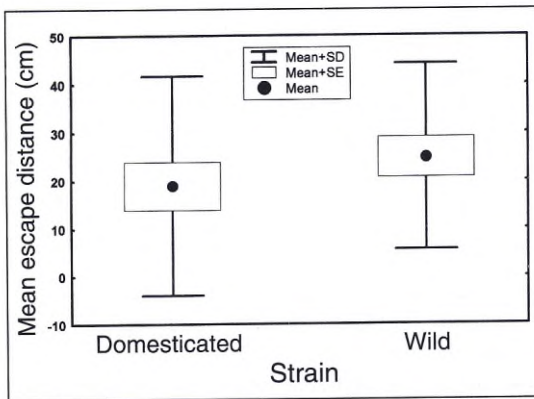


Fig. 2. Mean 'escape distance' in domesticated and wild juveniles when attacked by the dummy predator.

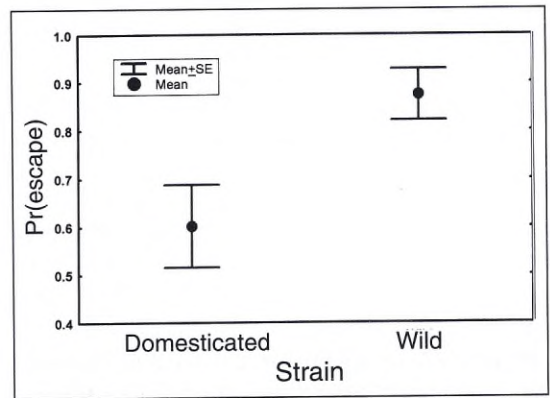


Fig. 3. The mean estimated 'probability of escape' in domesticated and wild juveniles when attacked by the dummy predator.

or between domesticated and wild juveniles (Table 1, Fig. 2). There was, however, a significant difference between the two categories of juveniles regarding the choice of behaviour in response to predator attacks. Wild fish reacted more often with an 'escape reaction' than domesticated fish (Kruskal-Wallis ANOVA,  $H=7.5$ ;  $P<0.01$ ; Fig. 3). Domesticated juveniles 'froze' on the other hand more often in response to the approaching dummy than wild juveniles ( $H=4.8$ ;  $P<0.05$ ; Fig. 4).

### Discussion

Several studies have shown that domesticated salmonid juveniles are more prone to take risks in order to obtain food than juveniles from a wild strain (e.g. Johnsson and Abrahams 1991,

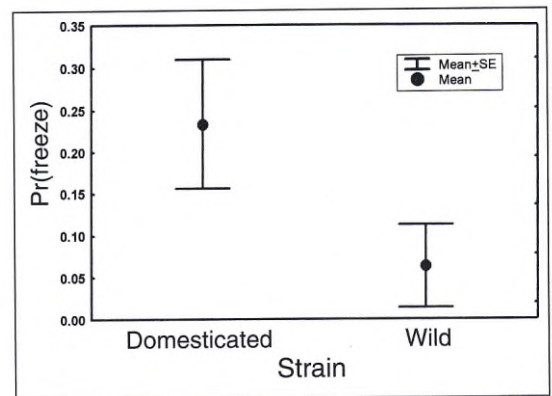


Fig. 4. The mean estimated 'probability of freeze' in domesticated and wild juveniles when attacked by the dummy predator.

Johnsson et al. 1996). In this study a difference in the actual response to an attacking predator was observed between the progeny of wild and sea-ranched sea trout. When attacked, domesticated juveniles more often swam or sank to the bottom and remained there than wild juveniles, whereas wild juveniles more often escaped by panic swimming. Although 'freezing' under some circumstances is regarded to be less risky than fleeing (Ydenberg and Dill 1986), it seems reasonable to assume that the behavioural option of 'freezing' instead of 'panic swimming' is a more risky anti-predator behaviour, when the prey is conspicuous to the bottom as in our experimental arena.

To our knowledge all studies up till now show that domesticated fish are more risk-taking than wild fish (e.g. Johnsson and Abrahams 1991, Johnson et al. 1996), indicating that the change in response to an attacking predator observed in this study is caused by a relaxed selection pressure for anti-predator behaviour in hatcheries. Juveniles in hatcheries are not preyed upon, and the accumulated energy gain and the growth advantage of risk-prone individuals could be considerable. A strong response to food in the rearing environment may give a competitive advantage, leading to more rapid growth (Johnsson et al. 1996) and lower mortality (Handeland et al. 1996).

To conclude, this study demonstrates a difference in the responses of wild and sea-ranched strains of sea-trout towards an attacking predator, and supports earlier findings that the hatchery environment selects for more risk-prone individuals. Although there is a complex interplay between predatory experience, social environment and genetic variation (Tulley and Huntingford 1987, Huntingford and Wright 1993, Järvi and Uglem 1993, Berejikian 1995), the differences observed between the strains are presumably of genetic origin, as the fish were raised under identical conditions in tanks and all fish were predator-naive. The selection pressure in hatcheries seems to lead to genetically based changes in anti-predator behaviour in spite of the facts that the sea-ranched strain has been in cul-

ture for only five generations and that the fish are subject to stabilizing selection in the natural environment from the smolt stage onwards.

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# Variability in Age Estimates of Whitefish (*Coregonus lavaretus* (L.)) from Two Baltic Populations — Differences between Methods and between Readers

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## Abstract

The reliability of the age determinations of two populations of Baltic whitefish (*Coregonus lavaretus* (L.)) — slow growing and fast growing — was tested. Four readers aged 50 individuals from both populations. The fish were aged from scales following the normal practice. In addition, three of the readers aged the same fish from otoliths, although the readers had limited experience of otoliths. There was a lot of variation in the ages determined by the readers. The readers aged the slow growing whitefish older from otoliths than from scales, and, surprisingly, two out of three aged the fast growing whitefish older from scales than from otoliths. A number of marked whitefish from the fast growing population were caught during the ageing test. On the basis of their calcified structures, three of the four readers overestimated the age of the whitefish from scales due to misleading false annuli. When ageing slow growing Baltic whitefish, otoliths must be used to get the most reliable estimates of age. However, the ageing can only be validated by using known-age fish. In the ageing of fast growing migratory whitefish, it is recommended to use not only scales, but also otoliths and opercular bones. The corrected ageing results of the migratory whitefish revealed overfishing, which had not been formerly found because of underestimated growth and mortality rates.

Keywords: ageing, scale, otolith, operculum, *Coregonus lavaretus*

## Introduction

Age and growth of fish are routinely determined in large numbers every year. However, the validity of the age readings is not unambiguous; measures are needed to determine the level of accuracy and to develop the ageing methods (Beamish and McFarlane 1983, Boehlert and Yoklavich 1984, Mann and Steinmetz 1985, Casselman 1987). Errors in ageing can lead to an incorrect figure of age distribution and bias the estimates of mortality and production. This may result in erroneous recommendations in fisheries (Beamish and McFarlane 1987, 1995).

In the Finnish Game and Fisheries Research Institute, whitefish (*Coregonus lavaretus* (L.)) have mostly been aged from scales. A testing of accuracy made by Salojärvi (1989) with 1–8-

year-old whitefish from Lake Oulujärvi showed that scales were reliable in age determination. In a study of other whitefish populations, the otolith age was greater than the scale age for 26% of the fish, and for 14% the otolith age was less than the scale age (Salojärvi and Huusko 1990).

In the comparisons of scale age and otolith age by Barnes and Power (1984) with *C. clupeaformis* and Skurdal et al. (1985) and Raitaniemi et al. (1998) with *C. lavaretus*, the otolith ages of especially slow growing old whitefish often exceeded the scale ages. Several other studies on Salmonidae, like Jonsson (1976) with brown trout (*Salmo trutta*), Casselman (1983) with lake trout (*Salvelinus namaycush*), or Sikstrom (1983) with arctic grayling (*Thymallus arcticus*), have shown similar results with slow growing fish. For some species, it has been proved that older otolith ages



are more valid than younger scale ages (Beamish and McFarlane 1987). In some cases otolith reading may also lead to overevaluation of age (Casselman 1987).

In the Finnish coastal waters of the Baltic Sea, there are populations of both slow and fast growing whitefish. The slowest growth is found in the sea-spawning populations of the northern part of the Gulf of Bothnia. In these populations, the individuals do not usually exceed the total length of 30 cm and the weight of 200 g. The growth in anadromous populations is usually faster. The fastest growing sea-spawning and migratory whitefish live both in the archipelago and coastal waters of southern Finland, where more than 50 cm long whitefish with the weight of 2 kg are not rare.

In order to assess the reliability of the age determinations that are regularly conducted for whitefish among these populations, we compared the age readings by four different readers experienced with whitefish. They were asked to determine the age from scales according to their normal routine, and in addition, separately from otoliths (sagitta), in which, however, they were inexperienced. One slow growing and one fast growing whitefish population were included in the study.

Unfortunately, known-age whitefish from the populations were not available in the comparison. However, in the autumn of 1996, when the ageing study was still in process, 24 marked (hot-branding) individuals (known age 5 summers) of migratory whitefish were caught and compared with the samples from the same population in the ageing test.

## Material and methods

The samples for the test were taken from two populations, of which the slow growing, sea-spawning whitefish population lives in Kalajoki area in the Gulf of Bothnia. The fast growing migratory whitefish were caught at the mouth of the River Vantaanjoki by the Gulf of Finland. Due to damming that prevents migratory whitefish from reproducing, the River Vantaanjoki is yearly stocked with one-summer-old fingerlings of the

River Kemijoki stock. A random sample of 50 individuals was taken from the catches of both stocks for the ageing test.

The readers were provided with 50 envelopes with scale impressions (five scales/individual or plate) from both samples. The scales were selected so that each plate included scales from the area between the tips of the pelvic fins and the area between the lateral line and the adipose fin. The readers used either a microfilm reader or a scale reader for the ageing.

In the preparation of otoliths for ageing, one otolith per fish was first burned and then ground to get a smooth cross section through the nucleus. After burning in the way described by Christensen (1964) and more precisely by Power (1977), the otolith was dropped hot into water. Before grinding, the otolith was glued to a piece of plastic plate and completely covered with epoxy two-component glue (method by K. Nyberg). This was conducted to make sure that the fragile whitefish otolith could be ground successfully and that it could stand the handling of all readers. The otoliths were aged under a stereo-microscope, and the cross section, covered with water or ethanol, was analysed in reflected light.

The scale and otolith envelopes were numbered in a different order, ensuring that the readers aged scales and otoliths separately. The readers were given written information of the whitefish on the envelopes: name of the stock, length, weight, and date of catch. In this way, the normal situation of ageing was imitated.

Four readers aged the scales, but only three of them were able to participate in the ageing from otoliths. Reader A aged only scales, B and C aged first scales and then otoliths. D aged first otoliths and then scales. Due to poor quality, one scale impression of migratory whitefish and one otolith of sea-spawning whitefish were excluded from the calculations.

The age determinations of different readers and ages determined from scales and otoliths were compared with each other. Wilcoxon's signed-ranks test (Sokal and Rolf 1981) was used to examine whether the differences were systematic or random. Chi-square test was used in comparing the age distributions resulting from the age

determinations. In this, small age groups 1–3 and 7–13 of the sea-spawning whitefish and 3–4 and 7–9 (6–9) of the migratory whitefish were combined.

Of the 24 marked migratory whitefish from autumn 1996, scales, otoliths, and in addition to earlier practice, opercular bones were studied carefully. The information from these was used in examining the sample of the ageing test again. This time, scales and otoliths were used together in the determination.

## Results

### Differences between structures

The differences between scale and otolith determinations of both sea-spawning and migratory whitefish were clear. Of the sea-spawning whitefish, 5–18 and of the migratory whitefish 10–25 fish were aged identically from scales and otoliths, respectively (Table 1). Similarly, the results of the readers differed from each other (Table 2).

The individuals of the sea-spawning population were commonly aged 1–2 years older from otoliths than from scales, but the difference between scale and otolith age was 4–8 years at most (Fig. 1). The highest scale age was 9 years, whereas the highest otolith age was 13 years. The differences between scale and otolith ages were greatest in fish with scale age older than 4 years.

Unexpectedly, there were also systematic differences between the estimates of scale and otolith ages of the migratory whitefish sample. Two out of three readers determined the fish on the average older from scales than from otoliths (Fig. 1, table 1).

### Differences between readers

In the sample from the sea-spawning population, systematic differences of several years between the readers were detected (Fig. 2, Table 2). The difference between scale and otolith ages resulted in a greater proportion of old age groups in the age distributions based on the otolith results (Fig. 3).

Systematic differences were also found between the estimated scale ages of migratory whitefish; otolith ages, in turn, were closer to each other (Fig. 2, Table 2). The age distributions based on otoliths were more alike than the age distributions based on scales (Fig. 3, Table 2).

### Known-age migratory whitefish

As a result of studying the calcified structures of the marked whitefish, there was an 84% agreement between the new reading of scales and otoliths by reader D and the previous ageing from scales by reader C (Fig. 4, no significant difference). This also revealed that the age distributions based on otoliths were closer to the actual age distribution than the scale-based age distri-

Table 1. The numbers of identical readings from scales and otoliths ( $N=49$ ). The significance of systematic differences between the readings (Wilcoxon's signed-ranks test) and the differences between the resulting age distributions ( $\chi^2$ -test) is presented with stars (\*\*\*= $P<0.001$ ; \*\*= $P<0.01$ ; \*= $P<0.05$ ; o= $P<0.1$ ; NS = no statistically significant difference).

Reader	Sea-spawning whitefish			Migratory whitefish		
	Identical readings	Wilcoxon's test	$\chi^2$ -test	Identical readings	Wilcoxon's test	$\chi^2$ -test
B	5	**	*	10	**	***
C	18	**	NS	25	**	o
D	9	**	***	14	**	**

Table 2. The numbers of identical readings between the readers A, B, C, and D. With the scales of migratory whitefish and the otoliths of sea-spawning whitefish 49 readings were conducted, and with the scales of sea-spawning whitefish and the otoliths of migratory whitefish 50 readings were conducted. The results of statistical tests are presented as in Table 1.

Reader	Sea-spawning whitefish		Migratory whitefish	
	scale	otolith	scale	otolith
A–B	21	–	15	–
Wilcoxon's test	**	–	**	–
$\chi^2$ -test	*	–	NS	–
A–C	22	–	6	–
Wilcoxon's test	NS	–	**	–
$\chi^2$ -test	NS	–	***	–
A–D	17	–	23	–
Wilcoxon's test	**	–	**	–
$\chi^2$ -test	NS	–	**	–
B–C	21	13	4	22
Wilcoxon's test	*	**	**	NS
$\chi^2$ -test	NS	NS	***	NS
B–D	14	16	10	20
Wilcoxon's test	**	NS	**	*
$\chi^2$ -test	*	NS	***	NS
C–D	12	20	17	21
Wilcoxon's test	*	**	**	*
$\chi^2$ -test	NS	NS	***	NS

butions by A, B, or D, who overestimated the scale age of the fish.

The examination of the marked whitefish also revealed that the opercular bone of fast growing Baltic whitefish is in many cases more readable than a scale or an otolith, because it is easier to distinguish false rings from annuli.

## Discussion

The ageing results of the sea-spawning population were similar to earlier findings with salmonids (Jonsson 1976, Casselman 1983, Sikstrom 1983, Barnes and Power 1984), according to which age determined from the otoliths of slow growing fish can be greater than age determined from scales. As scale ages of some fish species have been proved to underestimate the actual age of old individuals and there is some

evidence of otolith ages being more reliable (Beamish and McFarlane 1987), the ageings from otoliths were probably closer to the real ages of old sea-spawning whitefish. This is also supported by the thickness of their otoliths when compared with the thin otoliths of the fast growing migratory whitefish (cf. Beamish and McFarlane 1987, Simoneau and Dion 1992).

The great differences in all comparisons with sea-spawning whitefish — between structures and between readers with both scales and otoliths — indicate that the reliability of the determinations was poor regarding both scales and otoliths. The annuli in the scales were difficult to distinguish and the readers were inexperienced with otoliths. However, the reliability of ageing could be improved, at least when using otoliths in training with known-age individuals.

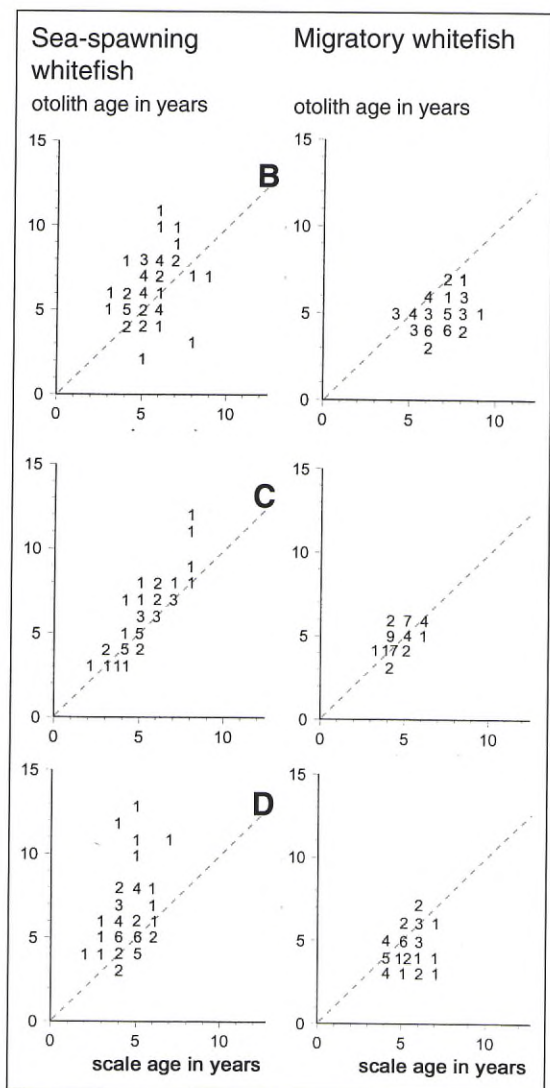


Fig. 1. Estimated ages from scales and otoliths of sea-spawning whitefish and migratory whitefish by the readers B, C, and D. The numerals indicate the number of fish falling within each cell of the matrix.

At present, age determination of a sample of slow growing Baltic whitefish cannot be reliably used to determine which year classes are strong or weak, for example. This could be difficult even if 80% of the fish were aged correctly, but most of the rest would systematically be estimated either younger or older than the actual age (Raitaniemi et al. 1998).

The discrepancies between the otolith ages and scale ages of the migratory whitefish were largely caused by a number of false rings in the scales that, in the readers' common opinion, are exceptionally difficult to distinguish from annual rings. Zones normally typical to annual rings, where "a zone of closely-spaced ridges is followed by a zone of widely-spaced ridges" (Bagenal and Tesch 1978), were often not situated close to the real annuli; instead, a certain kind of discontinuity of the ridges revealed the positions of annuli. This explains why a reader with experience of whitefish from lakes and with accurate readings in earlier ageing tests can get poor results when ageing fast growing Baltic whitefish. However, the indirectly found high level of accuracy of scale ages by the reader C, who was the most experienced with Baltic populations, showed that a fairly reliable ageing of fast growing whitefish from scales is possible, at least when the fish are not older than 4–6 years.

When considering the limited experience of the readers in ageing otoliths, the otolith results from the migratory whitefish population can be regarded as promising. The erroneous scale reading results from earlier studies should have been questioned earlier, if otoliths had been examined even without earlier experience of otolith reading. In addition, the opercular bones of migratory whitefish would have even more clearly shown the need of checking the scale age estimations. The use of several methods in ageing has been recommended by e.g. Bagenal and Tesch (1978).

According to our preliminary results, the earlier scale age estimations of the migratory whitefish population have caused an underestimation of the instantaneous mortality rate by about 20% and the growth rate by about 10% in length and 30% in weight. The new ageing results showed growth overfishing, which was earlier not found because of the biased ageing. This also affected the recommendations for fisheries management. On the basis of corrected ageing results, the migratory whitefish yield from stocking in the coastal waters off Helsinki could be improved by 50% by increasing the smallest permitted mesh size of gill nets from 45 mm to 50 mm (bar length).

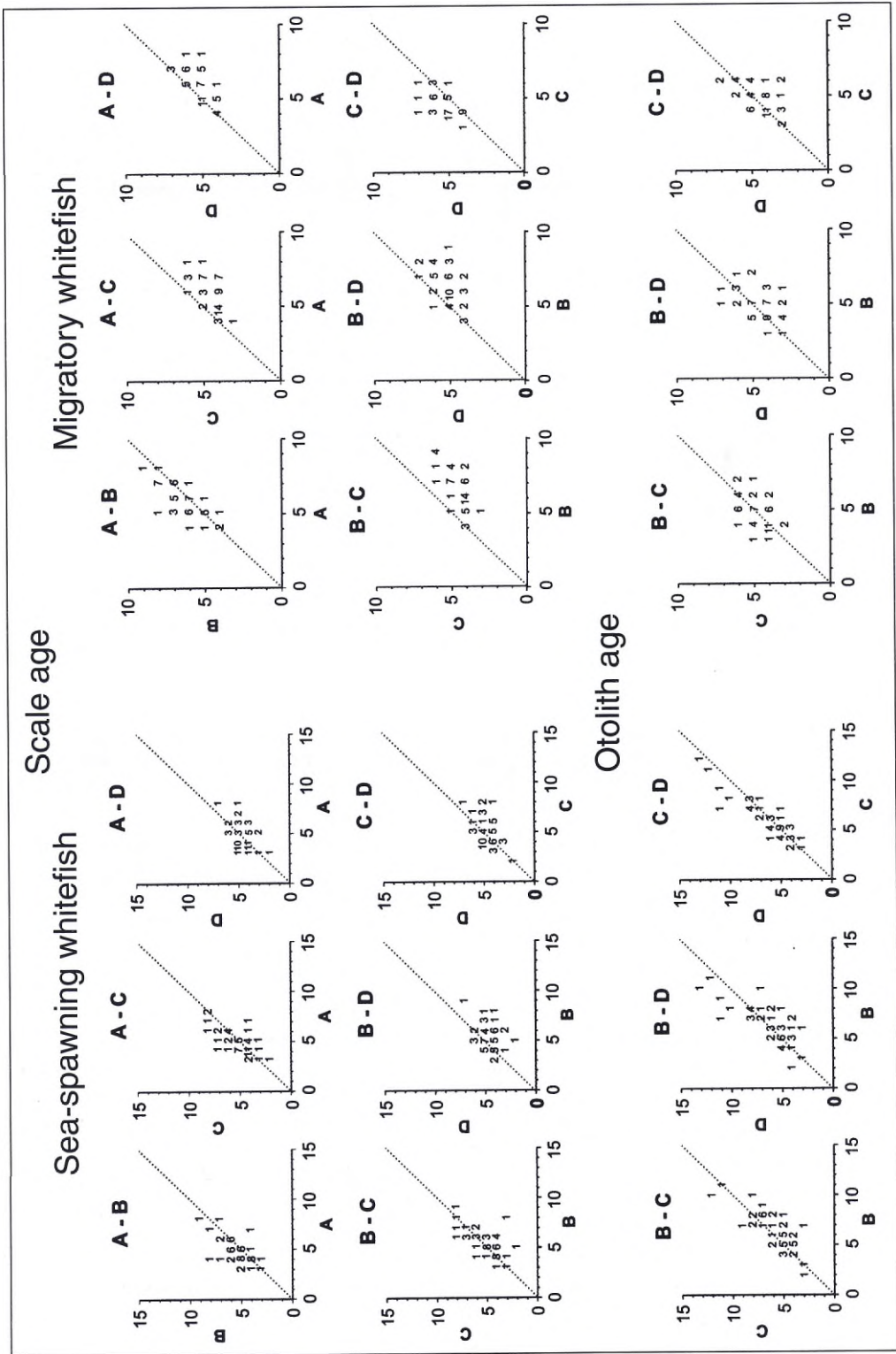


Fig. 2. The age determinations of sea-spawning and migratory whitefish in years by the readers A, B, C, and D in relation to each other. The numerals indicate the number of fish falling within each cell of the matrix.

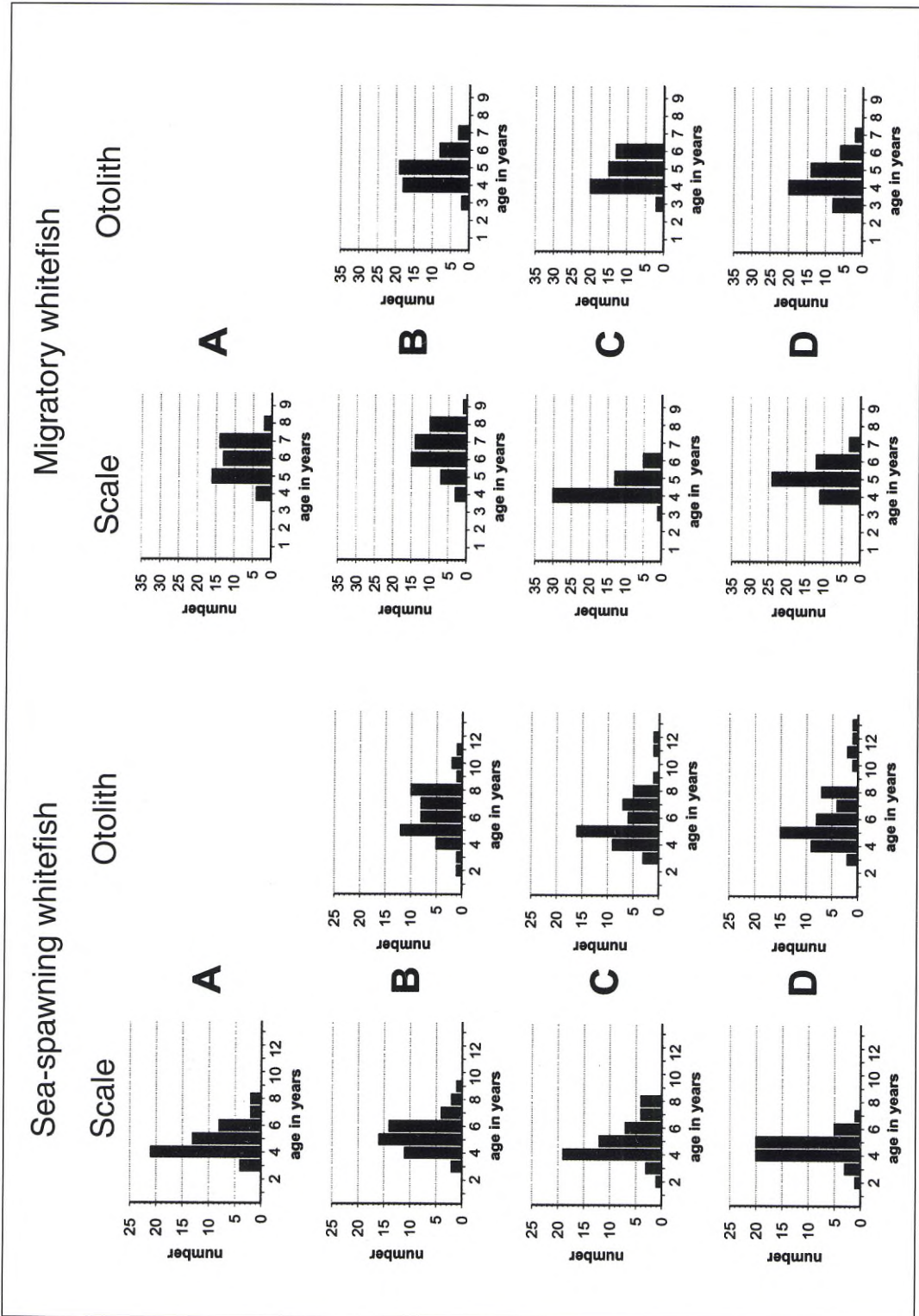


Fig. 3. The age distributions resulting from the ageings of the sea-spawning and migratory whitefish.

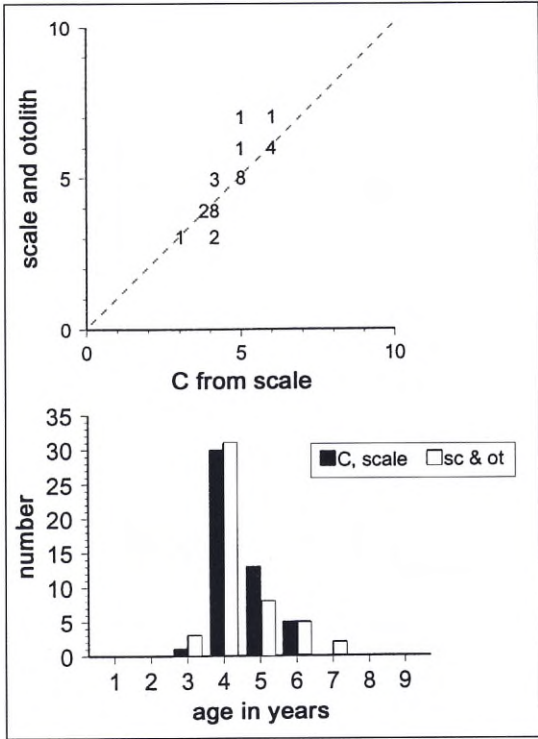


Fig. 4. Estimated ages of migratory whitefish from scales by the reader C in the comparison and from scales and otoliths by the reader D, after getting information from known-age individuals. Above, age determinations are in years and the numerals indicate the number of fish falling within each cell of the matrix. Below, age distributions resulting from the ageings.

### Conclusions

The calcified structures of different populations of whitefish can in extreme cases differ as if they were from different species; a reliable reader of some populations can be unreliable with others without especially training with them. For slow growing population of Baltic whitefish, scale reading tended to underestimate and for fast growing population overestimate the actual age.

In the ageing of especially slow growing whitefish, otoliths should be used. The opercular bones of fast growing whitefish may have less false rings than scales or otoliths and thus be easier to

age. If possible, marking fish and using marked fish to "calibrate" the age determinations is recommended; to use known-age fish is the only way to validate the ageing. Analysing several structures increases the reliability of ageing and is especially important when examining fish from populations that are unfamiliar to the reader.

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Alpo Huhmarniemi, Kari Hietanen, and Rauno Hokki took part in the age determinations and made this comparison possible. We got valuable comments to the text from Kari Nyberg and Magnus Appelberg. The Game and Fisheries Research Institute and the Employment and Economic Development Centre for Kymi Rural Department (Fisheries Services) financed the work. Helena Halme checked the language.

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# Individual Weight Estimates of Zooplankton based on Length-Weight Regressions in Lake Ladoga and Saimaa Lake System

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## Abstract

The length-weight regression was established for seven taxa of the Saimaa lake system, Finland and ten zooplankton taxa of Lake Ladoga, Russia. The biomass of measured species covered 80-91% of the total zooplankton biomass. Most of the variation in regression models was explained by length; the rest of this variation was supposed to be individual variation which was among adult copepods particularly large. The total carbon and dry weights of *Bosmina* were calculated in various lakes and seasons in order to clarify differences between the literature and our results. The dry weight differences of *Bosmina* between our study and the literature values were in general small. The size-specific dry weight of *Bosmina* was lowest in eutrophic Lake Biel, Switzerland and highest in mesotrophic Lake Ladoga where the biomass was three times that in Lake Biel. Furthermore, the weight in spring was higher than the weight of animals in late summer. In summary, the individual variation of zooplankton species and the changing environmental conditions in different lakes and seasons underline the necessity of establishing the length-weight regressions or measuring the populations under study directly.

Keywords: biomass, length, copepods, cladocerans

## Introduction

An ideal measure of biomass should give information about the elemental or energetic content of a population and should also allow the possibility of following the flow of these elements or energy through all the levels in the ecosystem (Latja and Salonen 1978). The total biomass of an organism or population can be weighed directly or estimated indirectly with the aid of length measurements. For crustacean usually only body length is measured and the body mass is predicted using published length-weight relationships. According to published studies the biomass estimates of same zooplankton species seem to vary significantly. Most of these studies are based on measurements of dry weight (e.g. Platt et al. 1969, Dumont et al. 1975, Bottrell et al. 1976, Culver et al. 1985, Vuille 1991, Vuille and Maurer

1991, Kawabata and Urabe 1998) and some on measurements of carbon content (Salonen et al. 1976, Latja and Salonen 1978, McCauley 1984, Duncan et al. 1985, Kankaala and Johansson 1986, Vasama and Kankaala 1990); nowadays biomass is rarely expressed as wet weight (e.g. Balushkina and Winberg 1979).

Many explanations have been suggested for the large variation in individual weight estimates (geographical, temporal, differences in biochemical composition of the zooplankton and lake-specific characteristics, or methodological differences). Variation in individual weight may be due to differences in food content, temperature or reproductive state of an individual animal. Length-weight regressions or weight conversion coefficients should therefore not be applied before their validity has been tested for the species and populations concerned.

The aim of the present study was to establish reliable length-weight equations for common zooplankton species of the Saimaa lake system in Finland and Lake Ladoga in Russia. The well-documented length-weight regressions of crustaceans are mainly measured lakes in samples from Central Europe, but in Eastern Fennoscandia there are only few equations available. The other purpose of this study was to describe the temporal variation of individual weight and to illustrate the weight differences which are due to lake-specific characteristics. Some practical advice is also presented for predicting crustacean weight from body length.

## Study area

Lake Ladoga is a large (17,891 km<sup>2</sup>), open and deep lake with a mean depth of 51 m and a maximum depth of 230 m (Fig. 1). In 1994 the total phosphorus concentration of the surface water was 4 mg l<sup>-1</sup> in the pelagic zone compared to 59 mg l<sup>-1</sup> in the nutrient loaded littoral areas. Total nitrogen concentration varied from 484 to 819 mg l<sup>-1</sup>. The Secchi depth of the water was less

than 2 m in the littoral areas, compared to 3.3 m in the pelagic areas. In the surface water the phytoplankton biomass varied between 218 and 3575 mg m<sup>-3</sup> fresh weight (Holopainen et al. 1996).

In Finland the Saimaa lake system (4,460 km<sup>2</sup>) consists of several interconnected basins and the Saimaa drainage basin forms 25% of the drainage area of Lake Ladoga. Lakes Pyhäselkä and Paasivesi are situated in the northern Saimaa lake system. Lake Pyhäselkä has an area of 263 km<sup>2</sup>, a mean depth of 9 metres and a maximum depth of 67 metres. In May 1990 the colour of the water was brown (70 mg Pt l<sup>-1</sup>). The nutrient content was low, indicating mesotrophy: average total phosphorus 15 µg l<sup>-1</sup> and total nitrogen 538 µg l<sup>-1</sup>. In the northern part of Lake Pyhäselkä the Secchi depth of the water was 1.7 metres. In 1991 the mean phytoplankton biomass in the surface water was 338 µg m<sup>-3</sup> and mean chlorophyll *a* content was 5.0 mg l<sup>-1</sup> (Holopainen et al. 1993).

Lake Paasivesi has an area of 101 km<sup>2</sup>, a mean depth of 21 metres and a maximum depth of 74 metres. In May 1990 the water was light brown (colour 40 mg Pt l<sup>-1</sup>) and the Secchi depth of the water was 3.4 metres. The nutrient content was low: average total phosphorus 8 µg l<sup>-1</sup> and total nitrogen 412 µg l<sup>-1</sup>. Lake Paasivesi was the most oligotrophic lake in the study area. In July 1991 the phytoplankton biomass was 332 µg l<sup>-1</sup> and the mean chlorophyll *a* content was 3.0 µg l<sup>-1</sup> (Holopainen et al. 1993).

## Material and methods

In Lake Ladoga zooplankton samples for biomass determination were taken in August 1994 and in Lakes Pyhäselkä and Paasivesi in February-May 1990. In 1995 the comparative samples for analyses were collected within a week; the first period was 26 June in Lake Ladoga and 3 July in Lake Pyhäselkä, and the second period was 10 August in Lake Ladoga and in 16 August in Lake Pyhäselkä. The samples were taken with a 120 µm mesh conical net with a mouth reducing cone (mouth diameter 25 cm, total length 120 cm) and with a centrifugal plankton pump (a nominal flow rate of 170 l min<sup>-1</sup>).

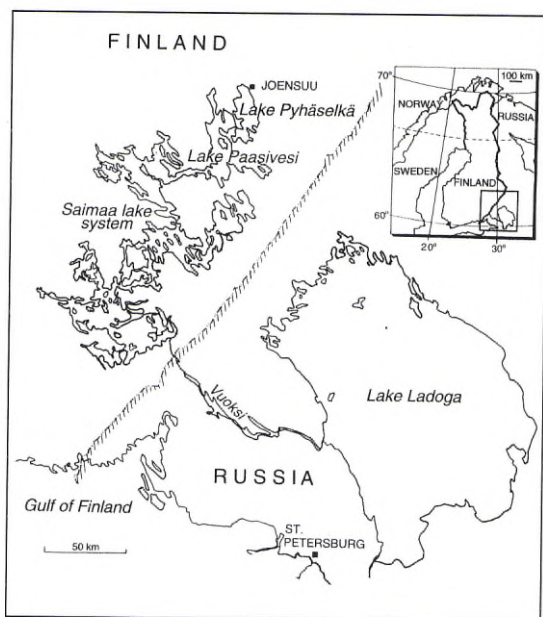


Fig. 1. Study area.

Immediately after sampling the animals were preserved in 4% formaldehyde and frozen at  $-18^{\circ}\text{C}$  for 1-8 months before the dry weight (DW) and carbon weight (CW) were analysed. Salonen and Sarvala (1980) observed no statistically significant differences in the carbon content of zooplankton preserved with this method. Thawed zooplankters were sorted by taxon, and some taxons were further sorted according to developmental stage and sex. The small cyclopoids *Mesocyclops leuckarti* and *Thermocyclops oithonoides* were treated as one taxon. After the animals were sorted from the samples, their length were measured in 1990 by inverted microscope and in 1994 and 1995 by an image processing system (Hamamatsu C2400 and Leitz Quantimet 500 -software). The measured lengths ( $L$ ) refer to the total length for cladocerans but do not include furcal rami in copepods. *Daphnia* was measured from the eye to the base of the tail spine. The measured individuals from Lake Ladoga were divided into size-classes.

Dry weights were determined only for the samples from Lake Ladoga. The number of animals used per weighing varied (1-10) according to the expected dry weight. To determine the DW of the animals, they were transferred to small oven-dried (2 hours at  $500^{\circ}\text{C}$ ) and pre-weighed aluminium cups. The animals were then dried for 24 hours at  $60^{\circ}\text{C}$  and allowed to cool in a desiccator before they were weighed on a microbalance (Sartorius Micro M3P). The sensitivity of microbalance was  $\pm 1\ \mu\text{g}$ .

In Lake Ladoga the measurements of carbon weight were made from the same animals as the dry weight determination. Carbon weight was determined with the high temperature combustion method of Salonen (1979). This method allows determination of carbon in single animals down to a size of  $0.01\ \mu\text{gC}$  (Latja and Salonen 1978). The animals were transferred to a high-temperature ( $+950^{\circ}\text{C}$ ) combustion tube. The released  $\text{CO}_2$  was measured by infrared gas analysis (URAS).

The length-weight relationships of planktonic crustaceans in the study lakes were described by a power function ( $y=ax^b$ ). In Lake Ladoga ten taxons were measured: four cladocerans (*Bosmina*

*longispina*, *Chydorus sphaericus*, *Daphnia* spp., *Limnospira frontosa*), five copepods (*Cyclops* spp., *Eudiaptomus* spp., *Eurytemora lacustris*, *Limnocalanus macrurus*, and small cyclopoids *Mesocyclops leuckarti* and *Thermocyclops oithonoides* together) and the large rotifer *Asplanchna priodonta*. In Lake Ladoga in 1994 these species made up more than 91% of the total zooplankton biomass. In the Saimaa lake system, four cladocerans (*Bosmina coregoni*, *Bosmina longispina*, *Daphnia cristata* and *Holopedium gibberum*) and four copepods (*Cyclops* spp., *Eudiaptomus* spp., *Eurytemora lacustris*, and small cyclopoids *Mesocyclops leuckarti* and *Thermocyclops oithonoides* together) were measured; these species made up over 80% of the total zooplankton biomass in Lakes Pyhäselkä and Paasivesi. Data of *Bosmina longispina* and small cyclopoids were gathered in 1995 and used to test the temporal variation and differences between the lakes by analysis of covariance (length as a covariate). The length-weight relationship and the statistical tests were performed using the SPSS program.

In order to clarify differences between lakes and seasons, the biomass of *Bosmina* was calculated from the data of various authors by means of the randomly selected population. Firstly, 100 lengths from the hypothetical populations were obtained randomly within the defined length range (0.3-0.57 mm). Then, different length-weight regressions were used to calculate the dry or carbon weights of the 100 animals of different sizes. Finally, the dry weights or carbon weights of all animals were summed up.

In addition to seasonal and interlake differences the estimates of dry weight between our equations (Table 1, August 1994) and the wet weights of Balushkina and Winberg (1979) were compared. The wet weights were transformed to dry weights by the dry weight-wet weight - coefficients of 0.11 and 0.03 for crustaceans and *Asplanchna*, respectively (Dumont et al. 1975). The calculations of the sums of dry weights were equal to the seasonal and interlake comparison except that in each taxon 10 simulations were made. The lengths of 100 individuals were obtained randomly within the length ranges given in Table 1.

Table 1. Dry weight-length relationship (mg/mm) in Lake Ladoga. Range of length measurements ( $L$ , mm), intercept ( $a$ ), slope ( $b$ ), number of observations ( $n$ ) and coefficient of determination ( $r^2$ ) are presented according to the power function  $w = aL^b$ .  $RMS$ = residual mean square. Statistically significant regression ( $P < 0.05$ ) are marked with an asterisk. Instars refer to nauplii (N), copepodites (C), and adults (ad).

Species	Date	$L$ (mm) <sup>1)</sup>	$a$	$b \pm SE$	$RMS$	$n$	$r^2$
<i>Asplanchna</i> spp.	Aug 1994	0.380-1.210	0.0032	0.69 $\pm$ 0.40	0.3005	19	0.16
<i>Bosmina longispina</i>	Aug 1994	0.330-0.870	0.0411	2.57 $\pm$ 0.47	0.2283	15	0.70*
<i>Bosmina longispina</i>	Jun 1995	0.290-0.565	0.0375	3.09 $\pm$ 0.51	0.1071	9	0.84*
<i>Bosmina longispina</i>	Aug 1995	0.270-0.775	0.0207	2.73 $\pm$ 0.20	0.0624	15	0.94*
<i>Chydorus sphaericus</i>	Aug 1994	0.205-0.345	0.0216	1.75 $\pm$ 0.74	0.1834	9	0.45*
<i>Daphnia</i> spp.	Aug 1994	0.430-2.110	0.0110	1.48 $\pm$ 0.15	0.1252	27	0.79*
<i>Limnospira frontosa</i>	Aug 1994	0.630-1.750	0.0094	2.69 $\pm$ 0.34	0.1996	40	0.63*
<b>Cladocera</b>	Aug 1994	0.205-2.110	0.0128	1.32 $\pm$ 0.09	0.2705	90	0.69*
<i>Eudiaptomus</i> sp. (C, ad)	Aug 1994	0.420-1.335	0.0100	1.48 $\pm$ 0.23	0.2146	35	0.55*
<i>Eurytemora lacustris</i> (C, ad)	Aug 1994	0.575-1.715	0.0072	2.57 $\pm$ 0.38	0.2085	30	0.62*
<i>Cyclops</i> spp. (C, ad)	Aug 1994	0.950-1.605	0.0061	3.63 $\pm$ 0.38	0.1111	31	0.75*
<i>Limnocalanus macrurus</i> (C, ad)	Aug 1994	1.905-2.585	0.0014	4.76 $\pm$ 0.89	0.1600	44	0.40*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad)	Aug 1994	0.340-0.930	0.0110	2.57 $\pm$ 0.15	0.0657	34	0.90*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad)	Jun 1995	0.340-0.845	0.0080	2.30 $\pm$ 0.33	0.1203	15	0.81*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad)	Aug 1995	0.355-0.945	0.0075	3.12 $\pm$ 0.29	0.1144	15	0.90*
<b>Copepoda</b>	Aug 1994	0.330-2.580	0.0100	2.27 $\pm$ 0.07	0.1774	151	0.88*

<sup>1)</sup> The lengths measured refer to total length and do not include furcal rami in copepods, and from the eye to the point of insertion of the caudal spine in *Daphnia*.

## Results

### Length-weight regressions

Regressions relating length (mm) to dry weight (mg) in several taxa of freshwater zooplankton were presented in Lake Ladoga (Table 1) as power functions  $w = aL^b$ , where  $L$  was length (mm),  $a$  was the intercept and  $b$  was the slope. The coefficients of determination ( $r^2$ ) for cladocerans indicated that 45-79% of the variation in dry weight could be explained by length (Table 1). In copepods  $r^2$  varied from 0.40 to 0.90. The relationship of  $DW$  to length varied greatly in *Limnocalanus macrurus* adults (Fig. 2). The general model explained only 44% of the observed varia-

tion in  $DW$  of *Limnocalanus macrurus*. The  $DW$ - $L$  regression calculated for all copepods ( $r^2 = 0.88$ ) fitted better than that calculated for all cladocerans ( $r^2 = 0.69$ ).

The carbon-length regressions of cladocerans and copepods are presented as power functions in Lake Ladoga and Lake Saimaa (Tables 2 and 3). In August 1994 in *Asplanchna* individuals the  $CW$ - $L$  relationship varied greatly. The power function explained only 68% of the observed variation in the carbon weight. In Ladoga the coefficients for the cladocerans indicated that 63-92% of the variation in the carbon weight could be explained by length (Table 2). The regressions include juveniles as well as ovigerous and non-

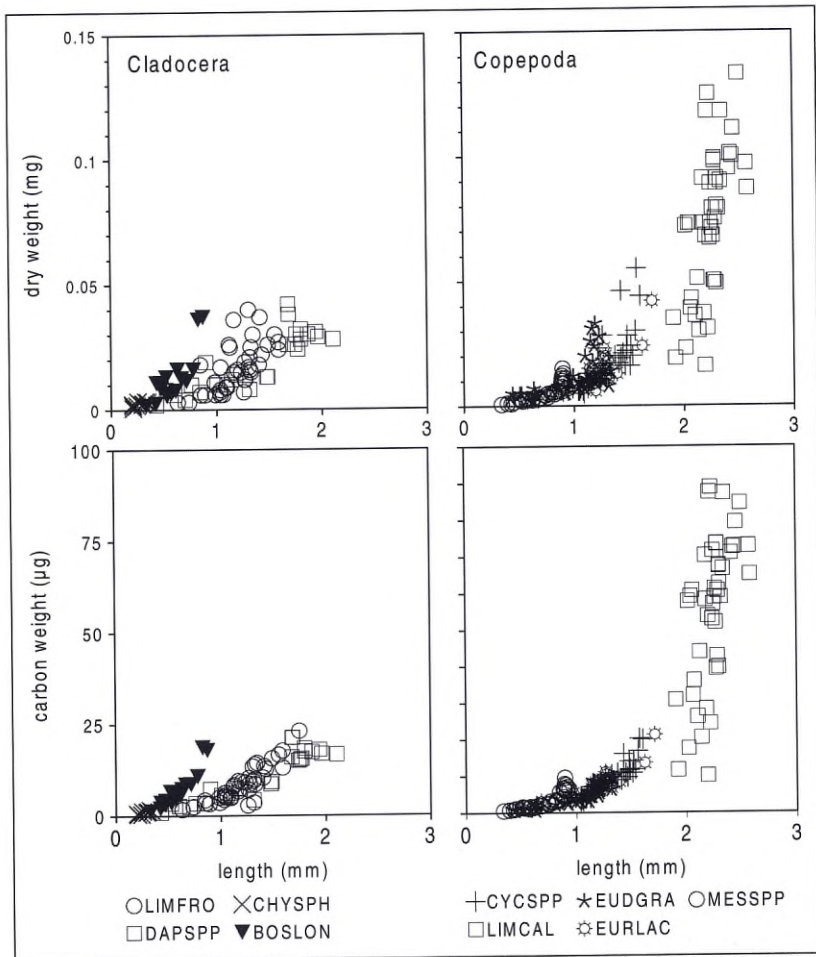


Fig. 2. Relationships between total length (mm) and mean individual weight expressed as dry weight (mg) and carbon weight ( $\mu\text{m}$ ) in four cladocerans and five copepods from Lake Ladoga.

(BOSLON=*Bosmina longispina*, CHYSPH=*Chydorus sphaericus*, CYCSPP=*Cyclops* spp., DAPSPP=*Daphnia* spp., EUDGRA=*Eudiaptomus* spp., EURLAC=*Eurytemora lacustris*, LIMCAL=*Limnocalanus macrurus*, LIMFRO=*Limnoscida frontosa* and MESSPP=*Mesocyclops leuckarti* and *Thermocyclops oithonoides*)

ovigerous adults. As in dry weight the regressions of carbon weight and length calculated for all copepods ( $r^2=0.91$ ) predicted carbon weight better than the regressions for all cladocerans ( $r^2=0.79$ ).

In Lakes Pyhäselkä and Paasivesi the carbon weight of similar-sized small cyclopoids (*Mesocyclops leuckarti* and *Thermocyclops oithonoides*) varied greatly and  $r^2$  was very weak. Otherwise, the power functions fitted well and length explained 32%–92% of the variation in the carbon weight of copepods (Table 3). In cladocerans the coefficients of determination were higher ( $r^2=0.73$ – $0.92$ ).

### Seasonal and lake-specific characteristics

Despite similar methods of measurement, the differences in the mean individual weight between the studied lakes were high. In order to explain these differences, two taxa were compared (Fig. 3). Temporal and lake-specific variation in the length-dry weight and length-carbon weight relationships for *Bosmina longispina* and small cyclopoids (*Mesocyclops leuckarti* and *Thermocyclops oithonoides*) were tested by analysis of covariance with year, lake, and month as factors and length as covariate. A significant seasonal

Table 2. Carbon weight-length relationship ( $\mu\text{g}/\text{mm}$ ) in Lake Ladoga. Range of length measurements ( $L$ , mm), intercept ( $a$ ), slope ( $b$ ), number of observations ( $n$ ) and coefficient of determination ( $r^2$ ) are presented for the power function  $w=aL^b$ .  $RMS$ =residual mean square. Statistically significant regression ( $P<0.05$ ) are marked with an asterisk. Instars refer to nauplii (N), copepodites (C), and adults (ad).

Species	Date	$L$ (mm) <sup>1)</sup>	$a$	$b\pm\text{SE}$	$RMS$	$n$	$r^2$
<i>Asplanchna</i> spp.	Aug 1994	0.380-1.210	1.34	0.98 $\pm$ 0.17	0.0537	18	0.68*
<i>Bosmina longispina</i>	Aug 1994	0.330-0.870	23.80	2.62 $\pm$ 0.21	0.0478	15	0.92*
<i>Bosmina longispina</i>	Jun 1995	0.290-0.565	40.42	3.83 $\pm$ 0.44	0.0789	9	0.92*
<i>Bosmina longispina</i>	Aug 1995	0.270-0.775	10.57	2.77 $\pm$ 0.20	0.0579	13	0.95*
<i>Chydorus sphaericus</i>	Aug 1994	0.205-0.345	19.80	2.41 $\pm$ 0.69	0.1620	9	0.63*
<i>Daphnia</i> spp.	Aug 1994	0.430-2.110	5.66	1.72 $\pm$ 0.12	0.0800	27	0.89*
<i>Limnospira frontosa</i>	Aug 1994	0.630-1.750	4.90	2.46 $\pm$ 0.23	0.0914	40	0.75*
<b>Cladocera</b>	Aug 1994	0.205-2.110	6.58	1.46 $\pm$ 0.08	0.2066	90	0.79*
<i>Eudiaptomus</i> (C, ad.)	Aug 1994	0.420-1.335	4.04	2.13 $\pm$ 0.16	0.0965	35	0.85*
<i>Eudiaptomus</i> (ad.)	Aug 1994	0.990-1.330	3.36	3.50 $\pm$ 0.70	0.0568	23	0.55*
<i>Eurytemora lacustris</i> (C, ad.)	Aug 1994	0.575-1.715	4.85	2.23 $\pm$ 0.15	0.0304	30	0.89*
<i>Cyclops</i> spp. (C, ad.)	Aug 1994	0.950-1.605	3.50	3.32 $\pm$ 0.25	0.0465	31	0.86*
<i>Limnocalanus macrurus</i> (C, ad.)	Aug 1994	1.905-2.585	1.35	4.48 $\pm$ 0.96	0.1835	44	0.34*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad.)	Aug 1994	0.340-0.930	7.18	2.56 $\pm$ 0.15	0.0684	34	0.90*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (ad.)	Aug 1994	0.510-0.990	8.12	3.08 $\pm$ 0.23	0.0621	29	0.86*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad.)	Jun 1995	0.340-0.845	4.88	2.62 $\pm$ 0.38	0.1627	14	0.80*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad.)	Aug 1995	0.355-0.945	3.78	2.98 $\pm$ 0.28	0.0973	15	0.91*
<b>Copepoda</b>	Aug 1994	0.330-2.580	5.38	2.56 $\pm$ 0.07	0.1661	151	0.91*

<sup>1)</sup> The lengths measured refer to total length and do not include furcal rami in copepods, and from the eye to the point of insertion of the caudal spine in *Daphnia*.

difference was detected for the dry and carbon weight of *Bosmina* ( $P=0.001$ ). However, there was no difference between the study lakes in 1995. Contrary to this, the dry weight and carbon weight of small cyclopoids did not differ seasonally, while there was statistical difference ( $CW, P=0.025$ ) between the study lakes. Between study years (1994-95) both *Bosmina* ( $DW, P=0.019$  and  $CW, P=0.003$ ) and small cyclopoids differed significantly ( $DW, P=0.004$  and  $CW, P=0.001$ ).

In order to further clarify the differences between lakes and seasons, the biomass of *Bosmina* (*Eubosmina*) is calculated from the data of the various authors. This generally observed variation is illustrated in Fig. 4. The other purpose was to point out possible mistakes when the length-weight regressions will be taken from the literature and used for the estimation of the biomass without any comparison. The estimated biomass ( $DW$ ) of *Bosmina* was lowest when calculated by use of the length-weight regression

Table 3. Carbon weight-length relationship ( $\mu\text{g}/\text{mm}$ ) in Lake Saimaa. Range of length measurements ( $L$ , mm), intercept ( $a$ ), slope ( $b$ ), number of observations ( $n$ ) and coefficient of determination ( $r^2$ ) are presented for the power function  $W=A L^B$ . RMS=residual mean square. Statistically significant regression ( $P<0.05$ ) are marked with an asterisk. Instars refer to nauplii (N), copepodites (C), and adults (ad).

Species	Date	$L$ (mm) <sup>1)</sup>	$a$	$b \pm \text{SE}$	RMS	$n$	$r^2$
<i>Asplanchna priodonta</i>	May 1990	0.540-0.900	1.72	1.94 $\pm$ 0.62	0.0761	7	0.62*
<i>Bosmina coregoni</i>	May 1990	0.360-0.625	14.67	2.92 $\pm$ 0.17	0.0188	29	0.92*
<i>Bosmina longispina</i>	May 1990	0.310-0.650	12.64	2.86 $\pm$ 0.17	0.0322	31	0.91*
<i>Bosmina longispina</i>	Jul 1995	0.255-0.805	13.31	2.65 $\pm$ 0.51	0.1612	18	0.73*
<i>Bosmina longispina</i>	Aug 1995	0.295-0.835	15.14	3.18 $\pm$ 0.28	0.1066	14	0.92*
<i>Daphnia cristata</i>	May 1990	0.385-0.915	5.17	3.05 $\pm$ 0.25	0.0535	27	0.86*
<i>Holopedium gibberum</i>	May 1990	0.445-0.575	7.47	2.98 $\pm$ 1.16	0.0656	6	0.62
<i>Eudiaptomus</i> spp. (N, C, ad)	May 1990	0.155-1.260	3.20	1.59 $\pm$ 0.05	0.0934	87	0.91*
<i>Eudiaptomus</i> spp. (ad)	May 1990	0.890-1.260	3.15	2.40 $\pm$ 0.36	0.0437	61	0.43*
<i>Eurytemora lacustris</i> (C, ad)	May 1990	0.205-1.945	3.35	1.56 $\pm$ 0.13	0.1800	14	0.92*
<i>Cyclops</i> spp. (N, C, ad)	May 1990	0.230-3.935	2.62	1.35 $\pm$ 0.12	0.1286	64	0.67*
<i>Cyclops</i> spp. (ad)	Mar 1990	0.935-1.320	2.10	4.45 $\pm$ 0.51	0.0443	25	0.76*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad)	May 1990	0.370-0.790	1.89	1.42 $\pm$ 0.23	0.0828	87	0.32*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (ad)	May 1990	0.530-0.790	3.03	2.94 $\pm$ 0.29	0.0290	40	0.73*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad)	Jul 1995	0.340-0.825	2.71	2.53 $\pm$ 0.35	0.1108	12	0.85*
<i>Mesocyclops</i> and <i>Thermocyclops</i> (C, ad)	Aug 1995	0.342-0.811	3.13	2.86 $\pm$ 0.34	0.1249	17	0.83*

<sup>1)</sup> The lengths measured refer to total length and do not include furcal rami in copepods, and from the eye to the point of insertion of the caudal spine in *Daphnia*.

derived from the eutrophic Lake Biel, Switzerland (Vuille 1991) and highest in the mesotrophic Lake Ladoga (Fig. 4A). Furthermore, the spring biomass were higher than the biomass of animals in late summer. Therefore, the possible mistake using the literature values may be in the worst case three times that of our own measurements. In general, the differences in the dry weight of *Bosmina* between our study and the literature values were rather small (Fig. 4B). The coefficient of variation between the data sets in Fig. 4 was 34% and thus, the average ratio between the estimated biomass of two different data sets was 1.4.

The carbon weights in different lakes were also rather similar (Fig. 4B). In the Saimaa lake system the difference between the lowest and the highest values was 1.3 times and in Lake Ladoga it was 3.5 times. The coefficient of variation between the data sets was 29% and thus, the average ratio between the total biomass of two different data sets was 1.3. The results clearly indicated that a researcher must carefully inspect the suitability of the length-weight regressions before using them for own data or measure dry or carbon weights directly from the populations under study.

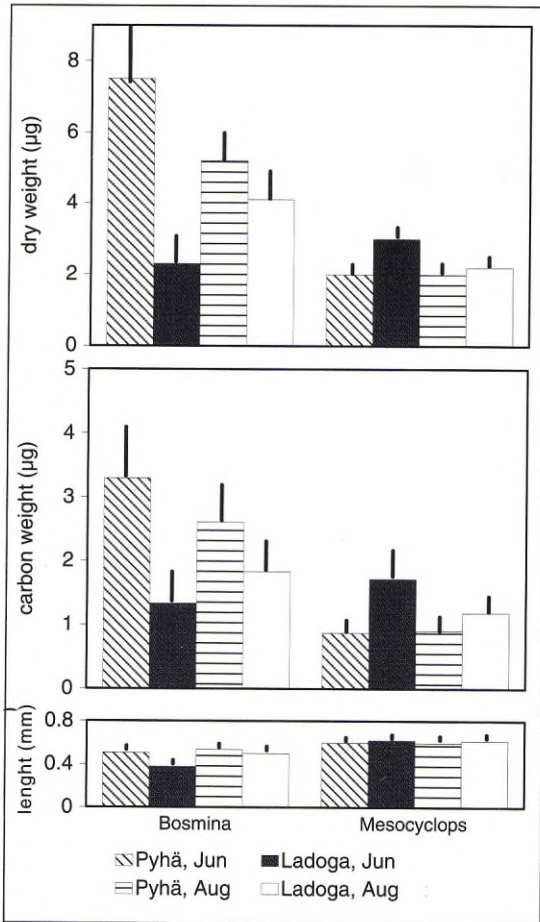


Fig. 3. Differences in mean individual weight ( $DW$   $\mu\text{g}$  and  $CW$   $\mu\text{g}$ ) and length (mm) of *Bosmina longispina* and small cyclopoids (*Mesocyclops leuckarti* and *Thermocyclops oithonoides*) between two sampling dates: June 1995 (6) and August 1995 (8) and two lakes: Pyhäselkä and Ladoga.

## Discussion

Culver et al. (1985) stated that "the differences between the length-weight relationships for a single species in different bodies of water are the norm, not the exception". These lake-specific variations in length-weight relationships were showed in this study. However, the variation in weight was generally well explained by the power regression with length; the coefficients of deter-

minations ( $r^2$ ) were in most cases high, except in the regressions of adult calanoids (cf. Latja and Salonen 1978). The relationship between body length and individual body weight depends on changing environmental conditions. Hessen and Lyche (1991) stated that the intraspecific variation in elemental composition was restricted, but in their study similar sized adult animals with corresponding egg numbers were used, on the contrary, in our material animals varied with size, age and egg numbers. The seasonal variation in food supply thus influences the size of lipid stores in cladocerans (Tessier and Goulden 1982) which store lipids as energy reserves (Goulden and Horning 1980). In Lake Ladoga the biomass-length regression of *Bosmina* for 1994 predicted higher biomass values for respective lengths than that of 1995. This was also true for other species in August 1994. The primary productivity and phytoplankton biomass in Sortavala bay were two times higher in August 1994 than in August 1995 (Holopainen and Letanskaya 1998). Water temperature was also in August 1994 higher than in 1995. The availability of food, the efficiency of the assimilation and finally the conversion of food to the growth was suggested to result in the differences in the length-weight relationship of *Bosmina*. Inter-lake variation is likely produced by the same factors although the trophic level of the lake seem not always to be the major factor e.g. in eutrophic Lake Biel, the sum of dry weights of *Bosmina* was lower than in meso- or oligotrophic lakes Ladoga and Saimaa (Fig. 4 A).

Inter-annual and seasonal variation in mean individual weight of *Bosmina* and small cyclopoids were more pronounced than lake-specific. Generally, both copepods and cladocerans (Manca et al. 1994) of the same length are heaviest in spring (Bottrell et al. 1976, George 1976, Culver et al. 1985, Geller and Müller 1985, Duncan et al. 1985, Kankaala and Johansson 1986, Vuille 1991). Vuille and Maureer (1991) stated that seasonal variations in body size with larger forms maturing during the colder periods in the year have been attributed to the influence of water temperature on development time (George 1976) but other factors as reduced food availability (Geller and Müller 1985, Duncan et



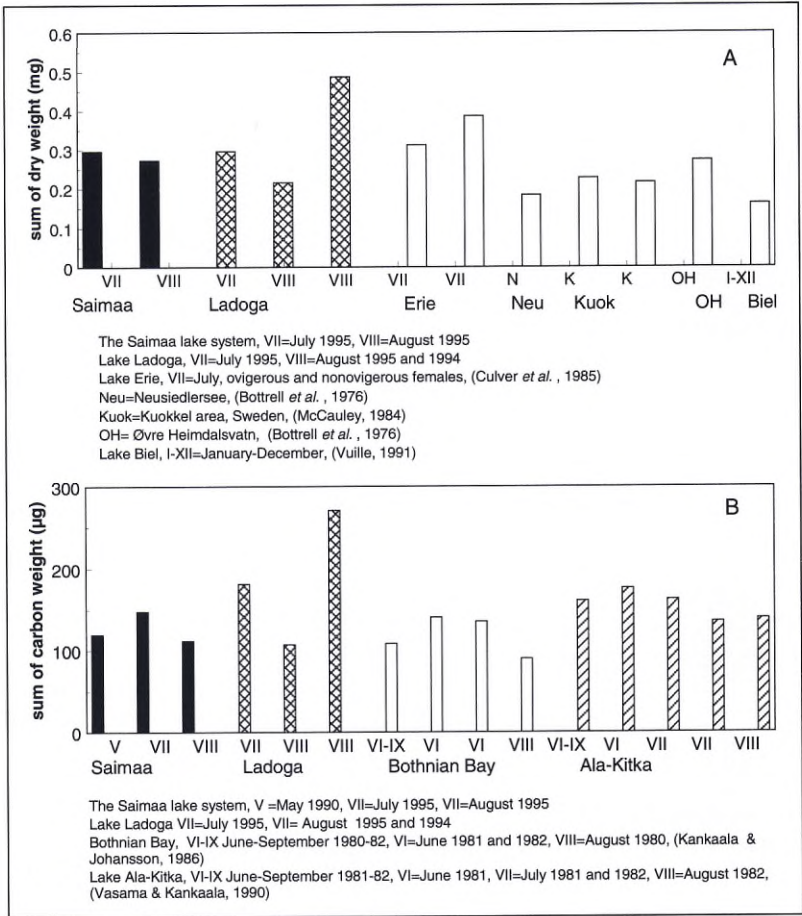


Fig. 4 A, B. Sum of the dry weight (mg): A and carbon weight (µg): B of 100 randomly selected *Bosmina* (*Eubosmina*) spp. calculated according to our own length-weight regressions in lakes Saimaa and Ladoga and comparable data from other investigations.

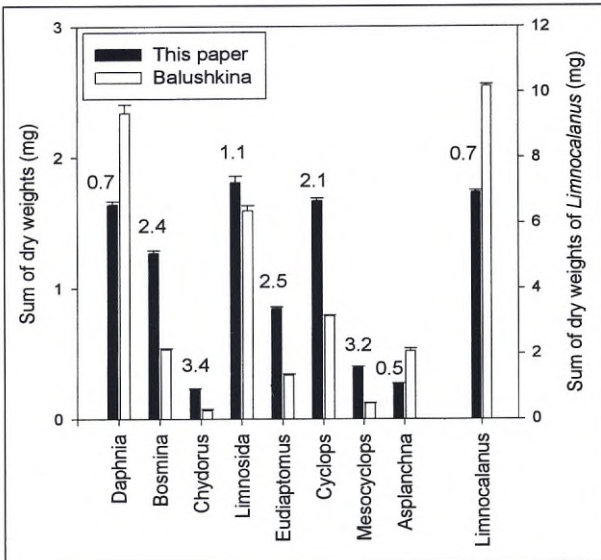


Fig. 5. The comparison between the sums of dry weights of 100 individuals in the hypothetical population calculated according to our and Balushkina's and Winberg's (1979) length-weight equations. The ratio between two equations (our equation : Balushkina's and Winberg's equation) of different taxa and the standard error (vertical line) of 10 simulations were also given.

al. 1985, Kawabata and Urabe 1998) or selective predation on larger animals (Brooks and Dodson 1965) might play an important role as well.

Thereby, the comparison of biomass estimates between different studies may be problematic. For example, the biomass estimates from Lake Ladoga made during the 1990s are based on the length-wet weight -equations of Balushkina and Winberg (1979). We compared the estimates of dry weight between our equations (Table 1, August 1994) and their equations. The average of the simulations is presented in Fig. 5. This comparison indicated that the general wet weight equations fitted poorly for the estimation of biomass in Lake Ladoga in August 1994. The ratio between the estimates calculated according to two equations varied from 0.5-3.2.

The part of residual variation may be caused by sampling and methodological differences or techniques. In our results the preservation method or time before the measurement should not affect the results, because the preservation and handling of samples was equal. The several studies indicated that freezing in 4% formaldehyde or 1-2% glutaraldehyde provided superior preservation for most aquatic invertebrates (Salonen and Sarvala 1980, Salonen and Sarvala 1985, Campbell and Chow-Fraser 1995).

Several studies have been performed for developing the different methods for the estimation of the zooplankton biomass. Bird and Prairie (1985) elaborated the practical guidelines for the use of zooplankton length-weight regression equations. They warned about the biases due to grouping animals, transformation and the variation in the precision of length measurements. Our results indicated that the seasonal variation (CV%) calculated between the different data sets of *Bosmina* was approx. 30%. The simulation models which produce a predicted size distribution including the variation in the biomass between individual animals at equal size should be developed. According to coefficient of determination and residual mean square of regression at least in copepods for rare or less abundant taxon it seemed to reasonable to use pooled equations

for Copepoda rather than to apply literature equation (Table 1 and 2).

In summary, without any comparison between own data and the regressions obtained from the literature the biomass estimates may include serious errors. Thus, we recommend that at least once in every sampling season the dry or carbon mass of 30-60 individual animals within the size range of a local population should be measured.

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# Behaviour and Sex Hormone Levels in Brook Charr\* (*Salvelinus fontinalis*) Males Paired with Females

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## Abstract

Brook charr male behavioural and endocrine responses to nest-digging females were examined and compared with males paired with juvenile fish of the same age and size. In addition, responses of intact and anosmic mature males were compared. The intact males courted ovulated and nest-digging females but did not show any interest for the juvenile fish. Intact males paired with ovulated females had also significantly higher concentrations of the sex hormones  $17\alpha,20\beta$ -dihydroxy-4-pregnen-3-one ( $17\alpha,20\beta$ -P) and testosterone (T) and enhanced volumes of strippable milt compare to males with juvenile fish. Anosmic males courted nest-digging females as readily as the intact males, but their volumes of strippable milt and plasma concentration of  $17\alpha,20\beta$ -P were significantly lower. There was no difference in the plasma concentration of T between intact and anosmic males. The study showed that brook charr males are willing to spawn though they are not able perceive odours. The lower levels of milt and plasma concentrations of  $17\alpha,20\beta$ -P in anosmic males suggest, however that ovulated females emit odours that have a stimulating effect on the activity in the testis. The lack of difference in T concentration between intact and anosmic males may suggest that some other sense(s) that register the behaviour or appearance of the female was sufficient to stimulate an increase in T.

Keywords: behaviour, milt, olfaction, pheromones, reproduction, salmonids, *Salvelinus*, steroid hormones.

## Introduction

Increasing number of studies have shown that chemical signals are important for synchronization of reproduction in teleost fish (reviews by Liley 1982, Stacey and Sorensen 1991, Lambert and Resink 1991). Previous experiments have shown that rainbow trout (*Oncorhynchus mykiss* Walbaum) and kokanee salmon (*O. nerka* Walbaum) males are strongly stimulated, both behaviourally and through the endocrine system, by exposure to nest-digging conspecific females. The males had significant enhanced sperm volumes and plasma concentrations of steroid hormones and gonadotrophin II (only measured in kokanee) (Olsén and Liley 1993, Liley et al. 1993). Anosmic males of these two species were still able to spawn, but had significantly lower vol-

umes of strippable milt and plasma hormone levels compared to sham operated fish, suggesting that ovulated females emit chemical cues with effects on the males within the two *Oncorhynchus* species (Olsén and Liley 1993, Liley et al. 1993). The chemical signals responsible for these responses in the males have not been identified yet but are in the rainbow trout females present in the urine (Scott et al. 1994, Vermeirssen et al. 1997). Female odours that stimulate enhanced sex hormone levels in males are also present in Atlantic salmon (*Salmo salar* Linné) and brown trout (*Salmo trutta* Linné) (Moore and Waring 1996, Olsén et al. 1998). Studies of pheromonal effects on the plasma hormone levels in males within the genus *Salvelinus* are lacking. However,

\* See Morton (1980) for common name and spelling.

it has been shown by electro olfactogram (EOG) that the olfactory sense in brook charr (*Salvelinus fontinalis* Mitchell) is sensitive to putative hormonal pheromones (Essington and Sorensen 1996, Bjerselius and Olsén pers. comm.) and spermiating Arctic charr (*S. alpinus*) males release odours that attract females (Sveinsson and Hara 1995). In the present study we observed the behavioural and endocrine responses of intact brook charr males paired with nesting females or juvenile fish of the same age and size. In addition anosmic males were paired with nesting females.

## Methods

### Fish

Brook charr (2+) (males:  $126.4 \pm 8.3$  g,  $n=26$ ; females:  $132.0 \pm 12.8$  g,  $n=18$ ; juvenile:  $125.0 \pm 11.8$  g,  $n=4$ ) were supplied by a local hatchery on 31 October, 1990. Males and females were immediately placed indoors in two separate fiber glass tanks at the Department of Environmental Toxicology, Uppsala University. Juvenile fish were placed together with the females. All males had running milt and were brightly coloured with parts of the ventral side of the body in black. The females were gravid and close to ovulation. Juvenile fish were slim and less coloured than the mature females. The juvenile fish were checked after the experiment and the gonads were rudimentary. The tanks were supplied with through-flowing aerated Uppsala tap water (10 °C). The automatic light/dark cycle corresponded to Hamburg's latitude and longitude.

### Experimental design

All experiments were performed in glass aquaria (102 cm long, 48.5 cm wide and 45 cm deep) supplied with tap water at a rate of 1 L/min. The bottom of the aquaria were covered with gravel (2-5 mm diameter). An ovulated female or a juvenile fish was placed in the aquarium at about 16:00, ca. 16 h before the male. The male was stripped of milt immediately before it was placed with the fish at 08:30 (this milt volume is called sample 1=S1). Eight of the males were made anosmic by

supply of vaseline with a pasteur pipette to the olfactory chamber, which surrounds the olfactory epithelium on each side of the head (Olsén 1993). The vaseline prevented water from entering the olfactory chamber. In total nine intact males were paired with ovulated females and eight intact males were paired with juvenile fish. Eight anosmic males were paired with ovulated females. All ovulated females were nest-digging. All females and juveniles were only used once. The frequency of the following behaviour patterns were observed: male "bouts of quivering" and "digging" by females (Smith 1941, Power 1980).

Each pair of fish was kept together from 08:30 to 15:30. Behavioural observations were done between 10:30 and 10:45 and between 15:15 and 15:30. The male was caught and anaesthetized (2-phenoxyethanol, 0.05%) immediately after the final observation session. Blood samples were taken and milt collected (this milt volume is called sample 2=S2).

### Blood and milt samples

Blood was collected with a heparinized syringe from *ductus cuvieri* of anesthetized males (2-phenoxyethanol, 0.05%). The blood samples were centrifugated for 90 s at 7,000 rpm. Plasma samples were kept at -80 °C. Anaesthetized males were stripped of milt by applying gentle abdominal pressure. The milt was drawn by suction into a glass tube, whereby care was taken to exclude urine (Olsén and Liley 1993). The amount of milt was determined by the difference in weight of the tube, before and after the supply of milt.

### Hormone assays

Testosterone (T) and  $17\alpha,20\beta$ -dihydroxy-4-pregnen-3-one ( $17\alpha,20\beta$ -P) were measured with specific radioimmunoassays (RIA) in unextracted plasma. Plasma samples (100 µl) were combined with 1.9 ml assay buffer and heated to 70 °C for 1 h (Scott et al. 1982, 1983). Plasma levels of T and  $17\alpha,20\beta$ -P were measured using the procedures described and validated by Van der Kraak et al. (1984). For further details see Liley et al. (1993). All plasma samples were first analysed regard-

ing the content of T before the  $17\alpha,20\beta$ -P analyses. In some males there were not enough plasma for both hormone analyses.

### Statistical analysis

Wilcoxon's two-sample test was used to analyse both behavioural and hormone data (Colquhoun 1971). The correlation among behavioural data, milt volumes and hormone concentrations were estimated by calculating the Spearman rank correlation coefficients and testing the significance of the coefficients (Siegel 1956). Tests are two-tailed unless stated otherwise. The level of significance was set at  $P=0.05$ .

### Reliability test of the vaselin nose plugging

The method to prevent odours to reach the olfactory epithelium was tested in an experiment with juvenile Arctic charr of just about the same size as the brook charr. Juvenile Arctic charr are strongly attracted to water scented by conspecifics and they are able to discriminate between odours from siblings and nonsiblings of the same population (e.g. Olsén 1989). Intact Arctic charr and fish treated with vaseline were tested according to the protocol of Olsén (1989) with siblings scenting one water current in the fluvium and only water in the other. Control fish were treated in the same way except no vaseline was applied. The fish were tested four days after treatment. A fish's preference for either water quality was determined on the basis of the number of observations in each. The three intact fish showed strong attraction to the water scented by siblings (ca. 70% of the time in the scented water, 30% in unscented water) but the six vaseline treated fish were indifferent (ca. 50% of the time in the scented water). The difference in behaviour was further confirmed by the significant difference in the number of observations in the scented water between intact and treated fish ( $P<0.05$ , Wilcoxon's two sample test). The fluvium test gave strong support for that the vaseline "nose plugging" method was reliable.

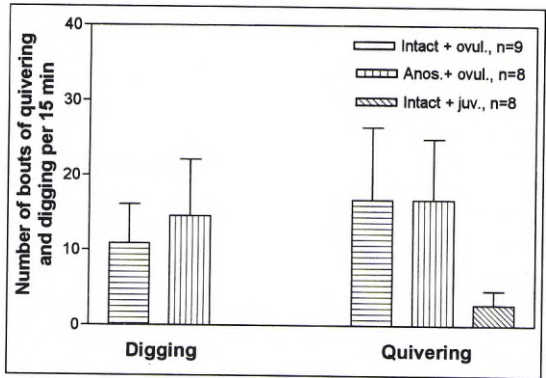


Fig. 1. Sexual behaviour of brook charr males and nest preparing of conspecific females (means  $\pm$ SD). Some males had been made anosmic by vaseline applied to the olfactory chamber. Both intact and anosmic males had significantly higher frequency of courtship quiver directed to ovulated nest digging females compare to males paired with juvenile fish (both  $P<0.001$ ).

### Results

Intact males courted nest-digging females but showed low interest for the juvenile individuals (Fig. 1). The amounts of strippable milt was also significantly higher in the males paired with digging females (Fig. 2).

Plasma concentrations of  $17\alpha,20\beta$ -P and T were higher in intact males together with nesting females compare to males paired with juvenile fish (Fig. 3a and b). Anosmic males courted the females as frequent as intact males. No significant differences in frequency of bouts of quivering were observed (Fig. 1). Anosmic males had, however, significantly lower sperm volumes and lower plasma concentrations of  $17\alpha,20\beta$ -P compared to intact fish (Fig. 2 and 3b). No significant differences in plasma concentrations of T were observed between intact and anosmic males (Fig. 3a). A significant positive correlation was observed between the frequency of digging in females and frequency of quivering in intact males (Fig. 4). A positive correlation between the digging and quivering frequency was also observed in anosmic males, but the correlation was not significant ( $r=0.60$ ;  $P=0.21$ ;  $n=6$ ). The failure to get a significant correlation may be due to the fact

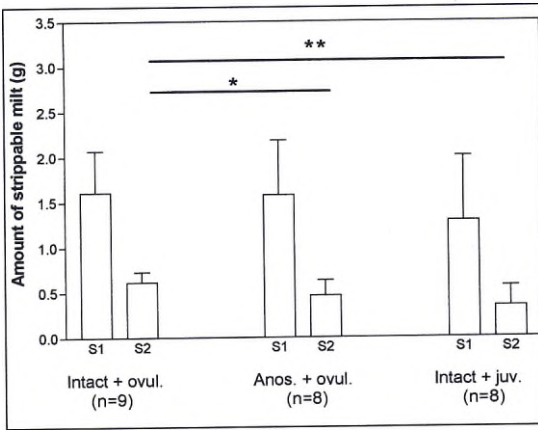


Fig. 2. Volume of available milt in intact and anosmic mature brook charr males paired with nest digging females or juveniles of the same age and size. Males were stripped milt immediately after they were removed from the holding tank containing only males (sample 1=S1) and before they were paired with a fish. Milt samples (Sample 2=S2) and blood samples were taken 420 min after pairing. Column, mean  $\pm$ SD. Significant differences: \* $0.05 < P < 0.01$ ; \*\* $0.01 < P < 0.001$  (one tailed).

that the most active male, which was paired with a low activity female, did not fit in the over all distribution.

No significant correlations were observed between milt volumes and size of the male; milt

volumes and hormone levels; milt volumes and digging frequency; milt volumes and quivering frequency; hormone levels and frequency of quivering; hormone levels and frequency of digging.

## Discussion

Previous studies with two *Oncorhynchus* species, rainbow trout and kokanee salmon, have demonstrated that ovulated nest digging females have strong stimulatory effect on the behaviour and the plasma sexual hormone levels and milt volumes of conspecific males (Liley et al. 1986, Olsén and Liley 1993, Rouger and Liley 1993, Liley et al. 1993). Experiments with anosmic males gave strong support for the hypothesis that an odour or a mixture of odours is acting as the priming signal or is an important part of it (Olsén and Liley 1993, Liley et al. 1993). Anosmic rainbow trout males had significant lower plasma concentrations of sex steroid hormones but courted and spawned with the females as readily as the sham operated fish. Scott et al. (1994) and Vermeirssen et al. (1997) have demonstrated that urine from mature rainbow trout females contain chemical cues with priming effect on conspecific males. The plasma concentrations of sex steroids and gonadotrophin II were enhanced in the males after exposure to female urine.

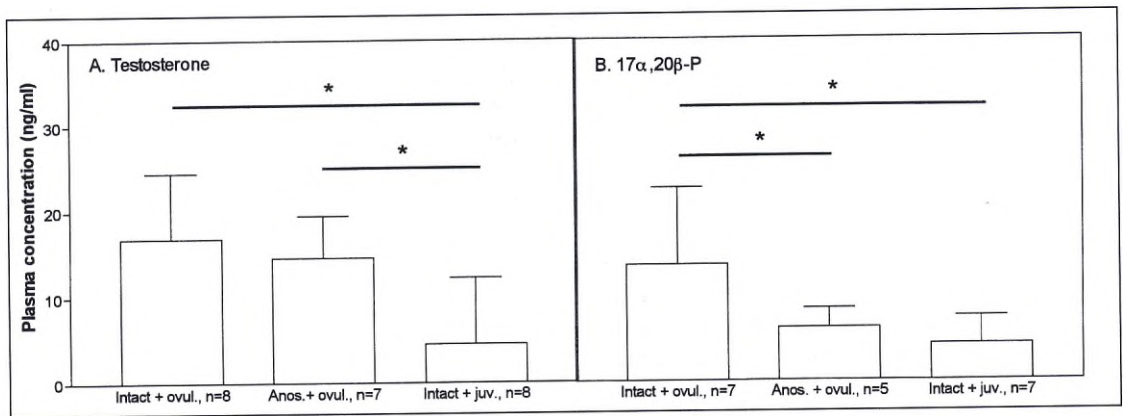


Fig. 3. Plasma concentrations of gonadal steroids in intact and anosmic mature brook charr males after 420 min pairing with a nest digging female. Intact males were also placed with a juvenile fish. The less number of hormone analyses done compare to the number of pairs studied (Fig. 1 and 2) was due to too small amounts of plasma from some males.  $17\alpha,20\beta\text{-P} = 17\alpha,20\beta\text{-dihydroxy-4-pregnen-3-one}$ . Column, mean  $\pm$ SD. \* $0.05 < P < 0.01$ .

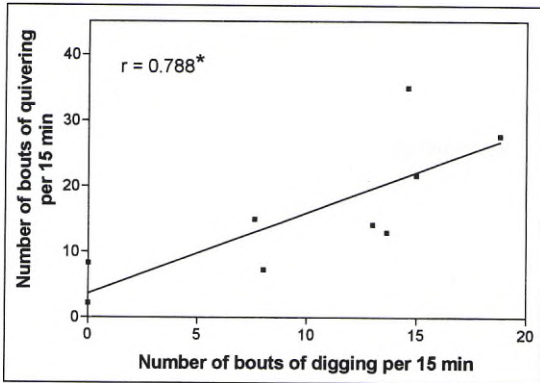


Fig. 4. Quivering frequency of intact males as a function of female digging frequency. The behaviour of males and females were studied during two 15 min periods (between 10:30 and 10:45 and between 15:15 and 15:30) per experiment which was run from 08:30 and 15:30. Each square represents the mean value for the two 15 min observations per female and corresponding male per experiment.  $**0.01 < P < 0.001$ .

In the present study we demonstrated that also within the genus *Salvelinus* are the endocrine system of males primed by ovulated and nest digging females. Milt volumes and plasma concentrations of T and  $17\alpha,20\beta$ -P were significantly higher in males interacting with digging females compared to those paired with nonvitellogenic individuals. The lower milt volumes and plasma concentrations of  $17\alpha,20\beta$ -P in anosmic males compared to intact individuals paired with a digging female points to the existence of a chemical signal with priming effects. *In vitro* studies have shown that salmon gonadotrophin stimulates  $17\alpha,20\beta$ -P production in the testes from rainbow trout and amago salmon (*Oncorhynchus rhodurus*) during the period of active spermiation (Sakai et al. 1989 a,b). This suggests that the effects of the chemical signal(s) on the testis and milt are through the pituitary as has been suggested for rainbow trout (Olsén and Liley 1993).

In contrast to the previous results with rainbow trout and kokanee salmon, the testosterone levels in anosmic brook trout males were not significantly lower than in intact males. These results may indicate that the behaviour and/or

appearance of the female is sufficient to stimulate the increase of testosterone. In fact there was a strong positive correlation between the female digging frequency and the frequency of quivering in intact males. However, no significant correlations were observed between hormone levels in males and the behaviour of females. There was also a positive correlation between quivering in anosmic males and digging in females, but the correlation was not significant due to one out of range male. The results may indicate that the female behaviour in combination with her appearance (great difference from the male in for instance colour) stimulate increased T levels of the courting male.

In conclusion, the present results give strong support to the existence of priming chemical cues emitted by ovulated females within the genus *Salvelinus* which have developed separated from *Salmo* and *Oncorhynchus* for about 20 million years (Behnke 1991). These and the previous results with rainbow trout, kokanee salmon, Atlantic salmon and brown trout (Olsén and Liley 1993, Liley et al. 1993, Moore and Waring 1996, Olsén et al. 1998) make us to suggest that female priming chemical signals are present within at least three salmonid genera. The priming odours may be important for the synchronization of the male spawning readiness (maximum amount of milt) with that of the female.

## Acknowledgments

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# Short-term changes of Crustacean Plankton Reproduction and Juvenile Survival in some Acidified and Limed High Mountain Lakes

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## Abstract

The reproduction of zooplankton was studied in four small lakes in an acidified high mountain area. The lakes have different liming management histories and only in the lake with the most intense liming management (Lake St. Rösjön), did a *Daphnia galeata* population become established. This population declined when liming ceased for some time. The rise and fall in the calcium+magnesium content coincided rather well with the short-time changes in the population. When liming ceased no deviation from normal clutch size in the *D. galeata* population could be observed, and the population decrease could not be related to reduced reproduction of the females (as defined). Mortality prior to reproduction was high during this episode. Lack of calcium at molting is a possible reason for this mortality. Higher calcium+magnesium content through liming also seemed to favour *Mixodiptomus. laciniatus* populations. When this content decreased in Lake St. Rösjön during the break in the liming, the *M. laciniatus* density was low again. The reproduction of *M. laciniatus* was not related to acidification in a simple way. Egg/embryo number per female was inversely related to population size, indicating an internal regulating mechanism in the population. Possible factors controlling hatching of resting eggs and survival of nauplii and/or copepodites are discussed.

Keywords: Cladoceres, diaptomids, reproduction, acidification, calcium, juveniles.

## Introduction

Among the factors involved in the reproduction of crustacean zooplankton the importance of food limitation in the trade-off between reproduction and other energy-consuming activities has been emphasized (Lampert and Muck 1985, Williamson and Butler 1987, Chow-Fraser and Maly 1991, Gliwicz 1991, Urabe 1991, Brandl and Wittingerová 1991 Ringelberg et al. 1991, Brett 1993, Branstrator and Lehman 1991).

Research into population development and reproduction of crustacean plankton in acidified lakes is reviewed by Brett (1989), Locke (1991) and Stenson et al. (1993). Toxicity of pH or aluminium is here added to the possible controlling factors. Locke concludes 'The pH at which re-

productive impairment is observed often seems to correspond better to field data than does the pH level for survival.'

The Fulufjäll area (Fig. 1, Table 1) is undergoing a process of acidification, and a number of fish and other animal species are on the verge of extinction. The area is favourable for a field study of acidification as several small, fairly similar lakes differ with respect to acidification and liming history (Lindström et al. 1984). This may perhaps outweigh the gap in the series of year in the methodology.

Sampling in the 1970's and in 1989-90 enabled a study of changes in crustacean plankton populations during this period (Lindström 1992) but the effects on reproduction could not be analyzed with that material. The present paper will test if

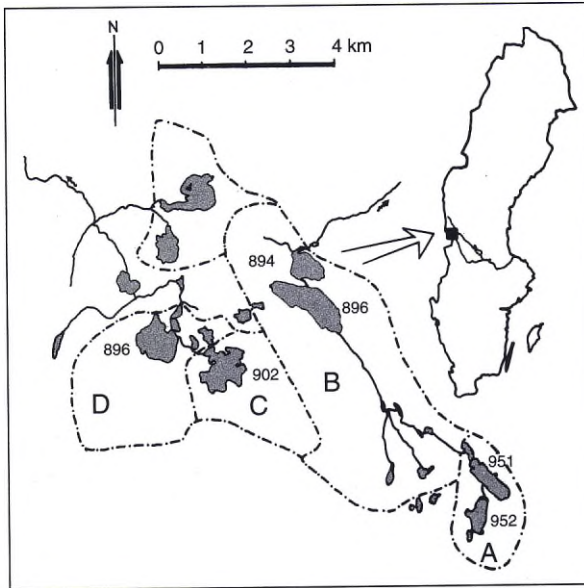


Fig. 1. Map of the Fulufjäll lakes, altitudes (metres) and drainage areas. A=Lakes Ö. Särnamannasjön and N. Särnamannasjön, B=Lakes St. Rösjön and L. Rösjön, C=Lake St. Harrsjön, D=Lake L. Harrsjön.

Table 1. Some characteristics of the investigated lakes when the development started that is reported in chapter Results. The most important zooplankton genus is underlined in each case.

Lake	Liming	Fish populations	Main crustacean plankton
L. Harrsjön	In autumn 1979 and again later, see text	Trout and occasional burbot	<i>Cyclops</i> , <u><i>Bosmina</i></u> and <i>Holopedium</i>
N. Särnamannasjön before 1975 and Ö. Särnamannasjön		No fish	<i>Mixodiatomus</i> , <i>Heterocope</i> and <u><i>Bosmina</i></u>
N. Särnamannasjön after 1975	In 1975 and again later	Char	<u><i>Mixodiatomus</i></u> and <i>Bosmina</i>
St. Rösjön	In 1962 and again later	Char	<i>Cyclops</i> , <i>Mixodiatomus</i> , <u><i>Bosmina</i></u> and <i>Holopedium</i>

the short time population changes of cladoceran species and *M. laciniatus* brought about by acidification and liming are the effects of changes in reproduction.

## Material and methods

The zooplankton material was obtained using a 5.3 litre plankton sampler, by the method fully

described in earlier papers (Lindström 1952, 1958, 1992). The content of plankton in a sample was allowed to settle and was then transferred by pipette to a plankton chamber. The size of the entirely new material is indicated in Table 2 but the results are also based on material from the 400 samples in the paper in Swedish (Lindström 1992).

Table 2. Numbers of samples in 1991 and 1992. The series from 1976-79 and 1989-90 have been published in Swedish (Lindström 1992) and includes some 400 samples.

	Lake St.Rösjön		Lake L.Harrsjön	
	Sampled depths	n	Sampled depths	n
24 Aug 1991	Surface	5		
	1 m	5		
	Bottom	5		
25 Aug 1991	Surface	4		
	1 m.	4		
	Bottom	4		
13 Sep 1991	Surface	3		
	1 m.	3		
	Bottom	3		
23 Jun 1992	Surface	2	Surface	2
	1 m.	2	1 m	2
			5 m	2
	Bottom	2	Bottom	2
6 Jul 1992	Surface	3		
	1 m.	3		
	Bottom	3		
28 Jul 1992	Surface	2	Surface	2
	1 m.	2	1 m	2
			5 m	2
	Bottom	2	Bottom	2
10 Aug 1992	Surface	3		
	1 m.	3		
	Bottom	3		
25 Aug 1992	Surface	2	Surface	2
	1 m.	2	1 m	2
			5 m	2
	Bottom	2	Bottom	2

The zooplankton reproduction was studied by counting the eggs/embryos of *Mixodiaptomus laciniatus* Sars and *Cyclops scutifer* Sars in the egg sacs and eggs/embryos of *Daphnia galeata* Sars, *Eubosmina longispina* Leydig (*Bosmina coregoni longispina*) and *Holopedium gibberum* Zaddach females in the egg chambers. Reproduction was also studied in terms of the proportion of females carrying eggs/embryos and number of juveniles. Loose sacs of *M. laciniatus* and loose eggs/embryos of Cladocera are included in the material.

The crest of *Daphnia galeata* is high in the summer but the denticle is low, in old females often insignificant. The taxonomy of some *Daphnia* populations in the region is treated in Lindström (1992).

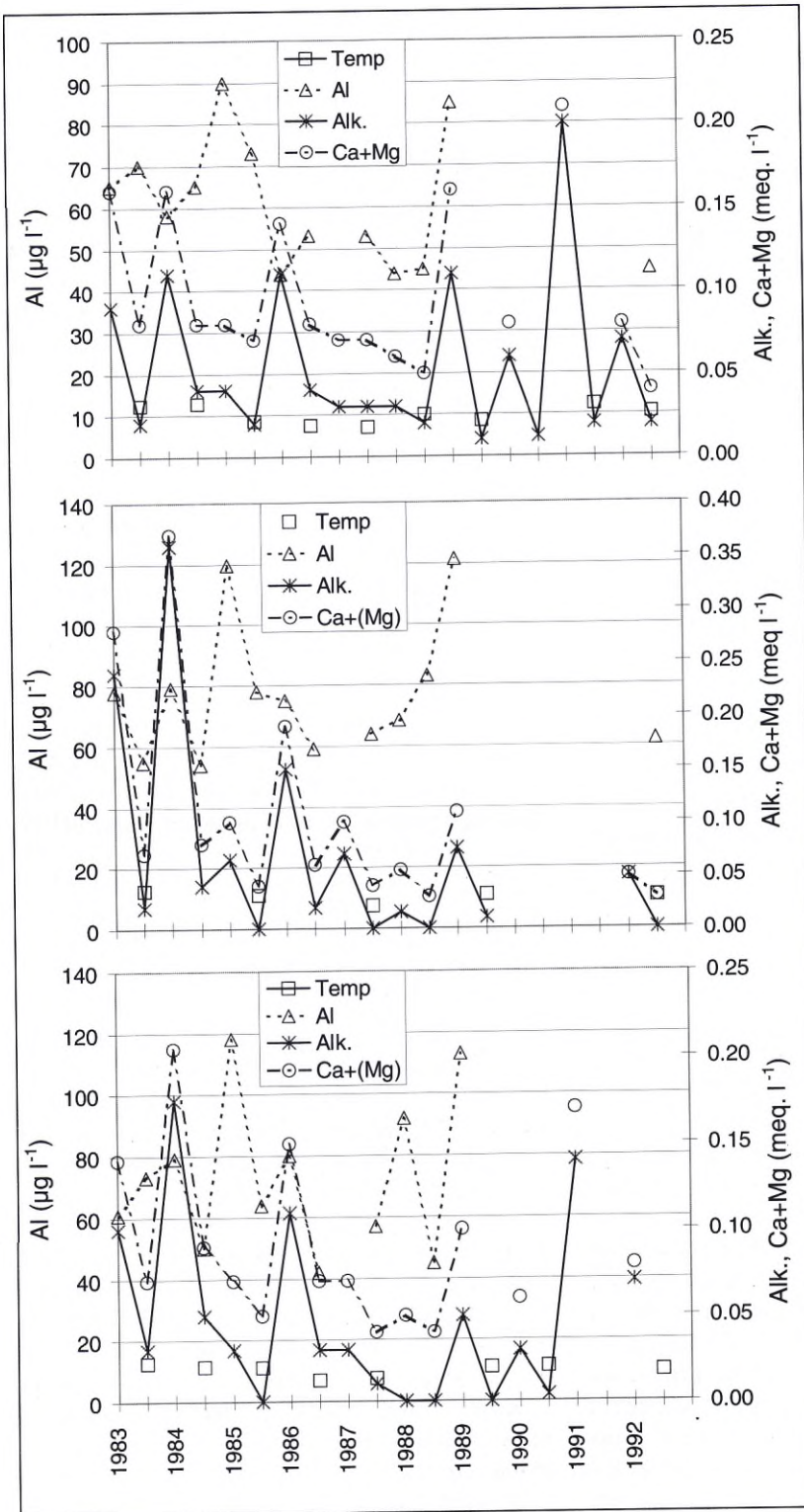
Furthermore the following anecdotic information is relevant: (1) The yearly trends in population density and reproduction of *H. gibberum* were difficult to reduce to a simple pattern (Lindström 1992). That report suffered from some printing errors but the general impression remains (2) Plankton samples from 1989 were obtained by vertical netting, and their densities should be corrected upwards by as much as a factor of 2 (Jensen 1988, Bottrell et al. 1976), cf Figs. 3,4 and 5 for comments.

Statistics: The significances of differences between groups are tested with Anova analysis, the binomial test or the Chi-square test for heterogeneity.

### The Fulufjäll area

The rock in the Fulufjäll area is a limefree sandstone. The effects of acidification in the area have been monitored by the Swedish Environmental Protection Agency (SEPA) since the year 1972, and the management of liming is planned accordingly. The annual fluctuations in water chemistry following liming up to and including 1982 are reported by Dickson (1975, 1981) and by Lindström et al. (1984). The lakes were limed from aircraft in the autumns of 1983, 1985, 1988, 1990 and there was also an automatic lime dispenser working at the inlet to Lake St. Rösjön for most of the open water season from 1983 up to 1991. The results in Figs. 2a-c are from unpublished SEPA data supplemented with information from the county administration for Dalarna and from the Institute of Freshwater Research. Magnesium forms only a very small part of calcium+magnesium content.

Liming was temporarily disrupted in 1991 as no lime was deposited in the autumn, and the lime dispenser in Lake St. Rösjön was out of order for most of 1992, so that the lake was not limed again until the late summer of that year. Precipitation in the summer 1992 was extremely low until mid-July (Table 3).



Figs 2 a-c. Water quality from 1983 onwards. Y-axis to the left: total aluminium content (in microgrammes per litre), and temperature, Y-axis to the right: alkalinity and calcium+magnesium (meq. l<sup>-1</sup>). Two occasions per year at most: late winter and summer.  
 a) Lake St. Rösjön,  
 b) Lake L. Harrsjön,  
 c) Lake St. Harrsjön (just upstream from Lake L. Harrsjön).

Table 3. Precipitation at Särna in 1992 according to the Metereological and Hydrological Institute of Sweden.

Month, whole or part	Precipitation sum (mm)	Precipitation % of normal
Jun	2.4	3
1-7 Jul	0.3	
Jul	88.9	105
Aug	168.5	237

The ice generally breaks up at the end of May or the beginning of June and temperatures oscillate around 10-15 °C from midsummer to the middle of August and then decline towards freezing by October, when the ice forms once again. The lakes are shallow and the turnover time is a couple of months.

The fish fauna consists of brown trout and/or arctic char (Table 1). The diet of the char contains chironomids, trichoptera larvae, *Eurycercus* and *Bythotrephes* but very little true plankton in the 1970's (copepodits of *Cyclops* and *Eubosmina* (Hanson 1976, Lindström et al. 1982)). When the fish population mainly consists of trout the predation pressure from fish on the zooplankton is still lower (Maria Hanson, pers. comm.). Among invertebrate predators *Heterocope* and *Bythotrephes* are known to occur, *Bythotrephes* mainly through fish food studies. A predatory role of *Mixodiaptomus* and *Cyclops* is not ascertained for here relevant species but possible (cf. Morgan et al. 1980, Anderson 1970). Other predators are Corixids and Dytiscidae larvae and they are very sensitive to fish predation (Eriksson et al. 1980) and the important char populations in the lakes should keep their densities low.

When the development started that is reported in Results the situation was as follows (Table 1):

Lake L. Harrsjön was the least acidified of the studied lakes. The composition of the crustacean plankton was not very different from that in naturally acid lakes in the high mountains of northern Sweden. The *E. longispina* specimens were (and are) large and the carapax regularly red-brown. The *M. laciniatus* population was small in the 1970's.

Lakes Ö. Särnamannasjön and N. Särnamannasjön were the most acidified of the studied lakes. All fish life was extinct when the first plankton samples were taken (Hanson 1974). The *M. laciniatus* observed in Ö. Särnamannasjön were bright brick red and not in very good condition. Lake N. Särnamannasjön differs from the other lake in that it was limed in 1975 and again later. The liming doses were kept small at the beginning of the project as in other lakes on Fulufjäll, in order to minimize the disturbance of the extremely dilute water chemistry.

Lake St. Rösjön had been subject to the most intense reclaiming programme in the Fulufjäll area from 1962 onwards. The aluminium and alkalinity values were kept at levels acceptable for the char population through continuous liming. Some information is available on phytoplankton (Hörnström 1979, E. Hörnström pers. comm.). Some single *D. galeata* specimens were observed in 1976.

## Results

### Annual cycles of the zooplankton.

#### Establishment of a *D. galeata* population

The annual cycles of the Crustacean zooplankton in Lake L. Harrsjön were taken to represent the general pattern in the Fulufjäll area (Lindström 1992). Annual cycles from August 1991 to August 1992 with respect to all the crustacean plankters in Lake St. Rösjön are shown in Figs. 3-6. Except for the cycle of *D. galeata* the annual cycles in Lake St. Rösjön do not differ much from those in Lake L. Harrsjön. The number of *M. laciniatus* eggs cannot be estimated in early August, but it reaches its final value towards the end of that month. There was no *D. galeata* population in the lakes before 1983 but the occurrence of one was verified through stomach analysis of char from 1984 in Lake St. Rösjön. The *D. galeata* density curve in 1989-90 culminated in August. The mean clutch size of *D. galeata* at the earliest date of the summer season in the material studied here, 14th June 1990, was=5.5 in Lake St. Rösjön and the number of eggs/embryos >25 per 5 litre and >1 per female (all females

included). Reproductive activity decreased during later seasons, and the clutch size did not exceed 2 again. *E. longispina* reproduction was also high on 14th June 1990 as the number of eggs and embryos approximately equalled the number of females (all females included). No clutch size figure can be given, as the *E. longispina* females dropped their eggs/embryos very easily during preparation. After a decline in the middle of the summer, their reproductive activity showed high values again in August-September in some cases (from 0.7 to 0.8 eggs/embryos per female).

### Density and reproduction of Cladocera populations

The *D. galeata* population was established in Lake St. Rösjön when the calcium+magnesium content rose in 1983 to a higher level than before (Chi-square analysis of heterogeneity in contingency tables for distribution of calcium+ magnesium content equal to or above 0.07 milliequivalents/l or lower and notations 1976-82 or 1983-91 give a  $P=0.00$ ). The annual density cycle in 1989/1990 followed the regularly occurring pattern over a wide region of Scandinavia. When the liming program was interrupted in autumn 1991 - late summer 1992 and the flow through the lake was low, implying a reduced spread of calcium from existing old moulds, the calcium+magnesium content dropped to the lowest level in ten years in August 1992 and the density of the recently established *D. galeata* population of Lake St. Rösjön decreased while the *E. longispina* density increased (Figs. 3 and 4, Anova analysis gives  $P=0.00$  for both comparisons). The clutch size in the *D. galeata* population remained between 1.00 and 1.36 until 23rd August in 1992 when the few remaining females had a mean clutch size of 1.6. The reproduction of *E. longispina* also increased towards the end of the summer (Fig. 4). When Lake L. Harrsjön was reclaimed by liming in 1979 and later, no population of *Daphnia* was observed, only some single dead specimens (in 1992) suggesting mortality before reproduction. *Daphnia* was not observed in Lake St. Harrsjön (Lindström 1992). The water chemistry data from Lakes L. and St. Harrsjön indicate only small dif-

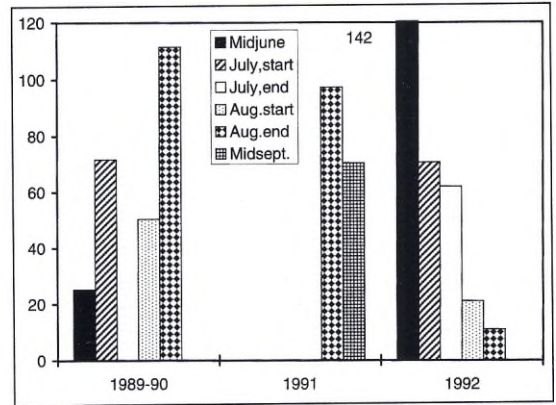


Fig. 3 a. Mean density of *Daphnia galeata* in a vertical column in Lake St. Rösjön in 1989 to 1992, numbers per 5 litres. The sample for 23rd August 1989 was obtained with a vertical net and corrected by doubling (cf. Material and methods).

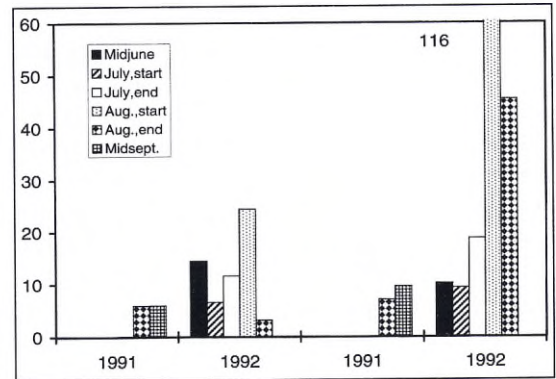


Fig. 3 b. Mean density of eggs and embryos of *Daphnia galeata* in a vertical column in Lake St. Rösjön in 1991 and 1992, numbers per 5 litres (left) and 100 times the mean numbers per female, all females included (right).

ferences relative to Lake St. Rösjön (Figs. 2a-c), but there was no lime dispenser in these lakes.

Among other factors within the present observations a drastic change in the phytoplankton was indicated by a mass development of *Melosira* in 1989 (Lindström 1992). In the years following after 1989 *Staurastrum* has replaced *Melosira* as the mass net phytoplankton in Lake St. Rösjön, with densities regularly above 10,000 per 5 litres, net mesh size 70 mikrons. For *Staurastrum* and products from its decomposition as a poten-

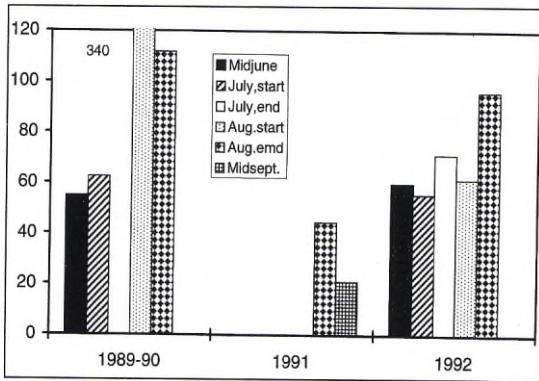


Fig. 4 a. Mean density of *Eubosmina longispina* in a vertical column in Lake St. Rösjön in 1989 to 1992, numbers per 5 litres. The sample for 23rd August 1989 was obtained with a vertical net and corrected by doubling (see Material and methods).

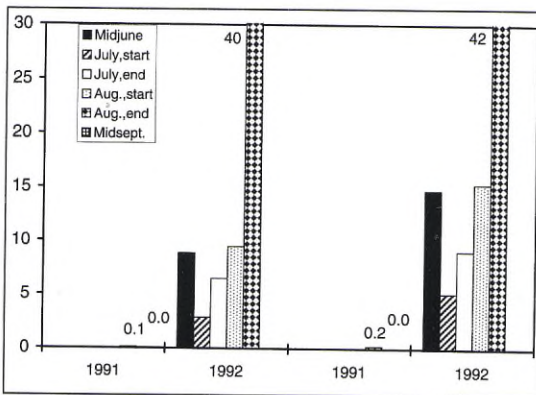


Fig. 4 b. Mean density of eggs and embryos of *Eubosmina longispina* in a vertical column in Lake St. Rösjön in 1991 (Aug. end and Midsept.) and in 1992, numbers per 5 litres (left) and 100 times the mean numbers per female, all females included (right).

tial *Daphnia* food see Lampert (1987), Hartmann and Kunkel (1991) and King and Shiel (1993). There was no observed effect on the phytoplankton in this lake when the *Daphnia* population decreased in 1992, as the mass development of *Staurastrum* that had started in 1990 continued and its density exceeded 10,000 per 5 litres in all the 1991 and 1992 samples. There are, however, no data on nanoplankton. No *Melosira-Staurastrum* community appeared in Lakes L. and St. Harrsjön.

The char started to feed on *D. galeata* when they became available in Lake St. Rösjön in the 1980's but there is no relevant change in the char population. The char populations in Lakes L. and St. Harrsjön are smaller than that in Lake St. Rösjön.

## Density and reproduction of *M. laciniatus* in three lakes

Lake L. Harrsjön was limed repeatedly in the years following the summer of 1979, so that the calcium+magnesium content rose above those recorded before liming. Alkalinity and aluminium levels became equivalent to those in the lakes that had already been limed for some time, Lakes St. Rösjön and St. Harrsjön (Figs. 2a-c). Successful reproduction of char in Lake St. Harrsjön in 1980 meant that this population began to grow and to disperse downstream to Lake L. Harrsjön, forming a substantial part of the fauna of this lake in the 1980's. The character of Lake L. Harrsjön is also approaching that of the other reclaimed lakes in this respect. The small *M. laciniatus* population in Lake L. Harrsjön increased at some time between autumn 1979 and 1992. (Anova analysis for a comparison of late August values in the years 1976 to 1979 and those in 1992 give a  $P = 0.00$ ). In August 1992, when the density of this population was 5.5 per 5 litres, reproduction was almost equal to that in Lakes St. Rösjön and St. Harrsjön in 1979 (Fig. 5a).

After test liming of Lake N. Särnamannasjön with an extraordinarily high dose in 1977, leading to peak calcium+magnesium content in 1978-79, the population of *M. laciniatus* reached the highest density ever observed in any of the Fulufjäll lakes (Fig. 5a). Individual female reproduction fell to very low values, as did the number of eggs/embryos per female, all females included.

Lake St. Rösjön had been limed for many years. The *M. laciniatus* density increased from 1976 to 1979 and reached a peak in 1989 after a gap in the sampling series (Fig. 5b, Table 4). Reproduction per female was low in 1989. The density decreased in 1990 and 1991. As a result of the break in liming management, the calcium+



Table 4. Relation between *Mixodiaptomus* female size and number of eggs/embryos in the egg sacs. The length is measured between the top of the head and the apical end of the furcal rami, in ocular units (30 o.u.=1 mm).

	Lake St. Rösjön 23 Aug 1989	Lake St. Rösjön 13 Sep 1991	Lake St. Rösjön 23 Aug 1992	Lake L. Harrsjön 23 Aug 1992
Density	30.85	6.60	8.18	5.54
Eggs per sac	7.18	7.47	11.20	9.00
Eggs per female	3.50	3.73	6.09	6.93
Mean female length	42.43	43.14	42.64	44.24
SE of length	0.21	0.72	0.82	0.42

magnesium content in August 1992 was the lowest in ten years and on a par with those recorded in 1976-81, while the *M. laciniatus* density in August was comparable to those at the start of this study (Fig. 5b). Reproduction per female in

1992 was higher than during the period 1989-91. The decrease in copepodit density in late August from 1991 to 1992 was significant (Anova analysis,  $P=0.00$ ) but the adult density decrease was not significant.

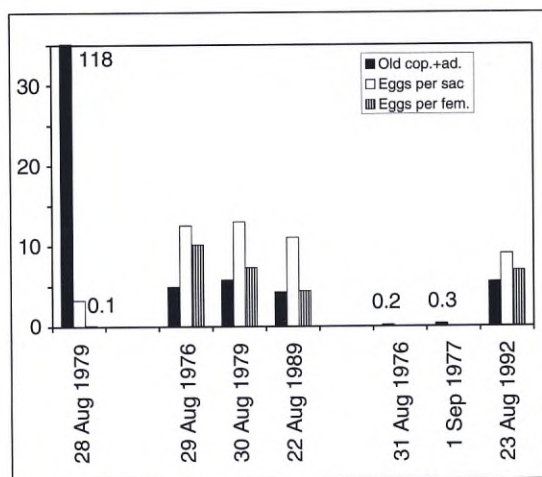


Fig. 5 a. Reproduction of *Mixodiaptomus laciniatus* in Lakes N. Särnamannasjön (left), St. Harrsjön (centre) and L. Harrsjön (right). Black bars indicate densities of old copepodites plus adults in a vertical column, numbers per 5 litres. There is no information about egg numbers in Lake L. Harrsjön in 1976 and 1977.

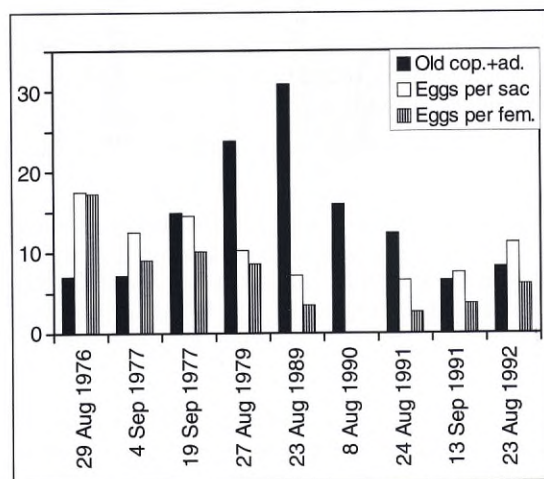


Fig. 5 b. Reproduction of *Mixodiaptomus laciniatus* in Lake St. Rösjön. Black bars indicate densities of old copepodites plus adults in a vertical column, numbers per 5 litres. The sample for 23rd August 1989 was obtained with a vertical net and the bar should be corrected upwards (not performed here). The egg sacs were incomplete on 8th August 1990, but the black bar indicates what a maximal density estimate for the end of August would be.

## Discussion

### Annual cycles of Crustacean zooplankton

The seasonal reproduction pattern of Cladocera in the Fulufjäll lakes in 1989-91 starts at the breaking up of the ice in May/June, with high reproduction by the females derived from the resting eggs. The development of Cladocera should be fairly slow at the temperatures prevailing in high mountain lakes (Bottrell et al. 1976, Bennet and Boraas 1989, Brett et al. 1992), but as post-embryonic development is dependent on both temperature and food (Bottrell et al. 1976, Kankala and Wulff 1980, Morgan et al. 1980, Gliwicz 1985, Brandl and Wittingerová 1991), there is a scope for variation - see e.g. Langeland et al. (1985) and Hrbáčková-Esslova (1962). A detailed analysis of the sequence of generations of Cladocera during the summer is not possible with the present material, but the study will gain support from research carried out in the region in or close to the Scandinavian high mountains. It appears that 1) bimodality in *Bosmina* density may occur, 2) the *Bosmina* and *D. galeata* density curves may reach their culmination in July, August or September, and 3) clutch sizes and/or

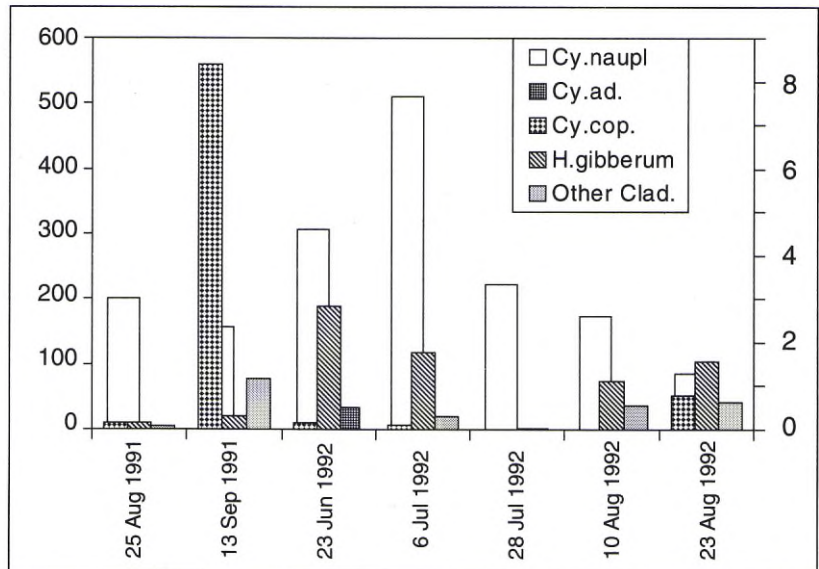
the number of eggs/embryos per total number of females are high in the first reproduction pulse, with clutch sizes decreasing to one or two in late summer (Lindström 1952, Axelson 1961a,b, Lötmarker 1966, Larsson et al. 1985, Jensen 1988). This summary of Scandinavian plankton research will be used as a reference when discussing the 1992 episode below.

The biology of the copepods is highly flexible, and their annual cycles are adapted to the predator pressure (Strickler and Twombly 1975, Stich and Lampert 1981, Hairston and Walton 1986, Hairston 1987, De Stasio 1990, Neill 1990, Hairston and Dillon 1990), i.e. characteristics of local validity. The fish predation pressure in the present Fulufjäll area is low and the prevailing conditions have led to annual cycles, in which *Cyclops scutifer* occurs only as nauplii for much of the summer and *M. laciniatus* is univoltine, overwintering as resting eggs, with the adults developing in late summer.

### Short-time changes in the *D. galeata* population size

There are lakes in the Fulufjäll area where neither *D. galeata* nor *H. gibberum* are observed, and lakes with a *H. gibberum* but without a *D.*

Fig. 6. Mean density of crustacean plankton in a vertical column in Lake St. Rösjön in 1991 and 1992, apart from *D. galeata*, *E. longispina* and *M. laciniatus*. Numbers per 5 litres. Y-axis to the left refers to *Cyclops* nauplii and adults only.



*galeata* population. Either *D. galeata* in Lake St. Rösjön was never completely exterminated but only very few, or else diapause eggs which had been resting for many years were activated (Carvalho and Wolf 1989, De Stasio 1990, De Meester and De Jager 1993) or a re-establishment resulted from some rare distribution opportunity and was perhaps delayed by invertebrate predators as shown by Henrikson et al. (1984); the theme of the present paper is not a comprehensive study of the factors controlling the *D. galeata* populations in the Fulufjäll area. Some clues to the problem of population control may, however, be obtained by a study of the development in Lakes St. Rösjön and L. Harrsjön.

The study suggests that the water qualities (Figs. 2a and b) are in the vicinity of the tolerance limits for the species. The aluminium content, however, was far below those reported by Brett (1989) and Locke (1991) in their reviews. If the aluminium content nevertheless was toxic to the *D. galeata* in this district (all the aluminium was in unchelated form, Lindström et al. 1984), it was yet not particularly high in Lake St. Rösjön in August 1992 (45 µg/l). The rise and fall in the calcium+magnesium content in Lake St. Rösjön and the time for occurrence of a lime dispenser coincide rather well with the increase and decrease in the *D. galeata* population. No other single factor within the present observations show covariation with the *D. galeata* population.

### Reproduction and juvenile mortality in Cladocera

When a *D. galeata* population was (re-)established in Lake St. Rösjön the pH latitude in 1983-91 was 5.4-6.8 (Table 5) and fits the region for successful *Daphnia* reproduction according to Locke (1991), whereas the latitude in Lake L. Harrsjön where no population occurred was lower in 1987-89 (5.2-5.6). The calcium+ magnesium content in Lake St. Rösjön was high during 1983-91 and not yet alarmingly low early in 1992. The *Daphnia* clutch size had probably passed beyond an early season maximum by the first sampling occasion in 1992 but this cannot be verified. The *Daphnia* density was at this oc-

Table 5. pH in three lakes in 1983-92.

St.Rösjön		St.Harrsjön		L.Harrsjön	
Date	pH	Date	pH	Date	pH
830405	5.9	830405	5.97	830404	6.2
830802	6.5	830802	6.25	830802	6.3
840331	6.3	840331	6.2	840331	6.5
840605	6.5	840605	6.44	840605	6.4
850331	5.6	850331	5.43	850331	5.7
850722	5.9	850722	5.64	850722	4.8
860401	6.1	860407	5.94	860405	6.1
860805	6.4	860805	6.29	860805	5.9
870406	5.5	870406	5.39	870406	5.6
870904	6.4	870903	5.67	870903	5.3
880328	5.4	880328	5.13	880322	5.2
880829	6.1	880829	5.58	880829	5.2
890403	5.9	890403	5.63	890403	5.7
890906	6.1	890822	5.2	890822	5.3
900330	5.8	900330	5.5		
900704	6.1	900704	5.6		
910403	6.8	910409	6.4		
910825	5.6				
920329	6.2	920327	5.9	920324	5.9
920824	6.3			920824	5.4

casion the highest observed in the present study and over 80 percent of the specimens were juveniles. One measure of reproduction employed here – number of eggs and embryos per female, all females included – varies i.a. with the density of juvenile females and the measure increased to the highest values observed in the lake in August 1992 when the calcium+ magnesium content was low (Fig. 3). Juveniles formed less than 50% of the low density at the start of August. Dead specimens were observed in the samples from 1992. The clutch size for the few remaining adult females attained its maximal value on 23rd August. No trend in the reproduction was observed that could explain the population decrease in 1992 but juvenile mortality may. This is in accordance with the views expressed by Walton et al. (1982), Nilssen et al. (1984): high egg numbers are not equivalent to dense populations as the ontogeny up to adult stage may mean great losses. The importance of access to a minimum calcium amount (necessary at molting or otherwise) is discussed by Havas (1985), Yan

et al. (1989) and Tessier and Horwitz (1990), and this explanation fits the population development better than does the pH-value separately - the pH was still high in August 1992, 6.3 (Table 5).

The *E longispina* population in Lake St. Rösjön increased until the latest sample occasion in 1992, and the normal reproduction rate per female would be responsible for an expected expansion when the competing zooplankton decreased in the deteriorating environment (Locke and Sprules 1993).

### Short-time changes in the *M. laciniatus* population sizes

Diatomids are often regarded as an acid-tolerant genus group but the present results don't comply quite well with this view as liming was followed by such important increases in population sizes. The difference between the Fulufjäll area and other acidified regions in Scandinavia (Stenson et al. 1993) is possibly an effect of the low calcium levels in the Fulufjäll area.

High-dose test liming in Lake N. Särnamannasjön and the start of liming in Lake L. Harrsjön were both followed by an increase in *M. laciniatus* density.

In Lake St. Rösjön, the automatic lime dispenser set up in 1983 provided a more continuous passage of lime into the water during the summer. The turnover time of the Fulufjäll lakes is only about a couple of months and the lime was now being introduced directly into the inflowing water rather than being present as a deposit in one bay of the lake as it had been before. The calcium+magnesium content reached a higher level in 1983-88 than earlier, and some very high values occurred in April 1989 and March 1991. In 1989 the *M. laciniatus* population reached a higher density than earlier, and in 1992, when the calcium+magnesium content dropped, density fell again to a value similar to that prevailing at the start (Fig. 5b).

The *Melosira/Staurastrum* responded dramatically to the new liming management, and the *M. laciniatus* peak in Lake St. Rösjön in 1989 could have been linked to the *Melosira* increase, as these algae may be desirable food objects

(Vanderploeg et al. 1988). There are only small amounts of other algae in the Fulufjäll lakes of length that suits the conditions reported by these authors (Lindström 1992, Table 10). Diatomids, however, also feed on many other objects (Nauwerck 1962, Williamson and Butler 1986, Vanderploeg et al. 1988, Williamson and Vanderploeg 1988, Hartmann et al. 1993), so *Staurastrum* may have been an acceptable food object in this lake up to the end of the study. The *Staurastrum* changes does not comply with the *M. laciniatus* population changes. The important expansion of the *M. laciniatus* population in Lake N. Särnamannasjön was not accompanied by any observed change in the phytoplankton.

Char was just becoming established at approximately the time when *M. laciniatus* increased in Lakes L. Harrsjön and N. Särnamannasjön. Rather than being a predator on *M. laciniatus*, char may have reduced the densities of some invertebrate predators (Stenson 1976, Eriksson et al. 1980, Hanson 1976) and thereby also favoured *M. laciniatus*. There was no major change in the char population of Lake St. Rösjön documented for the here relevant period, so the focus should perhaps be placed on the calcium+magnesium factor.

The colour of *M. laciniatus* in the fishless Lake Ö. Särnamannasjön may be explained as a sign of predation pressure from visually hunting predators that is low enough to allow the development of good protection against solar radiation (Hairston 1979b, Hobaek and Wolf 1991, Siebeck and Böhm 1991). The population was however small.

### Reproduction and juvenile mortality in *M. laciniatus*

The reproduction of *M. laciniatus* was not related to acidification in a simple way in the present material. When the population densities increased after start of, or increase in liming, the reproduction decreased and when the density of the *M. laciniatus* population of Lake St. Rösjön decreased during a break in the liming management in the summer 1992, the reproduction increased again. The egg/embryo number per fe-

male was inversely related to the population size. The population changes are not reflected in the mean size of adult *M. laciniatus* (as is shown for prosome length by Chow-Fraser and Maly 1991) because the size differences are insignificant. Thus no reaction of clutch size to mean thorax + abdomen length is evident but some kind of internal population regulation is indicated by the quoted inverse relation. If a high number reach the adult stage, the population may rise too high and some resources will not suffice for egg production (Williamson and Butler 1987), but these resources are not identified in the present case.

One may hypothesize that low reproductive effort of the females adjusts a possible surplus survival from resting eggs. When the low calcium+magnesium content increased through liming, it may somehow have stimulated the hatching of a larger than normal proportion of the resting egg reserve in the bottom sediment i.e. a particular form of reproduction (De Stasio 1990, though see the discussion in Redden and Daborn 1991). Moreover, the increased calcium levels favoured perhaps the bottom vegetation in these shallow lakes, and it is plausible to assume that the vegetation can protect the nauplii and copepodites against harmful solar radiation on days when this is strong (Hairston 1979a,b, Luecke and O'Brien 1981, Hobaek and Wolf 1991, Ringelberg et al. 1984, Williamson et al. 1994). A certain calcium level may also be important at molting etc. of *M. laciniatus* as well as for Daphnids (Havas 1985, Tessier and Horwitz 1990), although the critical level is probably much lower for *M. laciniatus* (Table 6 in Yan et al. 1989).

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# Moulting Strategies in Freshwater Crayfish *Pacifastacus leniusculus*

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## Abstract

Newly moulted soft-shelled crayfish run a very high risk of being preyed upon by other crayfish. If crayfish synchronise their moult, it would lower the probability for an individual of being injured or killed during the moulting period, by lowering the risk of being cannibalised. An experiment was thus conducted to test whether there is a difference in moulting strategy between isolated *Pacifastacus leniusculus* and socially kept *P. leniusculus*, by assessing moulting date, weight and length of isolated, and, socially kept adult crayfish of both sexes. Socially kept males moulted later than isolated males and socially kept females had a shorter moulting period compared to isolated females. Females moulted later and had a significantly longer moulting period compared to males. The crayfish in the isolated group increased more in length than socially kept crayfish. Isolated females also gained more weight than socially kept females. There was a correlation between the moulting dates of 1991 and of 1992 for each individual crayfish. The results indicate that the moulting periods for crayfish in groups are later and shorter in time compared to crayfish that are isolated from each other. Also the growth increment/moult is poorer for crayfish held in groups. The results from this study thus supports the occurrence of moult synchronisation. Further studies are however needed to reveal the actual mechanism behind the synchronisation.

Keywords: Signal crayfish, moulting, synchronisation, cannibalism.

## Introduction

Crayfish have to moult many times in their lives in order to grow. Moulting is thus an essential but also a very dangerous event in crayfish life-history. During moulting, and several days thereafter, crayfish are soft and therefore highly vulnerable to predation (Stein 1975) and cannibalism (Momot 1967, Momot and Gowing 1977, Brewis and Bowler 1983). Predatory fishes preferably prey upon recently moulted individuals (Stein 1975) and have a much shorter handling time for soft-shelled crayfish when compared to intermoult of the same size (Stein 1975). Cannibalism and non-predatory mortality at the time of moulting are sometimes regarded as more im-

portant than fish predation in controlling crayfish populations (Momot 1967, Momot and Gowing 1977).

Moulting has been shown to be influenced by a number of factors in crustaceans, e.g. hormones (Cheng and Chang 1994), damages to appendages (Ary et al. 1987), lunar rhythms (Skewes et al. 1994), diet (Jensen and Asplen 1998), reproduction (Weeks et al. 1997), water temperature (Tremblay and Eagles 1997), and water chemistry (Forward et al. 1997). Stressful conditions are also suggested to interfere with the induction or completion of some of the many steps of the moulting process, and may cause a flawed or fatal moult (Aiken and Waddy 1987). Pratten (1980) among others has discussed the impor-



tance of a potential mechanism inducing moult synchronisation in crayfish. By moulting fairly close in time fewer dangerous conspecifics will be in the vicinity of the individual. Furthermore, the soft-shelled and vulnerable crayfish will be only one of many potential prey for predators and cannibalistic conspecifics, depleting the risk of being predated, for a single individual.

The aim of this experiment was to investigate whether the presence of conspecifics would 1) lead to a synchronisation of the moulting period, 2) affect the growth increment per moult and, 3) to see if these effects differed between sexes.

## Materials and methods

The study was carried out between May 1991 and August 1992 at the Institute of Freshwater Research, Drottningholm, Sweden. The water used in the laboratory was pumped from a turbulent strait in Lake Mälaren (depth 8 m), cleaned via a dynamic sand filter and aerated. Mean temperature in the aquaria was 11.8 °C in June, 16.8 °C in July, and, in August 19.0 °C. The temperature in the laboratory during the experiment was on average 1.8 °C below the water temperature at the surface of the lake. Prior to the experiment computer controlled 60 W bulbs were used simulating outdoor light conditions. During the experiment the photoperiod was fixed to 14 hours of light and 10 hours of darkness with simulated dawns and sunsets. In September the photoperiod was again synchronised to the outdoor light conditions. Specimens of the signal crayfish (*P. leniusculus*), all uninfected by the crayfish plague (*Aphanomyces astaci*), were selected as experimental animals. On June 7, 32 males and 32 females were weighed (mean±SD: males: 35.8±6.2 g; females: 30.4±6.0 g) and measured (total length males: 102.1±5.5 mm, females: 101.8±6.2 mm) and divided into one isolated and one social setting. No significant differences in weight or length existed between experimental groups within sexes. All crayfish were marked individually on their carapace with permanent ink. None of the females mated the previous autumn, but, some of them may have produced sterile eggs at that

time. In the isolated group 12 females and 12 males were separated into 24 aquaria, divided into 3 racks. These aquaria (bottom area: 20×39 cm<sup>2</sup>) had separate water inlets and outlets, and, pieces of black plastic were placed between the aquaria to prevent visual contact between individuals. The crayfish in the social group were divided into four aquaria (bottom area: 60×130 cm<sup>2</sup>), 5 males and 5 females in each. Aquarium conditions were equal for both experimental groups (temperature; substrate: sand; density of crayfish: 12.8 crayfish/m<sup>2</sup>; shelter: 50×40 mm square shaped holes made of terracotta). In the social group there were 1.5 shelter/crayfish and in the isolated group 1 shelter/crayfish. The crayfish were fed *ad libitum* three times a week with corn, green peas and fish pellets. To avoid competition for food in the social group the food was scattered evenly over the bottom surface of the aquaria.

The moulting date was assessed for each individual. Newly moulted crayfish were identified by their coded exuvia, which were removed from the aquaria. To prevent cannibalism newly moulted crayfish in the social group were put into small refuge plastic mesh-boxes (W: 10 cm, L: 20 cm, H: 8 cm; mesh size: 10 mm) inside the aquaria for 5 days. The isolated crayfish also were held in mesh-boxes after moulting for 5 days in order to equalise the experimental treatments. The 5 day period of protection was chosen due to the fact that 50% of the calcification of new shells are completed 5 days after ecdysis (Wheatly et al. 1991, Wheatly and Gannon 1993). Therefore, 5 days after moulting the shells were regarded hard enough to reduce incidents of cannibalism at densities as in this experiment. By using the mesh-boxes we reduced the mortality in order to keep the density of crayfish in the aquaria fixed. Another reason for keeping newly moulted crayfish in the aquaria was the possibility that crayfish may be able to detect moulting of other crayfish by their 'smell' or by vision. Five days after ecdysis each crayfish were measured (carapace and total), weighed and marked with permanent ink on the carapace before being released back into the aquarium. A male in the isolated group

moulted as number one on July 10. This date was set to 'day 0' and all other data regarding moulting are related to this day. To compare if the moulting date of an individual is correlated to the date of moult for the same individual the next year, the individual moulting dates were also recorded in the summer of 1992.

Two males and two females in the social group were killed by the other crayfish and eaten during or shortly after moulting. None of them had yet been placed in a refuge mesh-box. The dead males moulted 1 day earlier than the mean moulting date of socially kept males. The dead females moulted 1.75 and 2.75 days later than the mean moulting date of socially kept females. The male in the isolated group who was the first to moult in the experiment (July 6) was the only crayfish who moulted twice this year (second moult: August 20).

To achieve a balanced design, required for statistical tests (Underwood 1981), data from one sex was excluded from two of the aquaria containing social sets of crayfish (chosen by random). Also, data from one individual of each sex was excluded by random from each of the remaining aquaria containing social sets. This was necessary since the aquaria of the social group contained one individual more per sex compared to the isolated group in order to achieve equal densities in the two groups. These exclusions resulted in a balanced design with data from 12 individuals of each sex in both experimental groups.

## Results

Socially kept females had a shorter moulting period compared to isolated females (Bartlett's test,  $P < 0.05$ ; Fig. 1). We found no significant difference in length of moulting period when comparing socially kept males with isolated males (Bartlett's test,  $P = 0.26$ ; Fig. 1). Males had a shorter moulting period than females (Bartlett's test, pooled groups:  $P < 0.001$ ; isolated group:  $P < 0.01$ ; social group:  $P < 0.05$ ; Fig. 1). Since there were significant differences in variances but no interaction between sex and treatment (Multiple ANOVA,  $P = 0.57$ ), Kolmogorov-Smirnov two-sample test by ranks was used for analyzing dif-

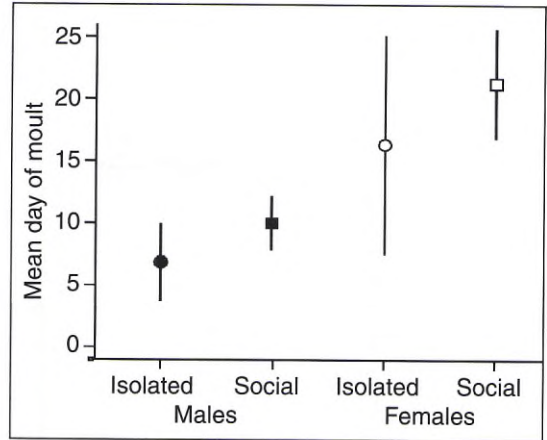


Fig. 1. Mean day of moult for isolated and socially kept signal crayfish of both sexes. Day 0 represents the first observed moult in the experiment. Bars denote SD values.

ferences in moulting dates. One-way ANOVA was used in the other analysis unless stated otherwise.

Socially kept males moulted later than isolated males (socially kept males: day  $10.0 \pm 2.2$ ; isolated males: day  $6.8 \pm 3.1$ ;  $P < 0.05$ , Fig. 1). We found no significant difference in mean moulting day when comparing socially kept females (day  $21.3 \pm 4.4$ ) with isolated females (day  $16.3 \pm 8.8$ ;  $P = 0.09$ ; Fig. 1). With isolated and so-

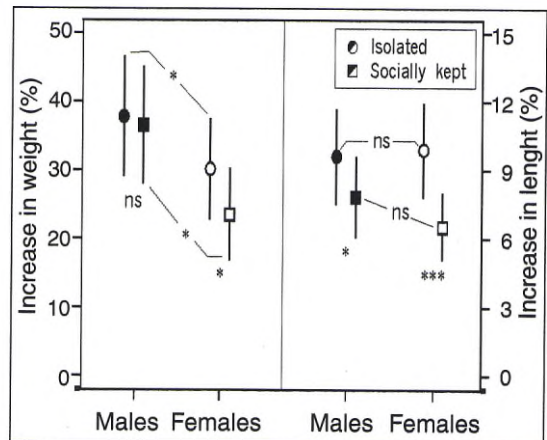


Fig. 2. Increase in length and weight during the moulting period for isolated and socially kept adult signal crayfish. Bars denote SD values.

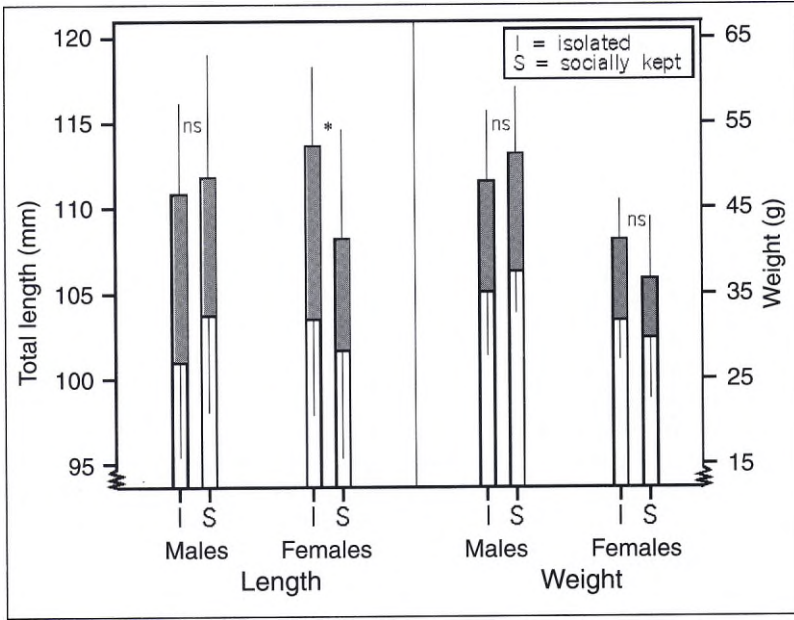


Fig. 3. Mean total length and weight of isolated and socially kept adult signal crayfish one month before □ and five days after ■ moulting. Bars denote SD values.

cially kept crayfish pooled, females moulted later than males (mean±SD: females: day 18.8±7.2; males: day 8.33±3.1;  $P<0.01$ ; Fig. 1).

Socially kept females gained less weight and length compared to isolated females ( $P<0.05$ ;  $P<0.001$ ; Fig. 2). The difference in weight increase between females in the different groups did not result in a significant difference in total weight after the moulting period ( $P=0.1$ ; Fig. 3). After moulting the socially kept females had a significantly smaller size than those in the isolated group ( $P<0.05$ ; Fig. 3). Socially kept males increased less in length compared to isolated males ( $P<0.05$ ; Fig. 2). However, there was no difference in increase in weight between males of different groups ( $P=0.98$ ; Fig. 2). The difference in length increase between males of different groups did not result in a significant difference in total length after the moulting period ( $P=0.56$ ; Fig. 3), and nor was there a difference in weight after the moulting period. Males increased more in weight (Kolmogorov-Smirnov,  $P<0.05$ ) but not in length ( $P=0.46$ ) compared to females (Fig. 2).

There was a correlation between the moulting dates of 1991 and of 1992 for each individual crayfish (Spearman Rank:  $r_s=0.67$ ,  $P<0.001$ ; Fig. 4).

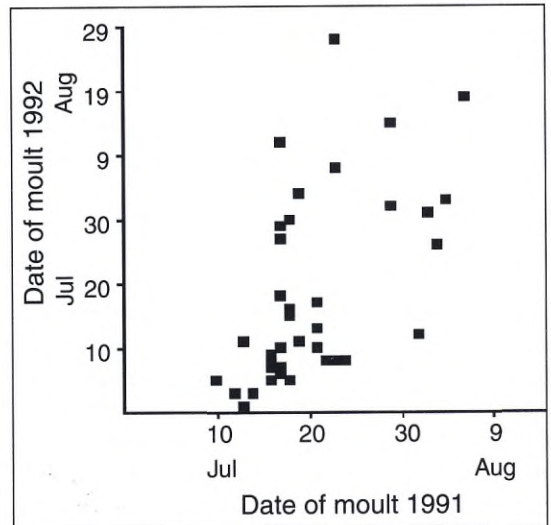
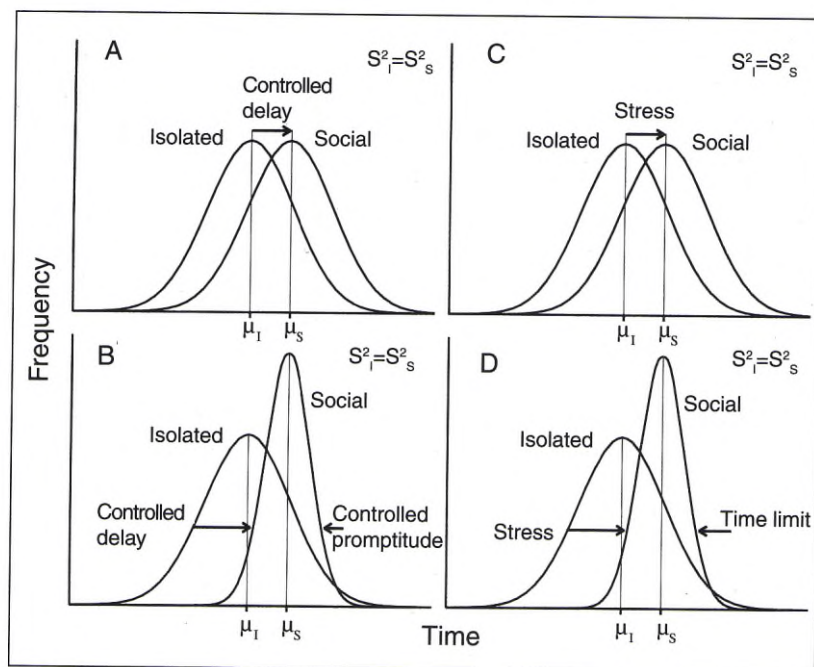


Fig. 4. The correlation between the moulting date in 1991 and 1992 for the individuals taking part in this study.

Fig. 5. Possible mechanisms behind the observed delayed and condensed moulting period.  $S^2_I$  and  $S^2_S$  denotes the variance for the isolated and social group respectively.  $\mu_I$  and  $\mu_S$  denotes the mean for the isolated and social group respectively. **A** describes an actual ability to delay moults and **B** an ability to both delay and rush moults. **C** describes a delay caused by stress and **D** describes a combined effect of stress and time constraints. The result in this study are similar to alternative **B** and **D**.



## Discussion

The results show that the presence of other crayfish delay the moult in signal crayfish. In addition, the presence of other crayfish also result in a shorter moulting period. Thus, in the presence of others, signal crayfish synchronise their moult. We suggest that there are two plausible mechanisms that could lead to the observed synchronisations. The first mechanism is a true ability to synchronise, meaning that crayfish can predict forthcoming moults of their conspecifics and synchronise their own moults according to this knowledge. However, this hypothesis includes that crayfish are able to both delay (Fig. 5A), and to rush their moults (Fig. 5B). The second mechanism is that stressful conditions associated with dense populations of crayfish, i.e., competition for resources, agonistic encounters, risk of injuries and predation etc., affect the premoult physiology of the crayfish negatively resulting in a later moult (Fig. 5C). This hypothesis can explain the delayed moulting period for the socially kept crayfish but not the shorter moulting peri-

od in this group. In order to explain the shorter moulting period found in this study, biological constraints have to be imposed, that are working against late moults by lowering the fitness of individuals moulting late. Such constraints would set a time limit to successful moults (Fig. 5D). In the temperate zone the growth period for crayfish are limited to the warmer months of the year. Moulting is followed by an energy build-up period before the mating season later in the autumn. A late moult may interfere with the reproductive season and lead to poor mating results, and also reduce the probability of surviving the winter. A decrease in temperature is believed to trigger the start of the mating season (Lowery 1988). However, the temperature did not drop and the light conditions were the same throughout the experiment of this study. To accept the stress-time constraint hypothesis one must argue the existence of a 'built in clock' or some factor other than temperature and light that are working against late moults. Further studies are needed to reveal if 1) an actual ability to delay or rush moults or 2) a combined effect of stress and time con-

straints, are responsible for the observed synchronisation in signal crayfish.

The later moult of females compared to males in this study, may be a general effect of intersexual differences in allocation of energy resources. The production of gametes is more energy consuming in females compared to males (Parker et al. 1972). It is likely that the egg production dislocates energy that could otherwise have been used for growth. This may be the reason why females in general moulted later and during a longer period than males. It is likely that the variation in reproductive effort in females also brings on variation in the amount of energy that is available for growth. Thus variation in reproductive effort of females may be reflected in variation in moulting date. In addition, female crayfish are engaged in parental care, first as berried females and later when offering protection for the 2nd-stage juvenile crayfish. These periods, 8 months and 1-2 weeks respectively in signal crayfish, are also energy consuming which will affect growth and, in turn, also the timing and duration of moult. A similar phenomenon, where allocation to reproductive effort affects the success of moult, has been found in i.e. birds, where females who failed in reproduction moulted earlier than females who did not (Klint 1982). Since gravid females were excluded in the experimental design, the effect of parental care on moulting date was not investigated in this study.

In spite of later moulting the socially kept females gained less weight and length during the moulting period compared to isolated females. This may be caused by the presence of other crayfish inducing stress, which results in inferior growth. During and after moulting soft-shelled crayfish enlargens its body size by increasing the water content in the tissues (Passano 1960, Aiken and Waddy 1992). The crayfish keeps the body enlarged until the new shell has hardened (Aiken and Waddy 1992). The new body size is now the limit of growth until the next moult. If the crayfish is disturbed during the phase prior to shell

hardening, it may fail in absorbing or in keeping the water concentration at a high level. To further support this interpretation, the increase in length was smaller in socially kept males compared to isolated males. The presence of other crayfish may restrain the absorption of water or the maintenance of the water content prior to the hardening of the new shell. This effect was probably more pronounced among the females who gained less weight than the males during the moulting period in the socially kept group. The data does however not reveal whether this was an effect of subordination due to size of the initially smaller females, or, an indication of that females are more easily stressed by the presence of other crayfish. In the isolated group such differences between the sexes was not found.

We found a correlation between the moulting dates for an individual crayfish between consecutive years so that an early moulting crayfish in 1991 also moulted early in 1992. This shows that there are other factors apart from the social situation that affect the moulting strategy in signal crayfish. This finding could be taken as evidence for an inherited, genetic component that influences when a crayfish will moult. There are however an alternative explanation. Moulting time one year may be affected more directly by moulting time the previous year. After the moult a crayfish has to eat and gain energy reserves for the next year, to use e.g. when moulting. A late moult one year will give less time to build up these reserves and thus in itself contribute to a late moult the year after. To critically test for a genetic component influencing timing of moult, parent/offspring analysis has to be conducted.

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## NOTES AND COMMENTS

# Conflicts between Cormorants (*Phalacrocorax carbo* L.) and Fishery in Sweden

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### Abstract

This paper presents data and discuss the interaction between cormorants and fishery in Sweden. Increasing numbers of cormorants in recent years have led to an intensified conflict. The aim of this study was to assess and quantify possible damage to the commercial fishery. Bite marks on fish in fisherman's gears occurs locally in Sweden and at certain times of the year. At the study sites (inland lakes in the province of Skåne, Västergötland and Östergötland, brackish water areas of Småland) the amount of injuries can at the moment be considered fairly low. Only in Lake Vänern and Lake Roxen, sometimes, a higher amount of the fishermen's landings (<8% by weight) are injured in such a way that it cannot be sold. A considerable number of cormorants regularly drown in fishing gears. Maximum number of drowned cormorants was 0.24 per fyke-net and day. Furthermore, there is no simple relation between cormorant densities and fish damage. Possible reasons for the existing injury pattern are discussed.

Keywords: Cormorant, predation, fishery, diet choice.

## Introduction

As a consequence of the rapidly increasing cormorant population in continental Europe, conflicts with human interests, particularly fishery, have increased dramatically in recent years (Moerbeek 1987, Zimmerman and Rutschke 1989, Staub and Ball 1994, van Eerden and van Rijn 1996). Cormorants are regarded as a problem among commercial fishermen in Sweden which is mainly due to that cormorants injure or consume fish in fishing gears. It is also asserted among some fishermen that when cormorant colonies are big, and large quantities of fish are being consumed, this can lead to an overall re-

duction in fish stock, and consequently reduced catches of economically important fish species. However, causes behind reductions (or fluctuations) in fish stocks are usually very difficult to establish and predation effects of cormorants on fish populations often rely on theoretical discussions (Birkhead and Furness 1984, Furness and Birkhead 1984, Staub and Ball 1994). More direct effects are reported in fish ponds and artificially stocked lakes, where high densities of fish often are reared (Osieck 1989). A further problem is when cormorants are fishing close to fishing gears, for example fyke-nets, and scares the fish. Fish can then be trapped, and die, in parts of the fishing gears that are not regularly emp-

tied. A very large number of cormorants get drowned in fyke-nets every year. In Sweden it amounts many hundreds and in Denmark many thousands (T. Bregnballe pers. comm.). At very rare occasions the cormorants can get stacked in the fykes in such away that they prevent fish from entering the fykes. Cormorants can also with their exceptionally sharp claws and beaks damage fishing gears. In many cases it has proved difficult to prevent or reduce damage and consumption of fish in fishing gears by cormorants (Cornelisse and Christensen 1993, for a review see Veldkamp 1996). The cormorants are very shy and operate over large areas.

In this investigation I have focused on the problem of damage on fish and drowning of cormorants in fishing gears. These are problems which has grown sharply in recent years. In Sweden the Great Cormorant *Phalacrocorax carbo sinensis* is found as a breeding species in lakes and shallow coastal areas up to around latitude 60°N. A few small colonies or single pairs breed north of latitude 60°N in the Baltic Sea. The core-area of distribution of Swedish cormorants is the southern part of Kalmar sound, where the cormorant became established in the late 1950's after having been absent as breeding species for almost 50 years due to human persecution (Jonsson 1977). Until around year 1985 the number of cormorants in Sweden remained very low but during the past 10 years a rapid increase in numbers has occurred.

## Methods and study sites

Six lakes and one coastal area were chosen for the studies, all sites being areas where a conflict between fishermen and cormorants currently exists. The lakes which are of different size and productivity have medium to high cormorant densities. Registration of injured fish was undertaken in co-operation with fishermen at each location. The fishermen was asked to fill in a protocol (once a week) giving the species, number and weight of all injured fish and the total catch of each species. The fishermen was also asked to register the number of drowned cormorants encountered in fishing gears. What can be classi-

fied as an injury on fish caused by cormorant predation was discussed in advance with the fishermen. Thus a standardised score was achieved. Several visits were made to the fishermen during the study periods to follow up the registration.

## Lakes Ellestadsjön, Vombsjön and Ringsjön

Lake Ellestadsjön (55°32'N, 13°44'E) 300 ha, Lake Vombsjön (55°41'N, 13°35'E) 1,200 ha and Lake Ringsjön (55°52'N, 13°34'E) 4,100 ha, are shallow eutrophic lakes situated in the south-east and central Skåne in south Sweden. Fish species of commercial importance for the fishery are; eel, zander, pike, perch and bream. The fishermen almost exclusively use poled fyke-nets.

Of the three lakes concerned, cormorants are breeding in Ellestadsjön only, where approximately 790 pairs bred in 1996. The colony established in 1991 and still continues to increase. Because of the small size of Ellestadsjön cormorants regularly forage at other water systems including Lake Vombsjön and Lake Ringsjön. The distance from the cormorant colony in Lake Ellestadsjön to Lake Vombsjön is 18 kilometres and to Lake Ringsjön 39 kilometres. The cormorants undertake both solitary and group fishing. Group fishing which is commonly practised in Lake Ellestadsjön can sometimes include several hundred birds.

Interference between cormorants and fishermen are regularly reported from all three lakes but is especially intense in Lake Ellestadsjön. Data on fish damage were collected from commercial fishermen at each lake from 15 July to 30 September 1994. The fyke-nets were emptied on average every second to every third day.

## Roxen

Lake Roxen (58°30'N, 15°40'E) 9,700 ha is a shallow mesotrophic lake in south-east Sweden. Fish species of commercial interest are: eel, zander, pike, perch, vendace and bream. The fishermen use poled fyke-nets and gill-nets.

The cormorant population in the lake has increased dramatically in recent years, now num-



bering about 460 pairs (1996). The first colony was established in 1993. The conflict between fishery and cormorants is very intense at the moment.

The registration of injured fish was undertaken once a week at 19 occasions by one commercial fisherman during the period 15 June to 24 October 1996. The fishing gears used 16 poled fykenets, 15 gill-nets which were emptied once a day.

## Vänern

Lake Vänern (570,000 ha) is the largest lake in Sweden with about 100 licensed fishermen. On overall, Lake Vänern can be considered oligotrophic; however many inlets close to cities are quite nutritious. The maximum depth is 106 m. Fish species important for the fishery are; perch, pike, zander, eel, salmon, trout, vendace and whitefish. Vendace, which is caught mainly in late November early December when spawning, is for many commercial fishermen the economically most important fish during the whole year.

The number of breeding cormorants (580 pairs in 1996) is quite low in relation to the lake's size. In autumn the population of breeding cormorants is replaced by cormorants of the nominate subspecies, which sometimes over-winter in Lake Vänern if there is no ice cover. Cormorants of the nominate race breed at closest in central Norway (north of Trondheim).

The conflict between cormorants and some fishermen in Lake Vänern have accelerated dramatically in recent years, and predominantly occurs in the south-east corner of the lake. The study was undertaken at two areas Torsö (58°46'N, 13°48'E) at 18 occasions from 2 June - 27 September 1995 and Kållandsö (58°42'N, 13°12'E) at 28 occasions from 7 June - 13 November 1995. The fishing gears used were un-poled fyke-nets. The fyke-nets were emptied on average every second to every third day.

## Northern Kalmar sound

The coastal area of Northern Kalmar sound is a shallow brackish water moraine archipelago where cormorants have bred since in the early

1960's. In this area the man - cormorant conflict has been more intense than anywhere else in Sweden and some fishermen have claimed cormorants to cause severe effects on fish stocks and the environment due their high numbers. The peak in number of breeding cormorants was reached in 1993, when the colony at Gåsö (3,000 pairs) was exterminated by some frustrated fishermen. In the same year five new colonies were established at distance of 3 to 20 kilometres from the former colony at Gåsö and the total change in number of cormorants in the area became comparatively small. However, repeated disturbances and egg-picking at colonies have affected the cormorants negatively and possibly counteracted further population growth. The commercial fishery in the area is mainly directed towards eel. The other fish species caught are of much less economical importance.

Registration of injured fish took place by one commercial fisherman Vällö (57°05'N, 16°34'E) at 18 occasions during the period 21 May to 14 July 1995. The fishing gears used are poled fykenets which were emptied on average every second to every third day.

## Results

### Shallow eutrophic lakes

Injuries on fish caught in fyke-nets caused by cormorant predation occurred only on eel. The highest proportion of eels encountered with bite marks, 30% (by weight), were those caught in Lake Ellestadsjön where cormorants also breed. In East Lake Ringsjön and Lake Vombsjön, 10% and 5% respectively of the eels were found with bite-marks. The larger the distance from the cormorant colony in Lake Ellestadsjön the less bite-marks were found on fish in fishing gears, most likely reflecting diminishing predation pressure with distance from the colony. Still, bite marks on eel only rarely seem to affect the commercial value of the fish. During the registration period a mean of four (Lake Ellestadsjön) and two (Lake Ringsjön) drowned cormorants were encountered per emptying time (Table 1).

Table 1. Drowned Cormorants encountered in fyke-nets. The last column show the mean number of drowned cormorants per fyke-net and day.

Place	Period	No. of emptying times	No. of fyke-nets	Days elapsed between emptying	Tot. no. of drowned cormorants	No. of cormorants drowned per day and fyke-net
Ellestadsjön	940715-940930	14	5	3-4	58	0.24
Ringsjön	950509-950728	23	12	2	58	0.10
Roxen	960615-961024	19	16	1	94	0.31
Torsö (Vänern)	960606-960927	18	7	2-3	53	0.17
Vällö (Kalmar sound)	980608-980901	85	7	1	22	0.04
East Kallsö S:t Anna	960620-961001	20	3+97*	2-3	6	-

\* small fish-traps put at a water depth of 0.5-1.5m.

### Roxen

In Lake Roxen damage occurred at a varying degree on different fish species caught by the fisherman. Of the total daily catch a mean of 7.4% by weight was found injured. The most frequently encountered injured fish species was vendace and least frequently bream (Table 2). On average five cormorants drowned in fyke-nets each day during the study period (Table 1).

### Vänern

A mean of 7.3% (Torsö) and 7.7% (Kållandsö) (by weight) of fish of commercial value were encountered injured. At Torsö the mean catch of injured fish of the different species were as fol-

lows: whitefish 3.5 kg, pike 3.0 kg, perch 2.8 kg, eel 1.8 kg and zander 1.4 kg. The total mean catch per fishing time was 172 kg. At Kållandsö the total mean catch was 114 kg per fishing time, of which 4.5 kg whitefish, 2.4 kg zander, 1.6 kg perch and 0.3 kg eel were encountered injured.

The total mean catch at both Torsö and Kållandsö also include vendace. Vendace is sometimes caught in quite large quantities (ca 50% by weight). Injuries on vendace occurred sometimes frequently. However, due to the long handling time quantification of injured vendace was undertaken only occasionally and therefore not included in the injury statistics. At Torsö a mean of three cormorants was drowned in fyke-nets per fishing time (Table 1).

Table 2. The mean proportion of injured fish in relation to total catch in Lake Roxen.

	Bream	Vendace	Zander	Perch	Pike	Eel	Total
Catch per day of each species (kg)	13.2	2.6	0.7	32.2	13.8	16	78.6
Injured fish (kg)	0.4	1.3	0.1	1.2	1.2	1.6	5.8
Proportion injured fish (%)	3	50	13	4	8	10	7.4

## Northern Kalmar sound

At the brackish water locality Vollå in northern Kalmar sound the damage on fish caught in fishing gears was restricted to whitefish. The total mean catch per fishing time was 4.7 kg (5.9 individuals) of which 1.9 kg (2.4 individuals) was found injured. The mean weight of damaged whitefish was 0.8 kg. Less than one (0.3) cormorant was found drowned in fyke-nets per fishing time (Table 1).

## Discussion

Injuries on fish in fishing gears caused by cormorants occurred at all places studied. Differences between the places were found in the proportion of injured fish in relation to total catch and what species the cormorants attacked. Consistently however, was that the cormorants regularly attacked fairly large fish specimens (>0.5 kg) in the fishing gears which probably seldom occurs when cormorants are fishing in the open water. Cormorants generally feed on relatively small fish (<0.2 kg) (Jonsson 1977, Hald-Mortensen 1994, Veldkamp 1995). Injuries on fish in fyke-nets caused by cormorants can be created in two ways; when cormorants try to attack the fish through the meshes from outside the fykes or squares and when cormorants are hunting for the fish within the fykes or squares. The latter can sometimes lead to that the birds cannot find the way out from a fyke and get drowned. At very rare occasions, according to the fishermen, a drowned cormorant can get fasten in a fyke in such a way that it prevents further fish from entering the fyke. However, the extra work associated with regularly handling large numbers of drowned cormorants can sometimes be considerable for some fishermen.

Damage on fishing gears have been reported from some fishermen but seem to be a less common problem, and when it occurs it is mostly associated with gill-nets.

In the freshwater lakes studied in Skåne damage on fish in fishing gears was exclusively found on eel. The fact that eel regularly occurred with bite-marks, while almost not on other fish species, possibly is an effect of unsuccessful attacks

by the cormorants in the open water and not because of hunting in the fishing gears. This is supported by the fact that other fish species seldom are encountered injured in fishing gears which however frequently occurs in other lakes (cf. Lake Roxen, Lake Vänern).

A possible explanation for the circumstances under which the eels are subjected to cormorant predation is presented by van Dobben (1989). He concluded that the eel is especially prone for predation during sunny warm days due to its habit of lifting its head out of the mud making swinging movements and respiring vigorously. Reports of cormorants catching large eels are scarce (large eels being difficult to handle for a cormorant due to its power and large size) so most cormorant attacks on large eels most likely lead to escape, the only visible sign of the encounter being some scratches (white strokes on the front dorsal part of the eel). These scratches, which only rarely occur as open wounds, probably do not affect the survival of the eel, nor the commercial value.

Despite the large number of eels found with bite-marks, which clearly shows that cormorants hunt for eel, the cormorant diet contain only small amounts of eel (Table 3). However, the fisherman in Lake Ellestadsjön have experienced much reduced catches of eel since cormorants became numerous in the lake. Even if each cormorant only occasionally consumes eel, eel-consumption of the whole cormorant colony might be quite large and possibly have a significant impact on the eel population density. The stage at which eel are supposed to be most prone to predation is when they are newly released 'stocking eel' and not yet familiar with the conditions in the new environment. The eel is possibly also especially sensitive to predation in spring and early summer, when water still is cold, which makes the eel slow and less mobile. Almost no information is available on the instantaneous rate of natural mortality of stocked eels but in comparison to other fish species it is generally assumed to be low (H. Wickström pers. comm.). Therefore, in special cases, cormorant predation on eel may be considered a mortality factor of importance in small lakes holding large number of cormorants.

Table 3. Diet composition of cormorants from Lake Ellestadsjön colony. Data based on stomach samples ( $N=30$ ) from drowned and shot birds (940713-940901).

	No.	%
Bleak <i>Alburnus alburnus</i>	1	<1
Bream <i>Abramis brama</i>	1	<1
Burbot <i>Lota lota</i>	1	<1
Eel <i>Anguilla anguilla</i> *	-	
Perch <i>Perca fluviatilis</i>	33	30
Pike <i>Esox lucius</i>	1	<1
Roach <i>Rutilus rutilus</i>	64	58
Ruffe <i>Gymnocephalus cernua</i>	2	2
Sticklebacks <i>Gasterosteus/Pungitius</i> **		
Whitefish <i>Coregonus</i> sp.	3	3
Zander <i>Stizostedion lucioperca</i>	2	2
Undetermined cyprinid	3	3
Total	111	

\* not found in analysed stomach samples but regurgitated eels have occasionally been found on ground in Lake Ellestadsjön cormorant colony (Engström, H. unpubl.).

\*\* present but not quantified.

It also has to be explained why such large number of cormorants regularly drown in fykenets, if they do not fish there. It could be that the birds enter the fykes accidentally because of the very turbid water (secci depth in summer usually <50 cm), and not because of active food search. This seem at least to hold for ducks and other non-piscivorous bird which also regularly drown in fishing gears.

The large and rather deep Lake Vänern has a much lower productivity and fish biomass than the lakes in Skåne. The number of breeding cormorants is low in relation to lake size. Despite this the amount of injuries on fish in fishing gears is comparatively high. Causes behind this pattern can only be a matter of speculation, but probable causes could be related to the comparatively low fish biomass and high transparency (cf. lakes in Skåne). High transparency possibly makes fish easy to detect for the birds in the fishing gears,

and low fish biomass may mean that fishing in fishing gears is an easy and less costly way to obtain food compared to hunting for fish in the open water. Deep and clear water probably also makes it easier for the fish to detect an approaching cormorant and seek for hide. Large scale group fishing on pelagic shoaling fish, which is a very efficient way of foraging (De Nie 1995, van Eerden et al. 1995), and commonly practised by cormorants in Lake Ellestadsjön is only occasionally reported from Lake Vänern.

Lake Roxen shows injury-pattern similar to Lake Vänern. At both areas damage on fish has increased dramatically with increasing cormorant densities in recent years. Lake Roxen and Lake Vänern also harbour additional cormorants in late summer when cormorants having bred elsewhere, for example at the coast, fly inland. An affect of this is that damage on fish increases and more birds get drowned in fishing gears.

In common, for the investigations, in Lake Roxen and Lake Vänern there is a tendency for salmonides to be injured more often than other fish species. At Lake Vänern whitefish and vendace and at Lake Roxen vendace are the fish species most frequently encountered injured. It could be that salmonides, due to their high energy value, are particularly preferred by the cormorants and therefore more often are subjected to attacks. Alternative explanations are; 1) salmonides are more conspicuous and attracts cormorants more than other fish species, 2) salmonides are more powerful and therefore more often escape a cormorant attack, 3) the skin of salmonides is particularly sensitive and/or 4) the behaviour of salmonides makes them more vulnerable for cormorant predation compared to other fish species. However, no supportive data are yet available.

According to some fishermen the vendace fishing in Lake Vänern during late autumn and early winter is affected by cormorant predation. The vendace is caught during spawning for manufacturing of fish roe and caviar, and is the economically most important fishery for many fishermen in Vänern during the whole year. Vendace is caught either by gill-nets or by trawling, some-

times at rather large distances from land. It is asserted among some fishermen that large quantities of vendace regularly are encountered injured or withdrawn from gill-nets due to cormorant predation. To quantify the amount of lost fish is very difficult. Remnants from partly consumed fish in nets are most likely rather few in comparison to fish consumed not leaving any remnants. Those cormorants that are present in Vänern during late autumn–early winter are overwintering cormorants. The problem is particularly difficult to solve because of cormorants being spread out over a very large area and that they during this period tend to form very mobile flocks that consistently switch between different areas. However, the likelihood that cormorants could affect vendace population as a whole in Lake Vänern is not likely because of the small number of cormorants present in relation to total size of the vendace population.

At the study site Vällö, in northern Kalmar sound, only whitefish was regularly encountered injured in fyke-nets. Why only whitefish are subjected to cormorant attacks and hardly any other fish species is not clear, but fishermen often point at the habit of whitefish to approach the surface while caught in fyke-nets.

The results obtained from northern Kalmar sound indicate that damage on fish presently is a problem of minor importance despite the large number of cormorants present in the area.

It can of course be speculated if the described injury-pattern on fish can be attributed to cormorant predation only. Gulls *Larus* sp., Grey heron *Ardea cinerea* and Red kite *Milvus milvus* (Skåne) often recede close to fishing gears and also feed on fish. Therefore it cannot be excluded that at least some of the injuries on fish is caused by fish eating birds other than cormorants. Piscivorous fish also attack fish in nets. However piscivorous fish trapped in fykes do usually not predate upon other fish, with one exception the burbot. Bite marks on fish caused by piscivorous fish also usually look different from bite-marks caused by birds.

Other factors that could be of importance for the injury patterns shown are how regularly these

are emptied. A longer time in between emptying implies larger catches and probably more attraction on the birds.

To conclude, the situation when cormorants damage and consume fish in fishing gears is presently restricted to a few localities in south and middle Sweden. At these localities fishermen may encounter, at the most, a mean of eight per cent (by weight) damaged fish due to cormorant predation. How much fish that is removed from the fishing gears due to predation is not known, but most likely it mainly affect smaller fish specimens which are of less economic value for the fishermen.

With the aim of reducing the problems, local authorities have in some cases given permission for hunting. Hunting is presently allowed within close vicinity of fishing gears (<200 m) and on open water at Lake Roxen, Lake Vänern, Lake Ellestadsjön and Northern Kalmar sound. At Northern Kalmar sound licensed fishermen and landowners are also allowed to practise egg-picking except for two protected sites at the island of Gåsö and Svartingskär, respectively. So far hunting has been fairly limited (total number of shot birds/destroyed eggs, 3,000 and 1,500, respectively, in Sweden 1996, data from County Administration Boards). The effects of the hunting efforts have not yet been evaluated but it seems as if the hunting does not have had the desired effects.

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# Testing Hydroacoustics as a Method for Yearly Assessment of the Vendace (*Coregonus albula* L.) Stocks Spawning on the Swedish side of the Bothnian Bay

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## Abstract

The vendace (*Coregonus albula* L.) in the Bothnian Bay spawns in inshore areas. Spawning takes place at the end of October or in the beginning of November when the ice starts to form. The winter is spent in the inshore-areas and the vendace does not migrate offshore until after the ice has gone at the end of May. It is supposed that from October until the end of May the entire spawning-stock is concentrated in reasonably small areas. The purpose of this investigation was to find out whether it is possible to take advantage of this behaviour to estimate the Norrbotten stock by means of hydroacoustics. Echo counting was therefore conducted from outside, through and on the inside of two of the present commercial trawl-areas in both October (1990, 1991 and 1993) and at the end of May (1989). The results showed a range of 50-600 fish/ha larger than 80 mm in October, recalculated to represent surface area in the commercial trawl-areas and slightly more on the inside of them. A rough estimate built on fishing mortality and catch indicated that in these areas there should have been at least between 630-1,550 vendace/ha surface area. The echo counting recorded only lower numbers of fish. The only explanation for this must be a continuous immigration up to the very moment of spawning. Another attempt to assess the vendace population, just after the ice broke up at the end of May, failed. The vendace did not ascend from the bottom during the night, so that the echo sounder could not distinguish the fish from the bottom.

Keywords: Vendace, *Coregonus albula*, hydroacoustics, Bothnian Bay.

## Introduction

The only area of the Baltic Sea with a large self-sustaining population of vendace (*Coregonus albula* L.) lies in the Bothnian Bay, the most northerly part of the Baltic Sea. This bay has a low salinity, ranging from 0 to 4.5 per mille. The freshwater-fish vendace does not inhabit waters with a salinity exceeding 3 per mille (Järvi 1950).

The Norrbotten area of the Bothnian Bay is shallow with a large archipelago with more than 1,000 islands and skerries. A high percentage of the Bothnian Bay vendace population spawns in this archipelago in the autumn (Enderlein 1989).

For centuries man has used this opportunity to catch vendace when they gather for spawning. At the beginning of this century the yearly catch

varied between 50 and 100 metric tons. It has since then increased to 2,000 tons (1988) (Hasselborg and Karlström 1996).

Over the years the increasing fishing pressure has had consequences for the recruitment and size-distribution of the vendace stock in the Norrbotten area of the Bothnian Bay. The stock is not today in danger of biological overfishing but of economical overfishing since the proportion of larger vendace is decreasing (Hasselborg and Karlström 1996). This has stressed the need for a fast and reliable method for monitoring the vendace stock as a base for proper management.

Hydroacoustics are widely used as a monitor for assessing the abundance of marine fish species. The method is also frequently used to assess the abundance of pelagic fish species in large

freshwater lakes (Jurvelius and Heikkinen 1987, Jurvelius et al. 1988, Appenzeller 1998, Walline et al. 1992). In Sweden the Lakes Vänern, Vättern and Mälaren are monitored on a yearly basis. The method is well established and suitable for this kind of investigation (MacLennan and Simmonds 1992).

The aim of the present study was to test whether it is possible to assess the spawning stock of vendace, when it is concentrated in the archipelago, instead of being spread over the entire Bothnian Bay (3,600,000 ha). There it is also mixed with herring, *Clupea harengus* L., another pelagic planctivore of similar size, which is difficult to differentiate from the vendace using hydroacoustics.

## Material and Methods

Two survey areas were chosen for this experiment, the Storörfjärden-Pålångefjärden in the Kalix archipelago and the Germandöfjärden in the Luleå archipelago (Fig. 1). Storörfjärden-

Pålångefjärden has been heavily exploited during the trawling season (20 September-31 October) since the trawling started in the 1960s, as it is close to port for many of the licenced trawlers. The other trawl area, Germandöfjärden, is much smaller and more frequently used today than in the 1970s.

Both survey areas were investigated from the offshore side (called outside), through the allocated trawl area, and up to areas close to the mainland where trawling is forbidden (called inside) (Fig. 1).

The hydroacoustic surveys took place on 25 May 1989, the day after the ice broke up, (Luleå archipelago), the 24 and 25 October 1990 (Kalix archipelago and Luleå archipelago), the 23 and the 24 October 1991 (Luleå and Kalix) and the 4 and the 7 October 1993 (Kalix and Luleå).

The echosounder was a Simrad EY-M single beam with a 70 Kz transducer (Bayona 1984). All recordings were made on cassette-tape 1989 and on Digital Audio Tape (DAT) 1990, 1991 and 1993. The sounder was used with 40 log R

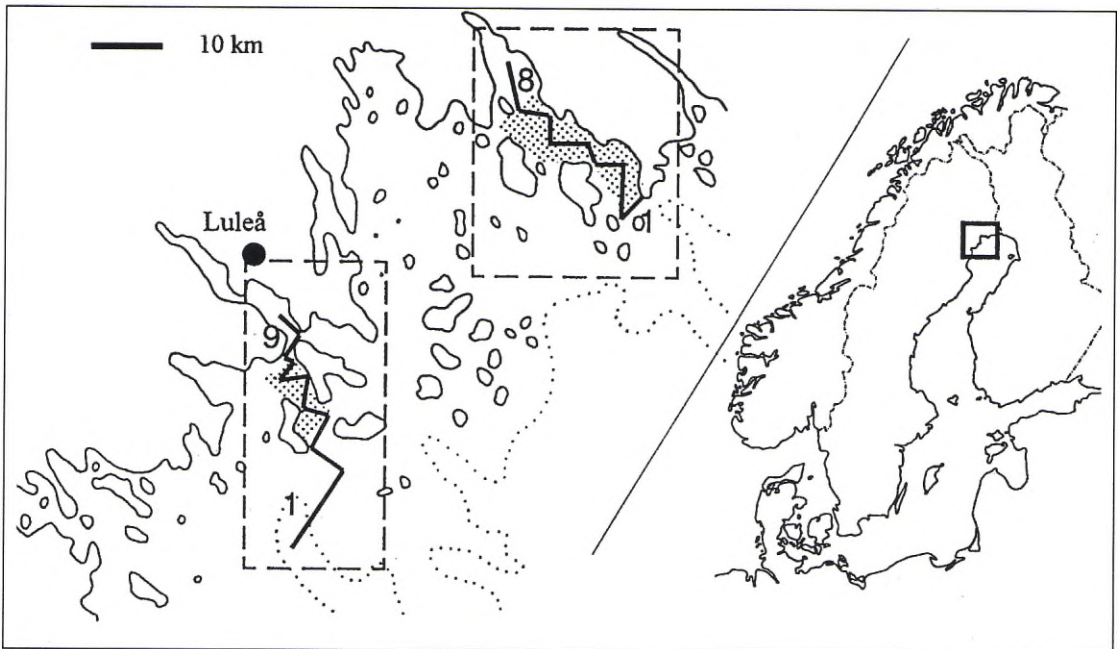


Fig. 1. The Norrbotten part of the Bothnian bay with the transects used. The northern shaded area is the Storörfjärden-Pålångefjärden trawl-area in the Kalix archipelago and the southern the Germandöfjärden trawl-area in the Luleå archipelago.



time varied gain control with a duration of the transmitted full pulse of 0.6 ms, giving a vertical resolution of about 0.8 m. The equipment was calibrated against a -39.2 dB copper sphere before each survey.

The recorded data was analysed by the Hydro Acoustic Data Acquisition System (HADAS) developed by T. Lindem (Walline et al. 1992) using the modified algorithm of Craig and Forbes (1969) for single fish targets to get a target strength distribution of the fish (Lindem 1983). The conversion from target strength to approximate fish-length was calculated according to the formula  $TS = 20 \log L - 68$  (Lindem and Sandlund 1984) where L is fish-length (in cm). The target-strength of the recorded echos were divided in two groups approximately corresponding to fish smaller and larger than 80 mm in all surveys. This was done in the knowledge that vendace in the Bothnian Bay normally exceed 80 mm after their first summer (Enderlein 1986).

Two metre vertical steps were used in the analyses of the hydroacoustic data. The number of fish/ha from each depth interval has been corrected for respective depth intervals part of the total surface area to give the number of fish/ha surface area.

The survey runs were conducted at night in darkness, except during May 1989 when it never became dark. At this latitude it is light enough to read during the night at the end of May. The boat used in 1989 was a small open one while in 1990, 1991 and 1993 the Luleå police-boat with the ordinary crew was employed. The main advantage of the police-boat is that it is equipped with radar and GPS making a precise repeatable survey track between years possible. The transducer was always hung beside the boat at 0.5 m depth. The survey-speed was five knots. Due to bad weather, which caused the transducer to turn over, some transect-recordings in 1991 and 1993 in the Kalix archipelago were discarded.

Three different methods were used in collecting samples for species composition and size distribution. In 1989 two sets of pelagic gill-nets with three nets in each were set, bottom and at the surface. The dimension of each net was 18·6 m with mesh sizes of 12.5 mm, 16.5 mm and 21.5

mm (knot to knot) respectively. In 1990 and 1993 trawl samples were taken from commercial trawlers. In 1992 nightly pelagic two-boat trawling with a small herring trawl was employed. The theoretical opening of the trawl was 4·3 m and the meshsize in the cod-end 5 mm (knot to knot). The trawl depth in Germandöfjärden was 0-3 m and 16-19 m (bottom) and in Pälängefjärden 0-3 m, 6-9 m and 17-20 m (bottom). The trawl depth was regulated by a buoy from the trawl to the surface and the actual depth recorded by a depth recorder. The trawl speed was around two knots. All collections of fish were made as close, in time, to the echo counting as possible, usually within 48 hours.

The fish collected were measured as total length in mm.

## Results and Discussion

Two prerequisites are necessary for using hydroacoustics as a method for yearly assessment of the spawning population on the Swedish side of the Bothnian Bay, i.e. knowledge of the actual proportion of vendace among the counted fish and the certainty that the entire spawning-population is counted.

Three sampling methods were used to determine the proportion of vendace in the fish community. Gill-nets were used the day after the ice broke in May 1989 in the Luleå archipelago. The total catch in the six nets was 13 fishes (5 vendace, 1 smelt (*Osmerus eperlanus* L.), 1 whitefish (*Coregonus lavaretus* L.), 5 four-horn sculpin (*Oncocottus quadricornis* L.) and 1 herring. The disappointingly small catch indicated a very low fish activity most likely due to the cold water. Of the other two methods, the collection of samples from trawlers was discounted. In these samples no fish smaller than 80 mm were collected due to the mesh-sizes of the trawls used by the fishermen. This method also had another drawback since the samples were from daytime bottom-trawling and were compared with the night-time distribution shown by the hydroacoustics. The night-time trawling, using the small trawl with the small-meshed cod-end, prob-

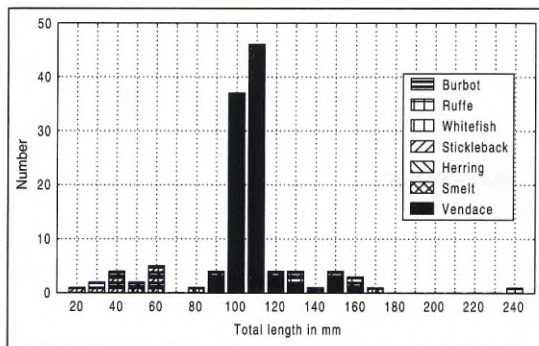


Fig. 2. The length-frequency distribution of the catch in the fine-meshed pelagic trawl from the Kalix archipelago during nighttime in October.

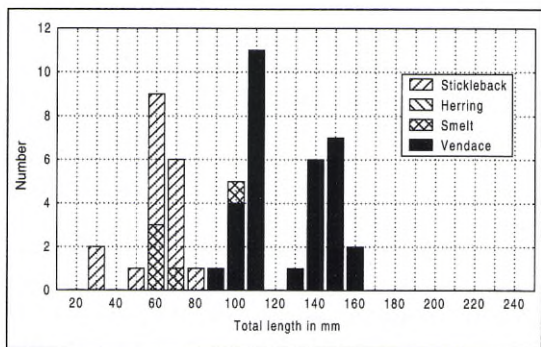


Fig. 3. The length-frequency distribution of the catch in the fine-meshed pelagic trawl from the Luleå archipelago during nighttime in October.

ably gave the most accurate picture of the species composition in the area when compared with the hydroacoustics. The five trawl-hauls resulted in rather few fishes (Table 1) but yielded a total of 7 species, vendace, smelt, whitefish, herring, 3-spined stickleback (*Gasterosteus aculeatus* L.), ruffe (*Acerina cernua* L.) and burbot (*Lota lota* L.).

The length-frequency distributions of trawl-catches in Kalix and Luleå archipelago also verified that the division of fish into groups smaller and larger than 80 mm when using hydroacoustics, was realistic. None of the vendace caught were smaller than 80 mm (Fig. 2 and 3). It also showed that the vendace is the most numerous species (Table 1). Of the fish larger than

Table 1. The trawl-catch of vendace and other species smaller and larger than 80 mm.

	Length 20-80 mm		Length >80 mm	
	No.	%	No.	%
<b>Luleå</b>				
Vendace	0	0	96	80
Other species	15	12.5	9	7.5
<b>Kalix</b>				
Vendace	0	0	32	61.5
Other species	19	36.5	1	2

80 mm vendace contributed with 97% (Kalix) and 91% (Luleå). Although the samples were small it could be said that the majority of fish larger than 80 mm were vendace at the time when the hydroacoustic surveys were conducted.

The first hydroacoustic survey was conducted on the post spawning-population of vendace the day after the ice broke up in May 1989 in the Luleå archipelago. The results from this survey were not promising, not because there were no fish, but because they stayed too close to the bottom (Fig. 4). If, as in this case, the fish are too close to the bottom the equipment has difficulty in distinguishing between bottom and fish with an underestimation as a result. The result was also supported by the low activity indicated by the small catch in the gill-nets. This problem was not experienced in the surveys conducted in October when the fish stayed well off the bottom

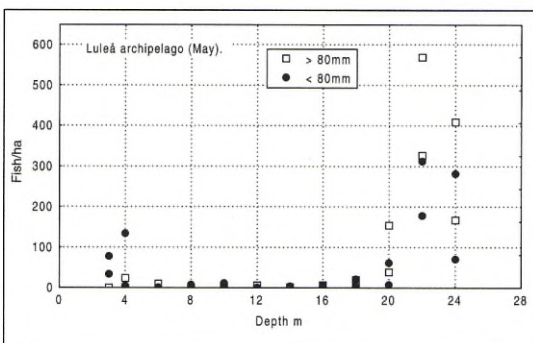


Fig. 4. The vertical distribution of fish along transect 5 in the Luleå archipelago in May.

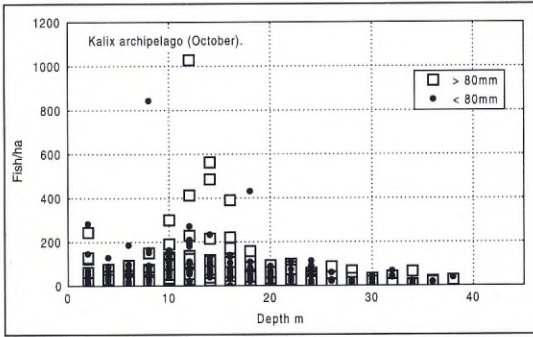


Fig. 5. The vertical distribution of fish along the transects in the Kalix archipelago in October.

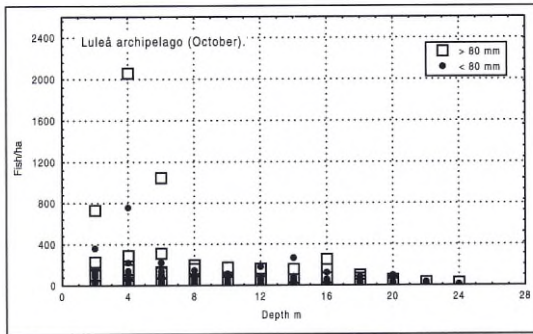


Fig. 6. The vertical distribution of fish along the transects in the Luleå archipelago in October.

both in the Kalix and Luleå archipelagos (Fig. 5 and 6) with a single fish resolution from 70 to 100%. For this reason May was discarded as a suitable month and efforts were instead concentrated on the month of October.

The hydroacoustics were always run from the outside of the area and towards the mainland in a zig-zag pattern where each straight line was called a transect (Fig. 1). In the Kalix archipelago transect 1 was outside the trawl-area and transect 8 inside. In the Luleå archipelago transect 1, 2 and 3 were outside and transect 8 and 9 inside the trawl-area. The results, fish/ha along each transect, were corrected for the different areas in each depth-zone before they were summed. The results then represent the number of fish/ha surface area along each transect. These data were plotted in Fig. 7 for the Kalix and Fig. 8 for the Luleå archipelago for all years (1990, 1991 and 1993), but note that due to bad weather in the

Kalix archipelago in both 1991 and 1993, when the transducer turned over, some transects were discarded. Both figures show a similar result, with a variation between 50 to 1,200 fish/ha except transect 3 in 1990 in the Luleå archipelago, when much higher densities were recorded (Table 2). This was probably due to the presence of schools of herring. The echograms from that transect differ in appearance from what elsewhere was interpreted as vendace. Note also that there is a higher fish density on the inside of the trawl-area than within it in both survey areas. The difference in fish/ha larger than 80 mm within the trawl-area between the years decreased from 1990 to 1993 in both areas (Fig. 9).

So far the hydroacoustic data does not verify the assumption that the entire spawning population of vendace was aggregated in the archipelago when the hydroacoustic surveys were conducted. However, using other available data an estimate can be made of what densities of vendace are needed to support the present fishery and these can be compared with what was found. If these densities are reasonably similar then it can be assumed that the hydroacoustics counted an aggregated spawning population of vendace.

Prior to 1980 catch statistics were recorded yearly from each trawl-area. Unfortunately this system was changed and from 1980 onwards

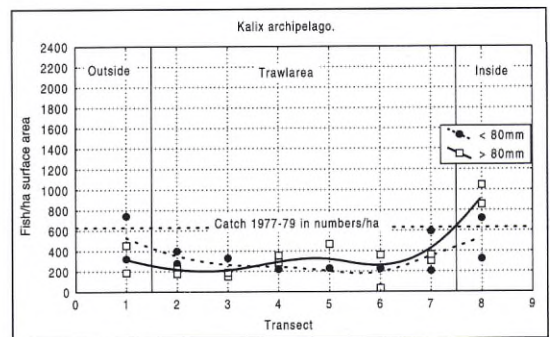


Fig. 7. The density of fish/ha surface area along each transect according to the hydroacoustics for fish smaller and larger than 80 mm. The vertical lines delimit the transects outside (number 1), trawl-area (2-7) and inside (8). The horizontal line indicates the average catch of vendace in numbers/ha for the Storöfjärden-Pålängefjärden 1977-79.

Table 2. The results from the hydroacoustics in fish/ha surface area along each transect. S=small (<80 mm), L=large (>80 mm).

Luleå				Kalix										
Date	890525		901025		911023		931007		901024		911024		931004	
Transect	S	L	S	L	S	L	S	L	S	L	S	L	S	L
1			287	375	60	93	146	231	323	455	xx	xx	742	189
2			329	523	80	130	73	169	278	227	xx	xx	399	179
3			1539	2539	118	218	164	183	158	152	xx	xx	331	190
4			220	431	107	156	71	49	219	288	xx	xx	332	356
5	144	100	341	507	207	257	99	78	231	467	xx	xx	xx	xx
6			235	587	156	213	107	174	225	359	xx	xx	42	35
7					254	366	187	164	529	302	205	364	xx	xx
8					606	771	920	238	720	1046	323	856	xx	xx
9					686	1256	269	740						

xx = data of poor quality due to bad weather, not used.

catch statistics were recorded from the much larger ICES-grids. In this study catch statistics from each trawl-area were needed and therefore old data from 1977 to 1979 have been used (Enderlein 1979). In Storöfjärden-Pålångefjärden the average catch for that period was 12.6 kg/ha and for Germandöfjärden 8.4 kg/ha. Assuming the average weight per fish was 20 g (Enderlein 1986) this should correspond to 630 and 420

vendace/ha. Since the total catch has increased from about 1,000 tons in 1977-79 (Enderlein 1986) to 1,700-1,100 tons in 1990-93 (Log-book statistics from Swedish National Board of Fisheries) the densities from 1990 to 1993 should be somewhat higher than those presented here. No consideration is given to any difference in average weight between 1977-79 and 1990-93 although the percentage of larger vendace in the catch has decreased from 1977-79 to 1990-93 (Karl-Bådo Johansson, pers. comm., Hasselborg and Karlström 1996). In Figs. 7 and 8 the mean

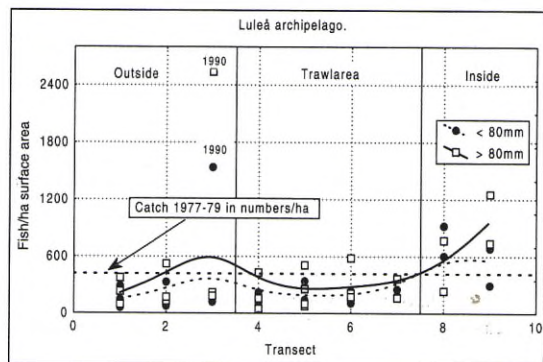


Fig. 8. The density of fish/ha surface area along each transect according to the hydroacoustics for fish smaller and larger than 80 mm. The vertical lines delimit the transects outside (number 1-3), trawl-area (4-7) and inside (8 and 9). The horizontal line indicate the average catch of vendace in numbers/ha for the Germandöfjärden 1977-79.

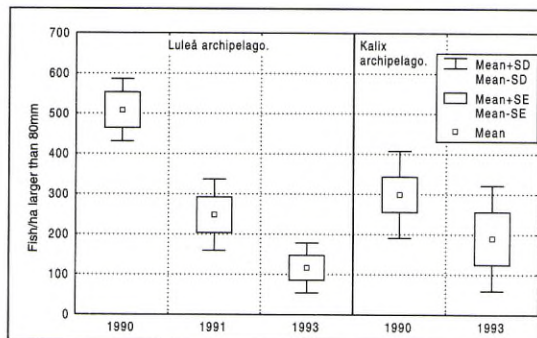


Fig. 9. The variation within the trawl-areas and the different years in fish/ha surface area, according to the hydroacoustics. Notice that the results from Kalix 1991 were excluded due to disturbances caused by bad weather.

numbers/ha of vendace caught in each trawl-area from 1977 to 1979 are shown as a horizontal line. From this it appears as if the hydroacoustic figures are somewhat low especially since they show all fish. If we take it a step further, i.e. calculate the minimum numbers of vendace/ha needed to maintain the present fishery, we get a figure of 1,600 in the beginning and 900 at the end of the trawl-season in the Pålångefjärden-Storöfjärden. Similar figures for the Germandöfjärden would be 1,100 and 600 vendace/ha respectively. (The assumptions behind these calculations are: a) that only 10% of the one summer old vendace survive to 6 years and more (Hasselborg and Karlström 1996),  $Z = -0.46$  (Gulland 1969), b) the one summer old vendace are fully recruited to the fishery, c) all mortality is fishing mortality in the autumn, d) that the average catches in 1977-79 equal the catches 1990, 1991 and 1993.) These calculated figures are much higher than those recorded by the hydroacoustics. The only explanation is that there is a continuous immigration into the spawning (trawl)-areas up to the very start of the spawning in the end of October or in the beginning of November.

The possibility of using hydroacoustics as a method for yearly assessment of the vendace spawning stock in the inshore area of the Norrbotten part of the Bothnian Bay can be ruled out. The vendace were not all present in October and were not countable in May.

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## Referees, 1998

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# Guide to authors

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Submit the manuscript in triplicate.

All manuscripts submitted are considered for publication on the understanding that they have not been published, submitted, or accepted for publication elsewhere.

Manuscripts are submitted to reviewers for evaluation of their significance and soundness. Authors will generally be notified of acceptance, rejection, or need for revision within three months.

Decisions of the editors are final.

Manuscripts are edited to improve communication between the author and the readers.

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Fifty reprints are supplied free of charge. An additional number may be ordered at cost. Price list and order forms for reprints are sent with proofs.

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Manuscripts should be in English. Linguistic usage should be correct. Write in a clear style. Avoid extensive reviews in the Introduction and Discussion. Cite only essential sources of a theory or opinion.

### Title

The title should be brief and contain words useful for indexing and information retrieval.

### Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article.

### Keywords

Five keywords should be given for indexing and information retrieval.

## Text

The first page should contain only the title and author's name and address. Begin the text on page two. The manuscript should be type-written, double-spaced with wide margins and on one side only of good quality paper. Word processor generated manuscripts should be in upper and lower case letters of typewriter quality font. Manuscripts printed by 7 x 9 or 9 x 9 dot matrix printers will not be accepted for publication or review. Underlinings in the text should be avoided. After re-submission please enclose a diskette containing the final version of the manuscript in any DOS-wordprocessing program (e.g. wp 5.1, ws, ms-world).

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Submit each diagram, graph, map or photograph in one original and three copies. All illustrations should bear author's name. Tables and legends of illustrations should be written on separate sheets. Do not incorporate the legend in the figure itself. Tables and illustrations should be comprehensible without reference to the text.

Colour plates may be included at the author's expense.

Plan your illustrations for the smallest size possible. Figures, letters, and other symbols on illustrations should be drawn so large that they will be at least 1.5 mm high in the final print.

## Units

Use SI units as far as possible.

## Nomenclature

Binomial Latin names should be underlined and used in accordance with International Rules of Nomenclature.

## References

In the list of references the following usage should be conformed to:

Journal

Svårdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshw. Res., Drottningholm 55: 144-171.

## Book

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology. An evolutionary approach. Third edition. - Blackwell Scientific Publications, Oxford. 482 p.

## Chapter

Krebs, J.R. and R.H. McCleery. 1984. Optimization in behavioural ecology. p. 91-121. - In: Krebs, J.R. and N.B. Davies (eds.) Behavioural ecology. An evolutionary approach. Second edition. Blackwell Scientific Publications, Oxford.

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Svärdson (1976) or, at the end of a sentence (Svärdson 1976).

Titles of journals should be abbreviated according to the World List of Scientific Periodicals. If in doubt, give the title in full.

Do not refer to unpublished material.

## Acknowledgments

Keep them short.

## Symbols and Abbreviations

The following symbols and abbreviations, as well as others approved for the Systeme International d'Unités (SI), are used in this journal without definition. Any others must be defined in the text at first mention, as well as in the captions or footnotes of tables and in figures or figure captions. A variable divided with another variable should be noted as the following example L per min is  $L \text{ min}^{-1}$ .

### Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h", "min", and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

### Prefixes

giga ( $10^9$ )	G
mega ( $10^6$ )	M
kilo ( $10^3$ )	k
milli ( $10^{-3}$ )	m
micro ( $10^{-6}$ )	$\mu$
nano ( $10^{-9}$ )	n
pico ( $10^{-12}$ )	p

### Time and Temperature

day	d
degrees Celsius	$^{\circ}\text{C}$
hour	h
(spell out for diel time)	
kelvin	K
minute	min
second	s
Spell out year, month, and week.	

In Table and Fig.:

year	yr
month	mo
week	wk

### Weights and Measures

centimeter	cm
gram	g
kilogram	kg
kilometer	km
liter (exception to SI)	L
meter	m

Spell out hectare and tonne.

### Mathematics and Statistics

all standard mathematical signs, symbols, and abbreviations base of natural logarithm	$e$
common test statistics ( $F$ , $t$ , etc.)	$R$
correlation or regression coefficient (multiple)	$r$
correlation or regression coefficient (simple)	$^{\circ}$
degree (angular)	df
degrees of freedom	$E$
expected value	$\alpha$
intercept	log
logarithm (specify base)	'
minute (angular)	NS
not significant	%
percent	$P$
probability	$P\alpha$
probability of type I error (false rejection of null hypothesis)	



probability of type II error (false acceptance of null hypothesis)	$P\beta$
radian	rad
sample size	$N$
second (angular)	"
standard deviation	SD
standard error	SE
variance	$V$ or var

### Physics and Chemistry

all atomic symbols	
alternating current	AC
ampere	A
becquerel	Bq
candela	cd
chemical acronyms listed in Webster's dictionaries (DDT, EDTA, etc.)	
coulomb	C
dextro	D
direct current	DC
electron volt	eV
equivalent	eq
farad	F
gray	Gy
hertz	Hz
hydrogen ion activity (negative log of)	pH
joule	J
levo	L
lumen	lm
lux	lx
molar	M
mole	mol
newton	N
normal	N
ohm	$\Omega$
ortho	$o$

para	$p$
pascal	Pa
per mille (per thousand)	$\text{‰}$
siemens	S
tesla	T
trihydroxymethyl-aminomethane	tris
volt	V
watt	W
weber	Wb

### General (some are restricted)

compass directions (maps and coordinates):	east E	north N	south S	west W
et alii	et al.			
et cetera	etc.			
filial generation	F			
for example	e.g.,			
international unit	IU			
months (tables, figures):				
first three letters				
(Feb, Jun, etc.)				
ploidy	n			
sex (tables, figures, hybrid crosses):	female ♀	male ♂		
that is	i.e.,			

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The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
$t$ -test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
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