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DROTTNINGHOLM

Report No 57

LUND 1979
BLOMS BOKTRYCKERI AB

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Speciation of Scandinavian Coregonus

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CONTENTS

I. INTRODUCTION

The *Coregonus* populations of temperate freshwater lakes have since long been a *crux et skandalon* for the taxonomists (FREIDENFELT 1933). The bewildering variety of forms has, however, also been a constant challenge to evolutionists. As was pointed out by STEINMANN (1950, 1951) they give a unique insight into ecological and zoogeographical aspects of the speciation process. So far, however, no agreed interpretation of this material has been arrived at.

STEINMANN thought hybridization between sympatric populations to be rare or nonexistent. He favoured the idea of postglacial sympatric speciation *in situ*, even in small lakes. SVÄRDSON (1949, 1957, 1965, 1970) on the other hand, stressed the proved introgression between sympatric coregonine populations and consequently saw the excessive variation as a decay process of an incomplete speciation in the past.

It may not be generally known that the majority of the coregonine populations of western Europe are to be found in Sweden. While Norway could be colonized by coregonines only in the southern and north-eastern parts of the country, because of sheltering high mountains and the too high salinity of the Atlantic, Sweden's parallel rivers, running from the western mountains to the Baltic, provided freshwater fish with excellent avenues for upstream dispersal. LUNDBERG (1899) sampled 3,960 lakes of Sweden and found whitefish in 422. If this sample is not biased, there should be some 8,000 lakes inhabited by whitefish or cisco within the country. So far, however, nobody has counted them.

There are many Swedish lakes with three different whitefish populations and quite a few lakes with four; some even have five populations. In most cases the local people, fishing for food, have acquired a good knowledge of the habits and spawning sites of the various forms, to which they have given local names. Some old and experienced fishermen are in fact highly expert at distinguishing different species of whitefish or ciscoes in mixed catches.

The southernmost Swedish lakes could be colonized from the north-west, during the warm Bölling interstadial, *c.* 12,300 yr BP, or even before that stage. Most of the northern lakes, however, could not be invaded until later, in the Ancylus period, *c.* 8,500 yr BP. Thus Swedish lakes have been open to new coregonine colonists during four thousand years.

The northern Swedish Baltic coast has been lifted up, by isostatic movements, to a maximum of 275 metres. This lifting process is still going on, though the rate has decreased. Obviously, the first fish colonists could swim upstream easily, whereas later shoals found rapids and waterfalls. The cisco, *Coregonus albula*, has a poor capacity to colonize upstream lakes and, in northern Sweden, is restricted to the coastal plains. Since this species has a tendency to dominate the whitefish populations (SVÄRDSON 1976), more of these populations have been saved in northern Sweden than in Finland or the Soviet Republic of Karelia, where ciscoes are abundant.

The existence of hybrids can be proved in every lake with two or more populations, if it is really searched for. This gene exchange is obviously a powerful obstacle for isolating mechanisms within the lake to create new species in the postglacial period. Since parallel rivers have much the same type of coregonine populations in their headwaters, mutually isolated for some 8—10,000 years, there is an overwhelming probability that the interpretation of original colonization by already different forms is the correct one.

The purpose of the research must primarily be to reconstruct what different forms were the common colonists to the lakes in which they now live. Some forms seem to have survived the glacial period in refugia in western Europe, while others are postglacial immigrants from the east. Ultimately, all coregonine forms have arrived in western Europe from the east, where the centre of their dispersal has been the non-glaciated Siberian coastal area with its abundant streams and lakes.

SVÄRDSON (1957) tried to relate the western to the Arctic and eastern forms. Because of the taxonomic problems involved in such evolutionary ideas, this attempt aroused much opposition, some of which was, no doubt, well founded. In the present paper a new, and it is hoped, more mature attempt will be made to suggest the evolutionary mechanisms behind "the coregonid problem". The principal difference is that now six, instead of five, whitefish species are identified in Scandinavia as well as the two ciscoes as recognized in the earlier paper. The identification of the six whitefish species is somewhat different from that of the 1957 paper, with several taxonomic consequences. Ultimately, the present paper should be looked upon mainly as a challenge made in the hope that it will evoke new studies on protein analyses of select key populations. Up to now, morphological and ecological studies have found an abundance of differences, while enzyme studies on *Coregonus* have mostly demonstrated similarities.

II. METHODS

The first method applied by the present writer to reveal coregonine evolution, was a study of the chromosomes. It was found that *Coregonus* had more chromosome disturbances than had other salmonid fishes and that these disturbances were similar to those of artifically produced hybrids between *Salmo* species. *Coregonus* from five localities all had chromosome fragments. Although the haploid number of chromosomes was 40, embryonic cells with subhaploid numbers were often found and these tended to have around 20 chromosomes. The evidence obtained suggested that salmonid fishes were old polyploids (Svärdson 1945). Recent protein studies have confirmed this hypothesis.

In the late 1940s, a series of transplantations were made, in order to check the statements by fishermen that while some somatic characters changed in a new environment, others remained stable and thus were probably genetically more firmly based. It was found that several of the systematic parameters most used related not only to body size (allometric) but also to growth rate, *viz.* height of body, length of snout and eye size (Svärdson 1950, 1951, 1952). The number of gill rakers, however, was reliable as a marker of genetic differences between populations. Later work was based on this circumstance.

Because of the great number of whitefish lakes in Sweden, it was important to acquire a regional knowledge of as many lakes as possible, above all the large lakes (Svärdson 1953, 1957, 1958). Gradually this explorative phase was concentrated on the headwater lakes of the bigger rivers, where the earliest colonists could be found. Lower lakes tended to have more introgressed populations, as had also smaller lakes as compared with big ones.

The phenomenon of dominance (Svärdson 1976) was found to be important since some whitefish species have a more evolved competitive edge. In some cases the dominance relation could even be used as an aid in identification.

Whenever possible, samples of spawning fish have been preferred. Spawners have already sorted themselves out, except for egg predators of foreign species. A gill-net catch in summer often gives a mixed catch of two or more populations. The separation of specimens then introduces a subjective, biased judgment.

In the last few years, emphasis has been laid on "the last species of the lake". It was found that less competitive species could survive in small numbers in deep water or be dwarfed or spawning on some inaccessible site and could therefore remain unknown to local fishermen. Since whitefish spawning often takes place when the ice is just beginning to cover the lake, there may be difficulties in getting boats out or walking on the ice. Some northern populations spawn in high winter, when the ice is very thick and may be covered by a metre of snow. In such cases explorative fishing for "the last species" can be extremely time-consuming and expensive.

In many cases only heads of whitefish have been secured, together with a scale sample and data on total length. Stomach analyses have also been performed but these are very cumbersome and normally give little further information. Gill rakers have always been counted in the laboratory under a microscope. Gradually, over the years, a tendency has grown up to include in the raker countings small lateral knobs. Because of this "human factor" older samples often appear to have about one gill raker fewer than younger ones from the same locality. Counts from investigators outside the Drottningholm Institute often display 1—3 fewer rakers. Only the first, left gill arch was used.

This human factor and the mixed samples, where hybrids and back-crossed specimens are included to an unknown degree, have discouraged the use of more powerful statistical methods. On the whole it has been thought more important to find similarities than differences between allopatric populations.

No analysis of the Scandinavian *Coregonus* forms can be performed without dealing with fish culture operations. Unfortunately, whitefish were among the first species to be introduced in new lakes when the technique of artificial fertilization spread in Scandinavia in the 1850s. Before that, it was customary to transport spawning whitefish, preferably from small-sized populations, on horse-drown sledges through the forests in winter to other lakes or tarns. The egg transport method begun in the 1850s was more efficient and resulted in long-distance transplantations. But permanent problems for later scientists were thereby created owing to the difficulty in knowing whether a local population was native or not. Time-consuming searches in scattered local literature and in archives, as well as interviews with elderly people, have been the methods used. As will be shown in a later section false conclusions have been drawn, based on incorrect statements about the original locality of important hatchery stocks.

III. THE NUMBER OF SPECIES AND THEIR VERNACULAR NAMES

SVÄRDSON (1957) divided the Swedish and European *Coregonus* forms into two main groups, the *lavaretus* group of whitefishes and the *albula* group of ciscoes. The first group was then supposed to comprise five species, the second two species.

It has now been found that the whitefish group actually consists of six species in Sweden. A further seventh species, *C. autumnalis*, has recently been identified as conspecific to the Irish pollan (FERGUSON *et al.* 1978). Whether this species is introgressed to other species in the British Isles and elsewhere is not known at present. East of Scandinavia there are also further species of ciscoes and some evidence has appeared that the British vendace *C. vandesius* may be a cisco of specific rank.

The principal addition to the list of Swedish species has arisen because it was found that one whitefish earlier thought to live at the coast as a large fish but also in upstream lakes as a dwarf, had to be split into two independent species. In addition the sparsely-rakered species have been found to consist of one large- and one smaller-sized form instead of two large-sized ones. The details of this reinterpretation will be given in later sections.

Nomenclature is, of course, dependent on what populations are thought to be conspecific. Owing to the introgression such homologies are at present often rather speculative, especially where lakes are inhabited by only one or two forms. The more forms there are that live sympatrically, the easier it is to identify them relatively to one another.

It is important to be able to speak about a *Coregonus* population irrespective of the taxonomic rankings of different writers. Otherwise, any new revision will confuse local or national discussion of whitefish stocks. Here vernacular names are of considerable value.

Swedish fishermen have created hundreds of local names for whitefish forms. In most cases these accurately distinguish biological species but around the Arjeplog lakes the sophisticated naming applied also distinguishes young fish from adult spawning specimens. In the Torne river valley the Lapps have names for different size-classes of whitefish, based on their suitability for rapid knife cleaning.

For national use six Swedish whitefish names have been selected. All of them circulate in local areas but some are used differently in different areas. They are listed below together with the names of the two cisco species. For international discussion English equivalents are also suggested. The pollan of Irish lakes is not included.

Swedish name	*Vernacular name in English*
Storsik	Large sparsely-rakered whitefish
Sandsik	Lesser sparsely-rakered whitefish
Älvsik	River whitefish
Blåsik	Blue whitefish
Planktonsik	Southern densely-rakered whitefish
Aspsik	Northern densely-rakered whitefish
Siklöja	Cisco or Baltic cisco
Vårsiklöja	Spring-spawning cisco

In later sections the nomenclature of these forms will be further discussed. For the description of the material on which the taxonomy can be evaluated, however, the vernacular names will be used throughout the main part of this paper.

IV. RESULTS

In the earlier paper (SVÄRDSON 1957) all material studied up till then was included in tables. Since that time the material has expanded widely and there seems to be no purpose in publishing all the figures from hundreds of lakes (except elsewhere for domestic use).

The principle adopted for this paper is to present the species in order. Lakes are selected to show why a form must be considered to be a separate species. Later the zoogeographical problems and the complexities of introgression in some river systems are presented.

Two sparsely- and one densely-rakered species in Lake Locknesjön

Lake Locknesjön is the headwater of the Gimån, which is a tributary of the River Ljungan. When the ice sheet still blocked the nearby River Indalsälven in its middle part, proglacial lakes, nowadays smaller and situated within the Indalsälven system, then drained into the River Gimån. When the Gimån and the ice-dammed lakes were colonized, the fish may, or may not, have made their way there via Lake Locknesjön. There were several step-wise stages of drainage. However that may be, Lake Locknesjön was early colonized and then isolated by falls and rapids. Pike and roach did not penetrate the river up to the lake (FAXÉN 1947, SVÄRDSON 1970, *cf* Fig. 28, p. 66).

Locknesjön is situated 328 m above sea level, its area is 27 km^2 and its maximum depth 53. A sparse population of char has survived. Because pike did not occur — which is a rather unusual situation in that area — the parasite *Triaenophorus* was also absent and the quality of the whitefish was thus higher than in other lakes of the region. The whitefish of Lake Locknesjön were already famous at an early date (OLSSON 1876); their picture on the door of the Lockne parish church (Fig. 1) is from the 16th century. Some time ago pike was introduced and since then the quality of the whitefish has deteriorated.

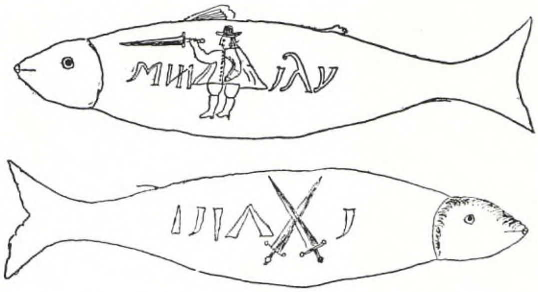


Fig. 1. Whitefish depicted on the door of Lockne Church in the sixteenth century.

The whitefish species of the lake were discussed by OLSSON (1876), LÖNNBERG (1922), HÖGLIN (1935), MODIN (1943), SVÄRDSON (1957, 1959) and HOLMBERG (1975). In the paper of 1957, the present writer knew only two species from the lake, though three were reported by LÖNNBERG and MODIN. But in 1958, the abundant and well-known, sparsely-rakered species of the lake was found to have a rarer, and bigger sympatric companion. That was the first clear-cut evidence of the occurrence of one larger and one smaller sparsely-rakered whitefish species living sympatrically in a Scandinavian lake. Since then the evidence for this has accumulated greatly, as will be shown in later sections.

Mr ELOF HALVARSSON of the Kälarne hatchery and field station has provided a wealth of information about the whitefish in Lake Locknesjön. A short summary is given below.

Large sparsely-rakered whitefish

The storsik is the rarest *Coregonus* of the lake. It is mostly found fairly deep and spawns on gravel with sparse vegetation, at a depth of 5—6 m around the promontory north of the Lokviken bay (Fig. 2), during the period January 15-February 20. The normal fish size is about 500 g, but now and then specimens of 2—3 kg are taken. The record weight was 3.5 kg. The diet is benthic: *Gammarus*, *Eurycercus*, *Pisidium*, trichopteran and ephemeropteran larvae, while chironomids are eaten mainly during the early summer (HOLMBERG 1975).

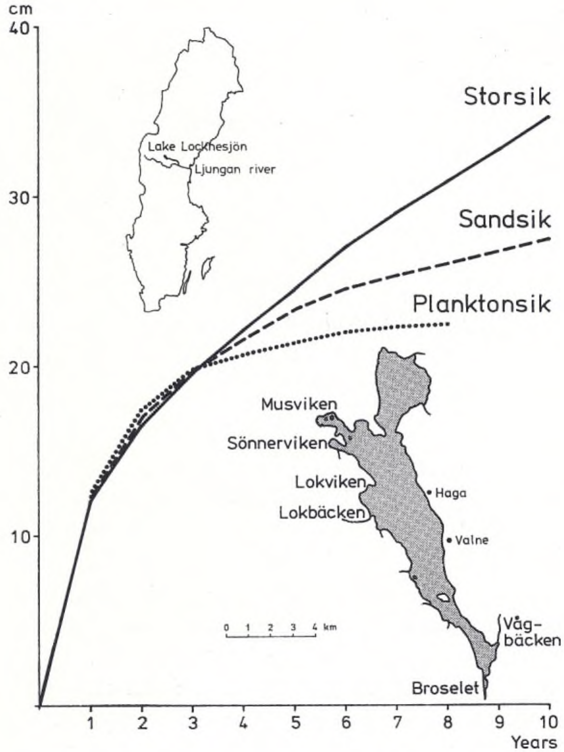


Fig. 2. Lake Locknesjön. Growth rate of the three whitefish species, back-calculated from scales readings.

Lesser sparsely-rakered whitefish

The sandsik is very common and is the species that made the lake famous. Generally it moves in shallower water than the storsik, especially when spawning. It used to spawn between Haga and Valne on the eastern shore (Fig. 2) but nowadays most fish seem to gather at the Lokbäcken stream and in a brook of the Musviken bay as well as in the associated bays. Spawning occurs during December 15—January 15. Modin (1943) pointed out that the sandsik were rather uniform in size, about 250—300 g, and they were formerly sold in numbers, not by weight. Nowadays the weight is lower, some 100—150 g, probably because of a denser population. There is a recent sport fishery for the sandsik. The record catch in one day, by a single angler, is 623 specimens. This fishing takes place from the ice in shallow water, not more than 1 metre deep. The diet of the sandsik is very similar to that of the storsik. The only difference found is that chironomid larvae are the sandsik's staple benthic food.

Southern densely-rakered whitefish

The planktonsik is also abundant. It lives pelagically and so is more difficult to catch by sinking nets. The size is the smallest of all species; formerly it was *c.* 175 g but nowadays it is less than 100 g. Spawning is very late, during February and the first week of March, at a depth of 5—10 m over firm bottom. The anglers may catch planktonsik instead of sandsik when they try deeper waters in the Musviken, Lokviken and Sönnerviken bays. Holmberg (1975) found the planktonsik to merit its Swedish name. The diet was almost exclusively zooplankton: *Cyclops* dominating in early summer, *Diaptomus* later, while *Daphnia* and above all *Bosmina* were taken in high summer. Insect larvae or *Pisidium* (*Sphaerium*) were utilized occasionally, mainly in April.

The late spawning of all three species was explained by Lönnberg (1922) as a consequence of the late cooling in autumn of this mostly spring-fed lake. This explanation is no doubt the correct one and the ice-covering of the lake is very late for the same reason.

Samples of spawners from several years prove the storsik to have 16—23 gill rakers, average 19, the sandsik 17—33, average 22 and the planktonsik to have 31—49, average 42. Some natural hybrids widen the span of variation (Table 1). The mouth is almost terminal in the planktonsik but clearly inferior in the storsik and sandsik.

The gill raker and mouth difference, the growth rate (Fig. 2) and the food habits, the various spawning places and periods all prove the three whitefish populations to be sympatric independent biological species.

The genetic background of gill-raker numbers, maturity, longevity, diet and growth

Lake Locknesjön is rather close to the Kälarne field station. This fact, and the wide difference in gill raker numbers between the storsik and the planktonsik, which have overlapping spaw-

Table 1. *Gill rakers of three whitefish species in Lake Locknesjön.*

Rakers / Sample	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	n	x̄
Storsik																																				
Febr. 1959	2	2	6	13	6	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	19.0
„ 1965	—	3	8	7	6	3	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	19.3
„ 1966	—	1	2	5	3	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	19.5
„ 1967	1	3	11	9	9	1	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	19.1
„ 1969	1	1	4	3	4	5	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	19.7
„ 1970	1	1	3	5	5	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	19.5
„ 1971	—	—	1	3	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	19.7
Total	5	11	35	45	36	23	11	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	168	19.3
Sandsik																																				
Jan. 1956	—	1	4	12	14	21	26	21	15	4	—	2	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	122	21.9
Oct. 1956	—	—	—	2	4	4	—	4	1	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	22.3
Dec. 1970	—	—	—	8	8	6	14	15	8	1	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	64	22.2
„ 1972	—	—	3	11	26	18	34	17	17	9	3	3	1	—	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	146	22.2
Total	—	1	7	33	52	49	74	57	41	17	5	7	4	—	2	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	352	22.1
Planktonsik																																				
Oct. 1956	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	3	3	6	1	4	1	1	—	—	—	22	41.8
Febr. 1957	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	3	2	15	19	12	12	17	10	6	—	—	1	—	98	41.3
„ 1959	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	2	40.5
Jan. 1964	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	4	7	12	15	15	17	13	7	7	1	—	—	100	42.1
Febr. 1965	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	2	1	8	6	6	5	5	—	2	1	—	39	42.4
„ 1966	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	2	40.5
„ 1967	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	4	4	5	3	5	2	1	—	—	27	43.1
„ 1969	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	5	4	1	5	3	11	5	2	1	—	1	1	42	41.7
Dec. 1970	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	4	2	1	1	5	2	4	2	1	—	—	—	24	41.0
Febr. 1970	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	8	6	5	7	4	5	3	2	1	—	45	42.4
„ 1971	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	2	1	3	3	6	5	16	14	14	16	7	6	3	—	—	99	41.9
Dec. 1972	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	2	2	2	—	1	—	—	—	9	42.6
Total	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	2	1	3	3	13	22	38	55	73	72	82	66	40	22	9	4	1	509	41.9

Table 2. *Examined one-summer olds from samples in the Hällesjö pond, where equal numbers of parent and hybrid fish were released as swim-up fry.*

	Storsik	Hybrids	Planktonsik
1964			
gill rakers	19.7 (16—24)	30.0 (26—34)	—
total length, mm	103.1	108.0	
number of fish	695	805	
1965			
gill rakers	19.5 (15—24)	28.1 (25—32)	40.4 (34—46)
total length, mm	99.4	100.6	95.2
number of fish	488	547	465
1966			
gill rakers	19.0 (16—23)	28.3 (24—33)	—
total length, mm	62.3	64.0	
number of fish	241	259	
1967			
gill rakers	18.6 (15—22)	29.4 (24—33)	41.2 (37—48)
total length, mm	112.4	116.0	110.9
number of fish	435	493	447
1968			
gill rakers	18.5 (14—22)	29.2 (25—32)	40.9 (36—46)
total length, mm	112.0	113.1	110.7
number of fish	74	99	121
1969			
gill rakers	20.0 (14—24)	28.9 (25—33)	39.7 (34—52)
total length, mm	103.6	103.6	106.9
number of fish	416	254	358
sex ratio ♂♂ : ♀♀	290 : 126	127 : 127	181 : 177
1970			
gill rakers	20.3 (17—24)	29.5 (26—32)	41.6 (39—45)
total length, mm	118.2	120.5	116.3
number of fish	65	38	18
sex ratio ♂♂ : ♀♀	38 :27	17 : 21	13 : 5
1971			
gill rakers	20.1 (18—24)	28.6 (25—33)	41.3 (35—46)
total length, mm	100.4	100.1	100.9
numer of fish	238	246	152
sex ratio ♂♂ : ♀♀	113 : 125	121 : 125	63 : 89

Note: In 1966 the pond wall was damaged and the fish were only half grown.

ning periods, provided excellent opportunities for experiments on the genetic background of some ecological and morphological characters.

Hybrids were artificially produced in the early winters of the years 1964—71. The hybrids and the parent species were incubated in the Kälarne hatchery. The swim-up fry of the hybrids and one or both parent species were picked in equal numbers and released into a natural pond 2 hectares in area. In autumn, samples from the pond were sent to the Drottningholm Institute for analyses. In the years 1969 and 1971 samples of living fingerlings were also released into Lake Storstensjön, some 10 km north-west of Locknesjön. In 1971 fingerlings were introduced in Lake Sillersjön 100 km south of Locknesjön. Both Storstensjön and Sillersjön were supposed to provide spawning facilities for whitefish. No new generation was, however, born in the lakes. A summary of the information obtained from the pond fingerlings is given in Table 2.

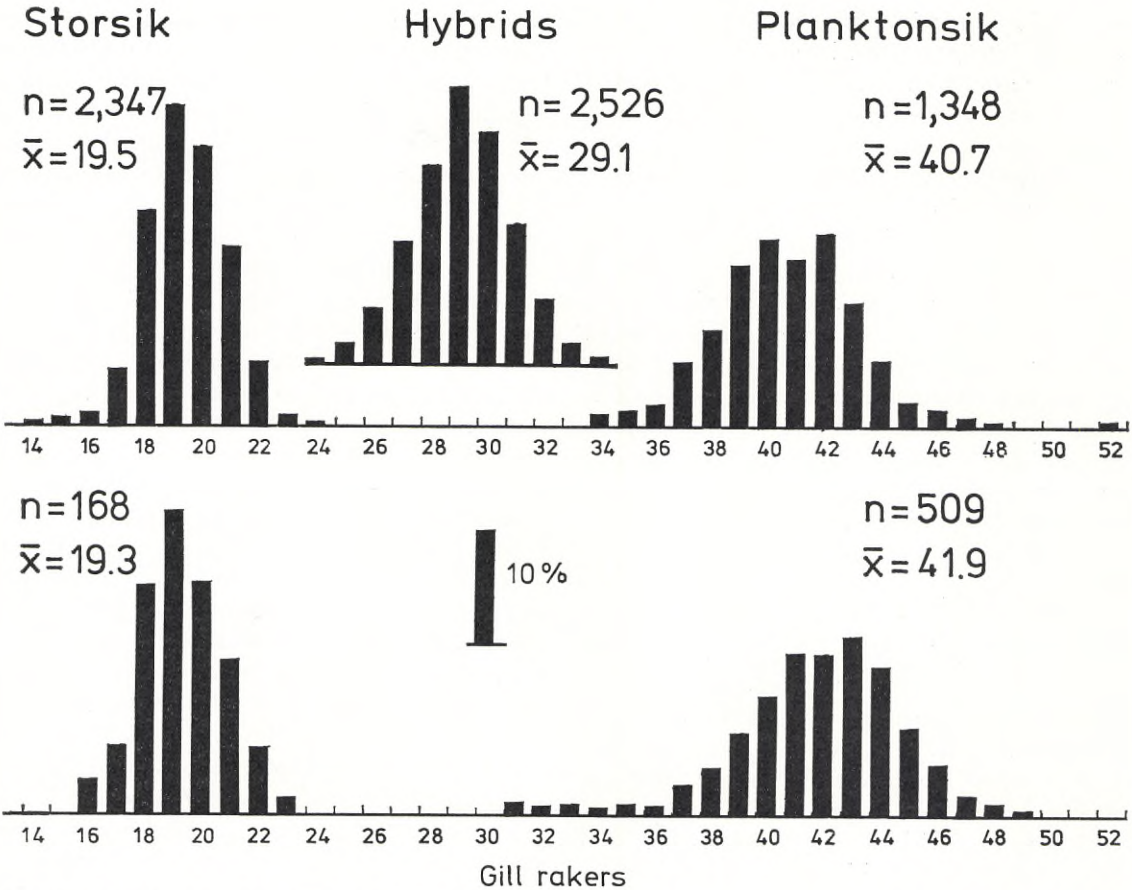


Fig. 3. Gill-raker number of adult (below) and fingerling storsik and planktonsik and their hybrids (*cf.* Table 2).

Many earlier experiments have proved that the number of gill rakers is genetically rather strictly determined. Again this was the case with the Lockne whitefish. Fig. 3 gives the percentage distribution of gill rakers in adult and fingerling pond fish of the same species, demonstrating almost no difference. It appears that the planktonsik fingerlings have on average one gill raker fewer (40.7 instead of 41.9), which seems natural in view of their much shorter gill arches. There is a saddle of both distribution curves (on 42 versus 41 rakers), possibly suggesting that one gene is responsible for more than one gill raker. The spawning planktonsik include specimens with 31, 32 and 33 rakers (out of a sample of 509), while there are no such rakers among the fingerlings (out of a sample of 1,348). Since the fingerlings do have fewer rakers than the adult fish, the low variants of the adult sample clearly suggest that they are natural hybrids. Table 1 also indicates hybrids included in the sandsik sample of spawners. As stated above, anglers fishing too deep may get planktonsik instead of sandsik and the gradual overlap of spawning habitats may produce natural hybrids.

Thus, while the Lockne whitefish are outstanding for their "pure" specific character, there is nevertheless some slight gene exchange between the populations. In most lakes the gene-flow is probably more intense than in Lake Locknesjön.

Fig. 3 demonstrates the intermediate morphological character of the F_1-hybrids. Only a very few specimens, with 23 and 34 gill rakers, overlapped the parent distribution. This possibility of identifying hybrids, living in the same pond as their parent species was, of course, the main idea of the experiments.

The hybrids were most numerous in five cases out of eight and they were the largest fingerlings in six cases out of eight. SVÄRDSON (1970) presented some of these results as evidence of hybrid vigour. The sex-ratio was studied in the 1969, 1970 and 1971 samples and was found to be normal, except for the storsik of 1969 where males outnumber females by two to one. There is evidence of such unbalanced sex-ratio in some other whitefish stocks, the mechanism of which is not known. No size difference was found between male and female fingerlings.

The transplantation to Lake Storstensjön

Gill-netting in Lake Storstensjön, in October 1970, produced 34 storsik, 30 planktonsik and 22 hybrids. The average total length was 222, 222 and 219 mm, *i.e.* they were all about the same size. It should be observed, however, that the planktonsik in two growth seasons (1969 and 1970, one of which in Lake Storstensjön) had already obtained the ultimate size of their home lake (*cf.* Fig. 2). Eleven planktonsik were sexually mature, as was one hybrid. On the other hand no storsik was sexually mature. If natural reproduction had been possible, the planktonsik would have filled the lake with progeny before any storsik had matured. This illustrates one of the most powerful mechanisms in whitefish competition: different generation turnover times.

The two-summer-old storsik specimens had fed on insect larvae and *Gammarus*, the hybrids on insect larvae and zooplankton, while the planktonsik had eaten *Bosmina* and *Daphnia*.

In the year 1971, the catch from Lake Storstensjön comprised 32 storsik (314 mm), 26 hybrids (296 mm) and 27 planktonsik (282 mm). The slower genetic growth rate of the planktonsik was now obvious, but so also was the strong modificational influence, since the fish of this species were considerably larger than ever in their home lake. Nine storsik males were still immature in their third summer while all seven females were ripe. Of 18 hybrids, all except two were sexually mature and ripe. All but three male planktonsik were noted as mature and ripe. The storsik had fed on *Gammarus*, *Pisidium*, insect larvae and *Corixa* (the lake had been rotenone-treated which had probably produced the rich *Corixa* population). Hybrid fish had copepods, some *Pisidium*, chironomids and very many *Corixa* in their stomachs. The planktonsik still concentrated on copepods, and *Bosmina*; some *Corixa* were also found but no insect larvae.

In 1972 all the planktonsik were gone. Their life span is the shortest of all the species. Of the fish released in 1969, six were storsik and four were hybrids. Diet differences were again noticeable, the storsik had fed on *Gammarus* and insect larvae but also on butterflies from the water surface, while the hybrids concentrated on *Corixa*, *Heterocope*, molluscs and some insect larvae. The storsik were 361 mm, the hybrids 331 mm long; weights varied from 400 to 600 g.

In 1973 smaller fish from the 1971 release dominated Lake Storstensjön. Nine were identified as storsik, eight were hybrids. The latter concentrated on *Eurycercus*, ephemeropteran larvae and *Corixa*, while the storsik fed on *Pisidium*.

It was a surprise that the food habits were genetically so firmly based and so different in fish, which, from the swim-up fry stage had lived in the same environment. Basically similar results, however, were described by VOLOSHENKO (1973) for *C. nasus*, *C. peled* and their hybrids.

In 1974 sixteen specimens were taken, weighing on average 1,000 g. Three were hybrids, all the others were storsik. In 1976 four fish were caught, weighing on average 1,180 g. Three were storsik, one was a hybrid. The last seven were taken in 1977 and consisted of one hybrid (1,375 g) and six storsik (865—3,070) of 425—570 mm total length.

The transplantation to Lake Sillersjön

In 1971 the second experiment was made to establish a reproducing population of storsik and planktonsik and their hybrids. Lake Sillersjön, in Ängersjö parish, was selected. Its area is 46 hectares, its maximum depth 12 m. Its fish fauna is dense, consisting of pike, perch and roach. In September 5,000 unselected fingerlings from the Hällesjö pond were released into Sillersjön. The subsequent test fishing, outside the feeding season, produced this result:

	Storsik	Hybrids	Planktonsik
1972	1	—	—
1973	28 (250 mm)	45 (250 mm)	34 (251 mm)
1974	10 (299 mm)	6 (288 mm)	3 (292 mm)
1975	no fishing		
1976	2 (373 mm)	4 (338 mm)	—
1977	5 (415 mm)	9 (369 mm)	1 (370 mm)

No reproduction occurred. Also the planktonsik specimen of 1977 was not born in the lake but was seven summers old. In 1977 the fishing effort was high in order to take the maximum possible amount of fish. Growth was slower than in Storstensjön, no doubt because of the competition from roach and perch. The hybrids tend to remain the most abundant even as adults. The life span of the planktonsik was again short, while the hybrids had the lifespan of the storsik.

Summary of experiments on Locknesjön whitefish

The evidence obtained from these field experiments can be summarized as follows:

1. The gill rakers are good markers on gene pools.
2. Hybrids tend to have better early growth and survival.
3. The diet tendency has a considerable hereditary component.
4. Age at maturity and span of life are partly under genetic control.
5. The growth rate may be strongly influenced by food availability but there is also some genetic basis, perhaps secondarily from the energetic value of the preferred food and the time for maturity.
6. The normal sex ratio is 1:1, but 2:1 in favour of males may occur.

Clearly, the evidence produced in these experiments on the Locknesjön whitefish can only strengthen the conclusion already formulated about the specific status of the three sympatric native whitefish populations of Locknesjön.

The river whitefish — a favourite object of transplantation

North of Stockholm a large anadromous whitefish runs the rivers of the Baltic coast in August to early October in order to spawn in rapids or over firm sediments in October or early November. According to the fishermen it returns to the Baltic Sea before the winter. It also occurs on the Finnish side of the Baltic. Taggings in both countries have proved that this species performs long movements southwards, from the top of the Gulf of Bothnia to the Åland islands, the northernmost stocks seem to be those that migrate furthest. It also homes to the stream where it has once spawned. Some females have been shown to spawn every second year.

Morphologically this species is characterized by a subterminal mouth and an intermediate number of gill rakers, as given in Table 3, mainly from SVÄRDSON (1957).

HANSSON and SANDSTRÖM (1968) and KARLSSON and LARSSON (1969) have provided more material from the north Swedish coast:

Torne	river	50 spec.	26—35 gill rakers,	average	30.2
Kalix	„	51 „	26—34 „ „	„	29.5
Lule	„	100 „	25—36 „ „	„	29.5
Rickleå	„	105 „	23—38 „ „	„	29.3

The Rickleå river lies between the Bure and Ume rivers.

The situation is similar on the Finnish side (JÄRVI 1928, VALTONEN 1976):

Iijoki	river	84 spec.	average	30.1 rakers
Oulujoki	„	95 „	„	29.1 „
Pyhäjoki	„	10 „	„	27.7 „
Kalajoki	„	9 „	„	28.4 „
Kokenmäenjoki	„	35 „	„	30.0 „
Kyminjoki	„	50 „	„	30.8 „

The last-mentioned river runs into the Gulf of Finland, all the others into the Gulf of Bothnia.

On both sides of the Gulf of Bothnia there is a second smaller and coast-spawning species with fewer gill rakers — a population of lesser sparsely-rakered whitefish — which locally is introgressed to the river whitefish. The Pite, Gide, Ume and Pyhäjoki river stocks may be influenced by such gene flow, or, alternatively, the samples are mixed up with the second species having 25—26 rakers.

For the commercial fishery the älvsik is impor-

Table 3. *Gill rakers in whitefish populations from Swedish Baltic rivers north of Stockholm.*

Rakers Sample	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	n	x̄
River																				
Torne	—	—	—	—	—	—	—	—	4	2	5	1	—	—	—	—	—	—	12	30.3
Kalix	—	—	—	—	2	4	18	15	23	13	16	12	10	4	2	—	—	—	119	29.7
Råne	—	—	—	—	4	3	8	10	13	16	15	8	3	1	—	—	—	—	81	29.4
Lule	—	—	—	1	3	5	3	10	5	5	8	2	1	1	—	—	—	—	44	28.7
Pite	—	1	4	11	9	22	19	14	1	4	2	3	1	—	—	—	—	—	91	26.6
Skellefte	1	—	—	1	—	3	1	7	11	2	5	2	—	3	—	—	—	—	36	29.1
Bure	—	—	—	1	6	15	11	17	16	13	12	6	1	—	—	—	—	—	98	28.4
Ume	—	—	—	8	12	17	18	27	8	7	6	4	—	1	—	—	—	—	108	27.6
Öre	—	—	—	—	—	—	4	6	11	15	9	5	1	1	—	—	—	—	52	29.8
Gide	—	—	1	4	2	16	7	10	5	5	4	—	1	—	—	—	—	—	55	27.4
Ångermanälven	—	1	—	1	3	4	10	20	22	28	26	33	19	12	6	—	3	1	189	30.6
Indalsälven	—	—	—	—	2	8	14	35	60	78	79	60	54	36	15	10	4	—	455	31.1
Ljungan	—	—	—	—	—	1	4	5	19	17	20	18	10	13	3	—	—	—	110	31.0
Ljusnan	—	—	—	1	—	1	2	1	5	7	12	7	3	6	2	2	1	—	50	31.3
Dalälven	—	—	—	—	—	6	5	1	8	11	10	4	3	6	4	3	—	1	62	30.8

tant. In former days the fish were caught in pole-nets where they accumulated in the first rapids in the lower part of the rivers. There were traditions of social gatherings and old rules of paying the fishermen, where part of the whitefish catch was smoked and eaten at the shore. The surplus was sold in the cities. Where the conditions were especially favourable, like the Torne river, up to 1,000 specimens could be caught in one day. The average weight was 0.5—1.0 kg, record specimens weighing up to 6—7 kg. The modern fishery has used big fyke nets and gill nets in the estuaries and seines in the rivers. The stocks have deteriorated in recent times.

The älvsik is a benthos-feeder with a good growth rate and a long life span. The age of Bure river male spawners is V—XII, of females VI—XVI (Svärdson 1951). The general ecology of the Indalsälven stock was described by Lindroth (1957), who also discussed the sympatric second species at the coast. Szczerbowski (1970) studied spawning samples in Indalsälven and analysed age and growth data.

There can be no doubt that Artedi, who was born the son of a clergyman and was brought up close to the Mo river (between Gide and Ångermanälven rivers) was thinking of this älvsik when he wrote about whitefish. Linnaeus (1758) referred to Artedi when he described "*Salmo lavaretus.*" *C. lavaretus* thus means the river whitefish of the northern Baltic Sea.

It is only rarely that the älvsik has spontaneously adapted itself to land-locked conditions and then only in large lakes. Lake Vänern has a long-snouted population with few gill rakers, 25 or 26 on average, and Lake Vättern is inhabited by a long-snouted population with 29—30 rakers. Lake Mälaren was up to historical times only a bay of the Baltic and its älvsik (30—31 rakers) has probably not changed in the last thousand years. Lake Siljan was almost connected to the Littorina Sea (a phase of the Baltic) and thus easily colonized. Its älvsik stock has some 27—29 gill rakers. All land-locked stocks are large-sized fish.

When the first wave of enthusiasm for fish culture swept over Scandinavia in the 1850s and 1860s the valuable älvsik stocks at the river mouths became popular. Hatcheries were built for salmon and this whitefish species.

A renewal of interest came in the 1940s and 1950s when the intensive expansion of hydroelectric power led to the creation of lake reservoirs in the upper parts of the rivers. The hydroelectric companies were compelled by the water courts to compensate actual or assumed damage to the whitefish stocks by abundant fry release. In order to rationalize fish-culture operations, eggs were secured where they were cheapest, *i.e.* at the coast.

Future zoologists will have much to say against the destruction of valuable natural variability by these fish-culture activities. In some cases, however, the analyses of transplanted älvsik stocks could produce new knowledge about the stability of whitefish population characters. The transplantation of the Bure river stock to lakes in Malå parish (Skellefte river) was studied (Svärdson 1951) as was also that of the Indalsälven river stock introduced in Lake Kölsjön (upper Dalälven) in the 1940s (Svärdson 1965, p. 96). The gill raker numbers, growth tendencies and spawning periods were not changed. Some further cases will be presented below.

Älvsik introduced in Lake Locknesjön

Lake Locknesjön has been presented above as a lake with three well-defined whitefish species. The lake ought to be regarded as a scientific natural reserve. Unfortunately the lake felt the impact of the vogue of the 1940s and acquired whitefish fry from various sources in the period 1943—51. According to records kept by the local fishery association of landowners, älvsik from the Ljusnan and Indalsälven rivers were released as fry. It was long thought that all these fry introductions had failed, as happily is often the case. However, when Annkristin Holmberg (1975), studying the diet of the Lockne whitefish, fished in summertime, her samples included 381 specimens referable to the three known species (*cf.* spawning samples in Table 1) but 29 fish had to be classified as "hybrids". The average number of gill rakers was 30 and the fish were fairly large and benthos-feeding specimens.

Mr Olov Jönsson, secretary of the local association, recently obtained information about a "new" whitefish in the lake. It is a large fish, spawning very early in places (Broselet, Vågbäcken, Fig. 2) where no whitefish spawning has been known before. In mid-October 1977 Mr Jönsson brought four whitefish heads to the Drottningholm Institute. One female of 1.9 kg was almost spent. The gill rakers numbered 17, 22, 24 and 29, suggesting that two of the fish were possibly storsik but that the others were älvsik or hybrids. Since the fishermen recognize the fish as a new kind, with spawning grounds in running waters of considerable volume, natural hybrids between only the native species are ruled out. There seems to be no escaping from the conclusion that the fry releases of the 1940s have given the lake a sparse älvsik stock as a fourth species, spawning earlier than the native ones.

Probably the new species will have difficulty in surviving in the long run, as seems to have happened to some of the other introduced älvsik stocks of upstream lakes. The fishermen are favourable to the new fish because it is large. In a small adjacent lake the same source of fry was introduced at the same time and a whitefish of 4 kg was recently taken. Catches like this are an encouragement to perpetuate fish-culture activity, which otherwise is out of fashion in the 1970s.

Älvsik introduced in Lake Sällsjön

It has long been known that, unfortunately, introduction of whitefish in this char lake took place about 1870 (Ekman 1910). The details of this management operation (whereby char was exterminated) were long poorly known. Nowadays this stock is abundant in many lakes of the River Indalsälven. The practical and scientific consequences have been important. Svärdson (1970) suggested, on the basis of the Sällsjön whitefish, that a new species could arise in so short a time as the postglacial period of 9,000 years. This interpretation was wrong, however, being based on incorrect information about the source of the Sällsjön whitefish stock in 1870.

The history of the uncovering of the mystery surrounding the origin of the Sällsjön fry has three stages, each of which had its effect on the general study of whitefish. First, the fry was supposed to have come from some nearby lake, with native whitefish stocks, in the same river system. The Sällsjön stock has 21—31 gill rakers, average 25—26 and it spread early to Lake Ockesjön, just downstream of the river. In Ockesjön there was a native storsik stock with 19—20 rakers. The old and new stocks were both large fish. They formed part of the main basis for assumpting that two large-sized sparsely-rakered species existed in Scandinavia (SVÄRDSON 1957), since the same situation also occurred in other lakes of the river.

Then the discovery in 1958 in Lake Ockesjön of a small-sized, almost dwarfed, third species, also with a low number of gill rakers, caused considerable confusion. At the same time the first samples of the rare, large sparsely-rakered whitefish of Lake Locknesjön proved the well-known abundant form of this lake to be a smaller-sized companion. In a short time during the late 1950s and early 60s the existence of native sympatric large- and small-sized sparsely-rakered species had been proved for headwaters of two rivers and other finds of new populations in Lule river lakes confirmed this interpretation. What, then, about the Sällsjön whitefish? Gradually it appeared that it was not native to the Indalsälven river system but, when introduced *c.* 1870, came from some remote locality.

The second stage began when light was thrown on the activities of CARL BYSTRÖM, a prominent fish culturist, who had been brought up not far from Lake Sällsjön. As he had published reports of introductions of whitefish into char lakes close to Sällsjön in the early 1860s it appeared that he was most probably also responsible for the Sällsjön introduction. Moreover, he later had access to whitefish foreign to the Indalsälven river, after he became head of the first national hatchery at Ed, lower Ångermanälven river in 1864. There he hatched salmon and whitefish from this river and char from nearby lakes. In his reports he described the introductions of whitefish fry in numerous lakes of lower altitudes. However, the gill rakers of the Ångermanälven stock did not fit those of the Sällsjön population. If BYSTRÖM was responsible for the fry released into Sällsjön, he must have got the eggs at the coast, where the second species of the Baltic, the sandsik, has about the same number of gill rakers as the Sällsjön stock.

It was then concluded that most probably BYSTRÖM had for some reason used the sandsik of the coast. When the presumed sandsik slipped down from Sällsjön to the Ockesjön, it lived there sympatrically as an independent third species, alongside the storsik and the native sandsik of the lake. Apparently it had evolved to specific rank during the mutual isolation lasting roughly 9,000 years (SVÄRDSON 1970).

The third stage started when the activities of a short-lived obscure hatchery within an agricultural school near Östersund became known. The industrious teacher of fish culture of that school, NILS BONDÉN, who was employed for only a few years in that capacity, has now been associated with the Sällsjön introduction on the evidence of travel-expense receipts and other documents found in the county archives of Östersund (SVÄRDSON 1977). Circumstantial evidence is available to show that in June 1870 BONDÉN released salmon and whitefish fry which originated from the second large national hatchery of the period, at the mouth of the River Gullspångsälven in Lake Vänern. The älvsik of this river was locally reknowned for its fatness and for this reason was called "fetsik". The same name was used for the Sällsjön whitefish soon after its introduction. Transports of the älvsik from Gullspång to places in southern Sweden are recorded but no transports up to central Sweden, where Sällsjön lies, are documented. The gill rakers of the Gullspång fish fit those of the Sällsjön stock.

Since BONDÉN can be held most probably responsible for an introduction of whitefish from Vänern, the sympatric coexistence of three species — all with few rakers — in Lake Ockesjön now seems natural, since they represent three different species which demonstrate their independent specific rank in other situations. The unusually low number of rakers in the Vänern stock of älvsik added to the confusion about the origin of the Sällsjön fry.

Rapid subspeciation by introgression

A fully-fledged speciation in postglacial times was thus a far-fetched conclusion that remains to be proved. But a rapid subspeciation by the same agent, introgression, is proved by the further spread of the Sällsjön whitefish. Owing to the building in the 1880s of a local hatchery at Lake Ockesjön, the Sällsjön stock was secondarily widely spread in the province. In a small lake, Siktjärn, almost a tarn, where it was put out as fry in 1906, test fishing was performed in 1977. The population was unchanged, with 26.4

gill rakers. In the big, deep and cold Lake Kallsjön, it was introduced in the 1920s. In various investigations of this lake, now a reservoir, a total of 737 specimens have been studied. The number of gill rakers, 19—34, average 25.9 prove that the stock has not changed.

In another tributary of the Indalsälven river than that of Sällsjön, Siktjärn and Kallsjön, the Sällsjön stock was introduced in the Lake Rönnösjön about 1915. It has not changed up to now. It spread to Lake Yttre Oldsjön and downstream to Lake Landösjön, which had two native whitefish species and a very sparse char population, (map in Svärdson 1970, p. 55). Soon the char was wiped out in all three lakes and the Sällsjön whitefish became known as the "new" whitefish of Lake Landösjön. It quickly became rather abundant but remained large-sized. In various investigations of this lake reservoir, a total of 779 whitefish attributable to the new whitefish were studied up to 1975. The first sample, from 1950, had 26.4 gill rakers, indicating that up to then no change had taken place. A sample from 1966 already had 28.1 rakers and in 1975 the number was 29.1.

A flow of genes between the introduced älvsik and the native planktonsik (with 39—40 rakers) has obviously taken place. The difference of gill raker distribution between allo- and sympatric Sällsjön whitefish (Fig. 4) demonstrates the subspeciation during 50 years of sympatry. So far the benthos-feeding habit of the älvsik in Lake Landösjön has not changed, which suggests that the subspeciation up to now is morphological more than ecological. It was argued (Svärdson 1959 b, p. 138) that "the morphological characteristics of the original populations tend to be eliminated first, thereby strengthening the ecological difference, which is under selection for persistence". It is hoped that the further evolution in Lake Landösjön will be followed by future biologists.

The contrast between on one hand the group of lakes where the älvsik from Lake Vänern introduced to Lake Sällsjön 1870 has not changed in 100, 70, or 50 years of allopatric existence and on the other hand the sympatric situation of Landösjön where it changed significantly in gillraker number in less than 50 years, is very strong evidence that introgression is the main factor in the postglacial evolution of *Coregonus*.

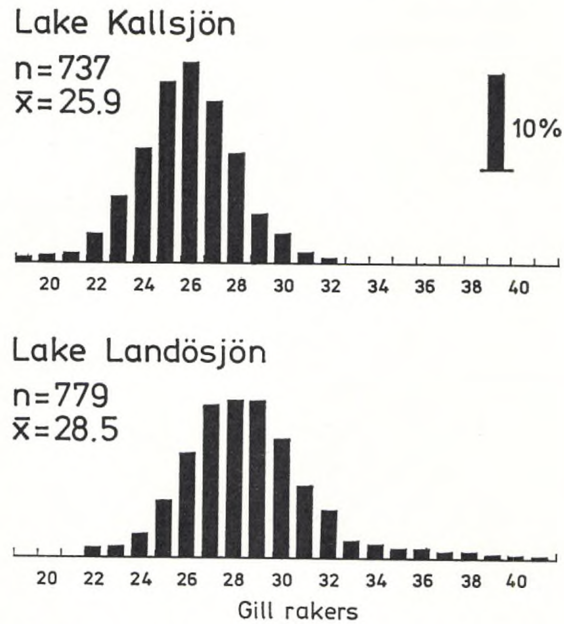


Fig. 4. In 50 years or less, introgression to sympatric stocks has modified the Lake Landösjön whitefish compared with the allopatric population of Lake Kallsjön.

The fifth species, northern densely-rakered whitefish

The known distribution in Scandinavia of the northern densely-rakered whitefish, or aspsik, is restricted to five North Swedish rivers, where it lives in seven large lakes (Fig. 5).

Ecologically the aspsik is a fairly large fish with a planktonic diet. It seems to be a surface-feeder in high summer, as has been proved in several populations. Since surface food is found in specimens caught in gill nets at a depth of 15—20 m a pronounced vertical dial migration is concluded. In some of the lakes the species is distinctly related to larger running waters for spawning.

Morphologically the aspsik is characterized by very long and numerous gill rakers, forming a series of population averages from 62 to 45. This change no doubt is caused by an increasing

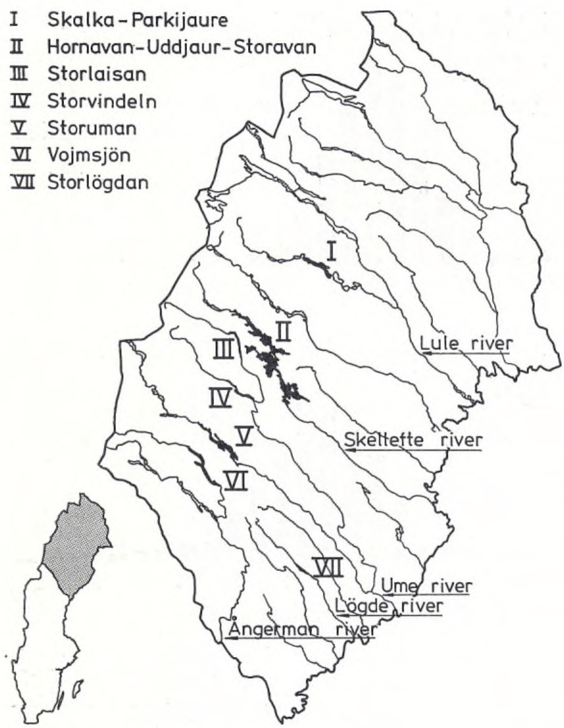


Fig. 5. The seven lakes from which the aspsik or northern densely-rakered whitefish are known.

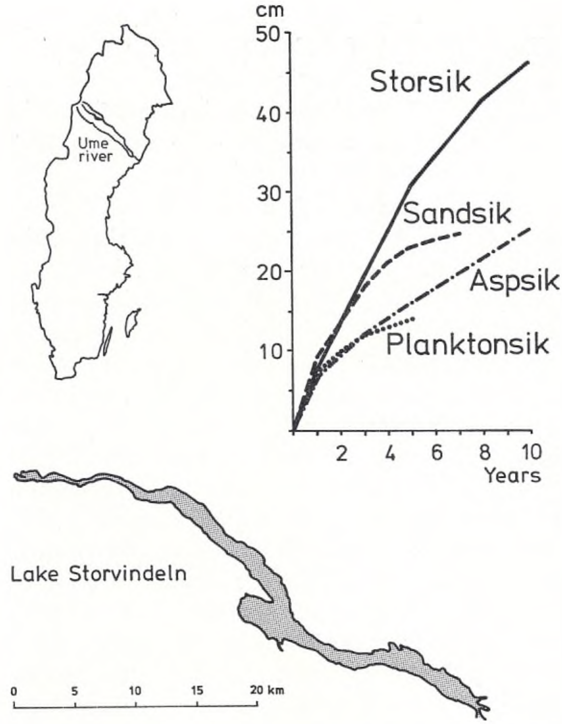


Fig. 6. Lake Storvindeln and the growth rates of its four whitefish species (*cf.* Table 4).

amount of introgression and is correlated to a parallel change of the mouth and snout. The least introgressed population has an almost cisco-like mouth with a longer lower jaw. The other demes have a terminal mouth with jaws of equal length or with the upper jaw slightly longer.

In 1882 SMITT described this species as *C. aspius*, after the Swedish local name "asp". The diagnostic criterion was the number of gill rakers, which should be more than 41. Later (SMITT 1886) he gave the range as 42—50 rakers and added that the snout is low (less than 61 % of its breadth). He also cites the religious reformer L. L. LAESTADIUS (1800—61), who in 1831 noted of the aspsik: "spawn in autumn in streams during October . . . similar to the (stor) sik but differs in having long and thin gill rakers". As a boy, and later as a young clergyman, LAESTADIUS lived close to Lake Hornavan.

All known lakes with aspsik, except those in Arjeplog parish, are briefly presented below, with their sympatric whitefish fauna.

Lake Storvindeln

The lake is the headwater of the Vindel river, a tributary of the Ume river. The area of Storvindeln is 5,500 hectares, its altitude 342 m and its maximum depth 36 m. Essentially it is a widened part of the river (Fig. 6).

The local people recognize four whitefish species, as cited by OLOFSSON 1930 in his very detailed field notes from the area. The local names are sik (=storsik), gertsbäckslöja (=sandsik), blajokk (=planktonsik) and storskallelöja (=aspsik). The aspsik is so named because of its large head. The growth rate of all species is given in Fig. 6 and their gill-raker numbers are summarized in Table 4.

The storsik is the largest fish; it lives to be rather old and may reach 2—4 kg. It spawns on some grounds in shallow water in mid-lake in November—December. The gill rakers number about 23. The sandsik has the same, rather protruding, snout as the storsik but a more curved

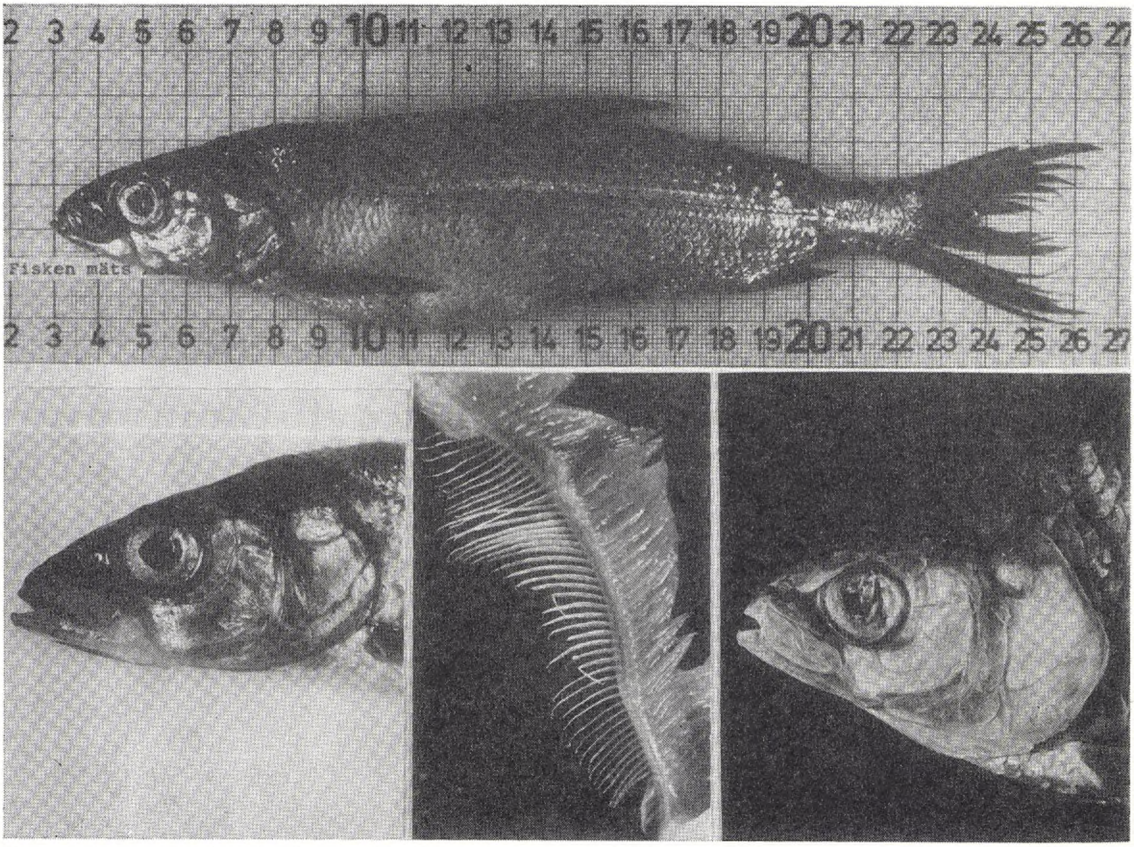


Fig. 7. The aspsik of Lake Storvindeln (above). Its mouth (left) is similar to that of the "river *peled*" of the Soviet Union (right). The gill rakers are long and thin, numbering more than 60.

head profile (like a goat says OLOFSSON). The fins are almost black, with a whitish base and the gill rakers, numbering 20—21, are short. The spawning occurs in December and the best-known spawning locality is a small stream, coming from Lake Gertsjaur. The local name of sandsik refers to this spawning site.

The planktonsik has a terminal mouth and the head profile is straight. The fin base is yellowish brown (OLOFSSON) and the fecundity of 16—19 cm specimens is some 2,000 eggs, against only 800 in sandsik of similar size. The planktonsik has 40 rather long gill rakers. Spawning is later, in November—January, at the shore or, locally, in the lower part of brooks or their outlet bays.

The aspsik of Storvindeln was not seen by OLOFSSON but it appears from his interviews that he regarded the species as being larger (older) specimens of the sandsik. This was quite wrong, however, as was shown when OLOF FILIPSSON in 1976 secured the first seven fish. They were some 25 cm in total length, and had very large eyes and extremely long and numerous gill rakers, numbering more than 60. Nothing like them had ever been seen by the experienced staff of the Drottningholm Institute. The most surprising detail was the distinctly longer lower jaw of these whitefish, giving them an almost cisco-like appearance (Fig. 7). In September 1978 more specimens were netted some 10 km from the entrance of the main inlet. They were mature but not ripe. The spawning grounds are so far unknown, even by the local people.

Stomach analyses proved the Storvindeln aspsik to be planktophagous but the specimens from 1976, taken in summer, had also fed from the surface.

Table 4. *Gill rakers of four whitefish species in Lake Storvindeln.*

Rakers / Sample		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Storsik																										
Nov.	1953	—	—	2	2	9	11	21	16	16	5	4	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Dec.	1956	—	—	—	1	2	9	7	9	5	6	8	2	—	1	—	—	—	—	—	—	—	—	—	—	—
Sandsik																										
Dec.	1951	—	2	1	3	11	6	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Oct.	1969	2	3	17	20	29	10	2	1	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Aug.	1976	—	—	1	1	1	2	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Planktonsik																										
Jan.	1952	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	5	9	13	18	13
Dec.	1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7	9	9	9
Oct.	1969	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	1	1
Aug.	1976	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	10
Aspsik																										
Aug.	1976	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sept.	1978	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 5. *Gill rakers of whitefish and cisco in Lakes Storlaisan, Storuman and Storlögdan.*

Rakers / Sample			17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Storlaisan																								
Storsik																								
Aug.	1976		—	—	—	—	2	4	6	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Nov.	1976		—	—	1	1	1	1	1	3	2	4	—	1	1	—	—	—	—	—	—	—	—	—
March	1977		—	—	1	4	6	7	9	6	1	1	—	1	—	—	1	1	—	—	—	—	—	—
Sandsik																								
Oct.	1956		—	—	—	—	13	24	21	24	11	8	—	—	—	—	—	—	—	—	—	—	—	—
Aug.	1976		1	4	4	9	31	44	59	50	31	17	10	4	—	1	—	—	—	—	—	—	—	—
Aspsik																								
Sept.	1956		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Aug.	1976		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—
Storuman																								
Storsik																								
Kaskeluokta		1953	1	1	3	6	8	5	10	9	3	1	1	—	—	—	—	—	—	—	—	—	—	—
Laisbäck		1953	—	—	4	1	12	7	12	7	4	1	—	1	—	—	—	—	—	—	—	—	—	—
Storströmmen		1953	—	—	1	3	5	4	8	8	9	8	1	3	—	—	—	—	—	—	—	—	—	—
Ankarsund		1975	—	—	—	1	3	3	2	4	4	2	2	1	—	—	—	1	—	—	—	—	—	—
Aspsik																								
Kaskeluokta		1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
"		1954	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Several localities		1975	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Storlögdan																								
Siklöja (cisco)																								
Aug.	1977		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Aspsik																								
Aug.	1977		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 4 continued.

41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	n	x̄
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	89	22.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	23.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	20.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	87	19.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	21.0
10	5	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	80	39.3
10	8	4	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	61	39.8
3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	39.2
7	1	4	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	40.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	1	—	2	—	—	7	62.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	3	—	2	3	1	1	14	63.0

Table 5 continued

39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	06	61	62	63	64	65	66	n	x̄
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	22.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	24.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	22.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	101	23.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	265	23.2
—	3	6	6	7	7	8	7	9	3	11	11	3	6	3	2	2	—	—	—	—	—	—	—	—	—	—	—	94	46.9
(1)	—	—	—	—	—	—	—	—	—	1	2	1	3	2	1	4	—	1	1	—	—	—	—	—	—	—	—	16	53.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	22.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	22.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	23.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	24.2
1	—	11	17	16	10	15	7	9	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	88	43.6
2	7	10	19	23	29	20	13	13	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	152	44.0
2	17	27	72	80	91	106	85	40	22	6	6	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	557	44.3
1	—	—	3	8	16	13	11	10	8	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	74	45.4
—	—	(1)	—	—	—	—	—	—	—	1	1	—	2	4	10	12	12	8	12	6	2	2	1	2	—	—	1	76	56.4

Lake Storlögdan

This is the biggest lake in the comparatively short Lögde river. The lake area is 1,230 hectares, its altitude 266 m and its maximum depth 38 m.

The lake is the only aspsik-lake also inhabited by the cisco (SMITT 1886). When OLOFSSON visited the lake in 1934 he wrote that there was a whitefish, called "hutchen", from which caviar was made and sold. The hutchen thus had economic value for the local human population. OLOFSSON saw only two hutchen and found them to have 60 and 65 gill rakers. He noted that the hutchen spawned at the inlet of the Lögde river and was obviously related to the well-known "asp" of the Arjeplog lakes.

In the late summer of 1977 Filipsson found hutchen abundant in Lake Storlögdan. His rich sample had an average of 56 gill rakers, the next highest known. The hutchen were 30—35 cm long, and thus larger than the aspsik of Lake Storvindeln. The mouth was terminal or the upper jaw slightly longer (Table 5).

The sympatric cisco had 45 rakers, just normal for the species. The cisco is a dwarf of only some 10 cm total length, just as in SMITT's time.

Lake Storlaisan

The lake is headwater for the River Laisälven, a northern tributary of the Vindel river just south of Lake Storvindeln. Its area is 2,770 hectares, its altitude 424 m and its greatest depth 45 m.

Three sympatric whitefish species live in the lake. The storsik has 23—24 rakers (Table 5) while the sandsik has 23, so they cannot be separated on the basis of the gills. The growth rates, however, are again different. The storsik is 25 cm long when 5 years old and grows to a considerably larger fish. The much more abundant sandsik is only 15 cm in total length at age 5.

Two samples of the aspsik, from different localities within the lake, had 47 and 53 gill rakers respectively. Some specimens with 36, and 38—40 rakers may be hybrids (aspsik x storsik) or stray remnants of a more or less swamped planktonsik. Actually, a surviving population of planktonsik may exist, though all sizes of meshes were used in the routine test fishing. The aspsik grows to some 30 cm (20 cm at age 5) and spawns in November at the inlet of Laisälven river at the northern end of the lake. According to OLOFSSON's notes the aspsik was formerly of economic significance for the local population and dominated the catch.

It should be noted that a few aspsik specimens from Lake Storlaisan do have a longer lower jaw whereas the bulk of the sample had terminal mouths or slightly longer upper jaws. It seems that introgression to the sparsely-rakered species has caused the reduction of gill raker numbers and the change of the mouth, as compared with the Storvindeln stock.

Lake Skalka-Parkijaure

These two lakes of the River Lilla Lule, which is a tributary of the Stora Lule river, have been united since they became a lake reservoir in 1970. The total area is 6,400 hectares, the altitude 295 m and the greatest depth 40 m.

In order to study the changes of the damming and subsequent water-level fluctuations, the lakes were fished thoroughly in the summer of 1970 and again in 1975. EVA BERGSTRAND (1977) analysed the population changes of all fish species, of which the whitefish are the most important. She is now analysing a wealth of stomach samples from various seasons and depths and — of course — from the different species.

There are four whitefish species in the lakes. Two of them are large-sized, *viz.* the storsik and the aspsik, while the other two are rather small. Their growth rates are given in Fig. 8.

The species were sampled outside the spawning season so gill rakers, growth histories and slight morphological details were all considered in order to identify the four populations (Table 6).

The storsik has more rakers than in most other demes, with an average of 27—28. No doubt introgression to the aspsik (of roughly similar size) is the reason for this. The aspsik, in turn, has some 49—50 rakers, which again reflects gene flow since it "should have been" higher. The storsik has a normal snout while the aspsik has a terminal mouth and low nose. The storsik is a pronounced benthos-feeder while the aspsik feeds on cladocerans and terrestrial food from the surface.

The pair of small-sized species, sandsik and planktonsik, just have the same span in gill rakers (21 against 38—39, only 35—36 in Skalka) as the larger species-pair and very different diets. The sandsik feeds on benthos of smaller item size than the storsik, while the planktonsik (maybe introgressed to the blåsik, to be presented later) is a plankton-feeder, taking cladocerans as well as copepods (indicating a skilled plankton-hunting fish).

The spawning habits of the four populations are not well recorded in the lakes but a gathering of spawning aspsik in the vicinity of the main feeding river is known. This ecological character thus reminds one of the corresponding aspsik habits in Lakes Storlögdan and Storlaisan.

Lake Storuman

With an area of 160 km², an altitude of 349 m, and a greatest depth of 135 m Storuman is the largest lake in the Ume river. There is a deep-living char population of large-sized specimens. Only two whitefish species are recorded from this lake. The sparsely-rakered one, giving the major share of the yield, is a sandsik with storsik genes certainly still recombining. There is some slight raker variation in different parts of the lake. The average size of the fish is only 200—400 g but some specimens of 2 kg are known.

Evidence for a former existence of two independent sparsely-rakered whitefish in Lake Storuman comes from Lake Långvattnet, just upstream of Storuman in the north-west. Test fishing during 1978 in Långvattnet produced 13 storsik and 34 sandsik. The former were 24 cm long at age 5, and 30 cm at age 8, while the sandsik were only 15 cm in total length at age 5.

The aspsik of Lake Storuman is certainly rather introgressed, almost to the limit of identification. It has a terminal mouth, and low snout, but only 44 gill rakers (Table 5), being a small-sized fish (15 cm) with pelagical life habits. No association to running water is observed. There have been rumours about a second "asp" in the lake but in spite of big efforts in 1975, when more than 500 pelagic whitefish were studied, no second form could be found.

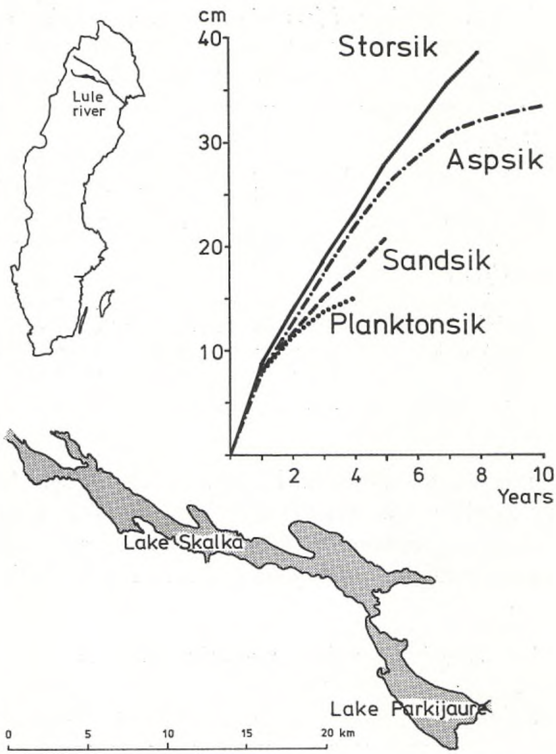


Fig. 8. Lake Skalka-Parkijaur and the growth rates of its four whitefish species (*cf.* Table 6).

Since no population of planktonsik has been found in Storuman, this species is probably swamped by the aspsik, which has itself been changed in the process.

Lake Vojmsjön

This lake is a widened part of the Vojmån river, a northern branch of the mighty Ångermanälven river (Fig. 5). The lake area is 78 km², its altitude 413 m and its greatest depth 145 m. Because of other investigations of this lake reservoir, many samples of its three whitefish species have been studied (Table 7).

Just as in Storuman there is in Vojmsjön an abundant sparsely-rakered whitefish which has been reported as a "storsik" in earlier papers from the Drottningholm Institute. It now appears that the fish in question is a sandsik, maybe with

Table 6. *Gillrakers of four whitefish species in Lake Skalka-Parkijaur.*

Rakers / Sample	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Skalka																							
Storsik	—	—	—	—	—	—	—	1	8	9	17	18	17	10	11	6	2	1	—	—	—	—	—
Sandsik	—	4	15	25	40	49	42	19	18	8	5	—	—	—	—	—	—	—	—	—	—	—	—
Planktonsik	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	1	1	—	3	1	—	4	4
Aspsik	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Parkijaure																							
Storsik	—	—	—	—	1	2	1	3	9	17	19	22	20	25	23	7	3	2	2	—	—	—	—
Sandsik	1	8	19	34	50	91	62	44	16	13	4	4	2	3	—	—	—	—	—	—	—	—	—
Planktonsik	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	4	8	13	34	51	66
Aspsik	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

some storsik genes still recombining though it is possible that storsik may survive as a very sparse population of its own. The majority of sparsely-rakered fish, however, are sandsik. Their average size is 250—300 g but specimens of 2—3 kg are known. In the summer of 1978 the upstream Lake Skikkisjaure was fished with a view to solving the problem and, again as in Lake Lång-

Table 7. *Gill rakers of three whitefish species in Lake Vojmsjön.*

Rakers / Sample	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Storsik																					
Nov. 1966	—	—	1	1	1	16	22	28	17	22	11	4	3	1	—	—	—	—	(1)	(1)	—
Dec. 1967	—	—	—	2	3	5	19	22	19	14	7	8	3	2	—	—	1	—	—	—	—
„ 1968	—	—	1	1	2	7	14	9	11	3	4	4	2	2	—	—	—	—	—	—	—
„ 1969	—	—	—	3	6	11	32	30	17	19	12	3	3	6	1	1	—	—	—	—	—
„ 1970	1	—	—	1	8	17	36	26	31	19	23	6	2	2	—	—	—	—	—	—	—
Nov. 1971	—	—	—	1	3	10	17	19	20	17	8	1	2	2	—	—	—	—	—	—	—
„ 1972	—	—	—	1	2	6	17	27	18	22	4	9	4	—	—	—	—	—	—	—	—
„ 1973	—	—	1	1	4	12	13	13	13	13	14	7	5	3	2	2	2	—	—	—	(1)
„ 1974	—	—	—	—	2	8	8	15	15	12	14	14	10	3	4	1	1	—	—	—	(1)
Dec. 1975	—	—	—	—	—	12	15	15	21	19	3	7	5	2	4	2	1	—	—	(1)	—
Nov. 1976	—	1	—	—	3	11	15	20	15	16	8	5	4	4	—	—	(1)	(1)	—	(1)	—
„ 1977	—	—	—	1	2	13	22	23	18	17	6	4	3	—	—	—	—	—	—	—	—
„ 1978	—	—	—	2	3	8	20	29	19	19	8	3	—	—	—	—	—	—	—	—	—
Planktonsik																					
Sept. 1949	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2
Aug. 1966	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
July 1971	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
„ 1977	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Aspsik																					
Dec. 1966	—	—	—	—	—	(1)	—	—	—	—	(2)	—	—	—	—	—	—	—	—	—	—
„ 1967	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
„ 1968	—	—	—	—	—	—	(1)	—	(2)	—	—	(2)	—	—	—	—	—	—	—	—	—
„ 1969	—	—	—	—	(1)	(1)	(2)	—	(3)	(3)	—	—	—	—	—	—	—	—	—	—	—
„ 1972	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)
„ 1973	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—
„ 1974	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—
„ 1975	—	—	—	—	—	—	(2)	(3)	(1)	—	—	—	—	—	(1)	—	—	—	—	—	—
Nov. 1976	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
„ 1977	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dec. 1978	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 6 continued.

39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	n	x̄
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100	27.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	225	21.2
5	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	35.6
—	3	6	6	9	17	11	16	25	33	36	59	41	43	30	14	11	7	2	2	1	—	1	373	49.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	156	27.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	351	21.3
86	69	32	17	13	6	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	406	38.7
—	1	1	3	1	5	2	5	5	8	14	16	17	16	12	13	6	2	2	2	—	—	—	131	50.4

vattnet upstream of Storuman, two populations were identified in Lake Skikkisjaure. The storsik were 40—50 cm in total length and 10—15 years of age while the sympatric sandsik were smaller and younger. At the age of seven, the storsik were calculated from the scales to have been 30 cm long or more while the sandsik were only 25 cm.

Table 7 continued.

36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	n	x̄
—	—	—	—	—	—	—	—	(1)	—	—	(1)	—	—	—	—	—	—	—	—	—	127	22.5
—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	105	22.9
—	—	—	—	—	—	—	(1)	(1)	(3)	(3)	(3)	(2)	(4)	—	(1)	—	(1)	—	—	—	60	22.4
—	—	—	—	—	—	—	—	—	(1)	(1)	—	—	—	—	—	—	—	—	—	—	144	22.6
—	—	—	—	—	—	—	—	—	—	—	(1)	(1)	(2)	(1)	—	(1)	—	—	—	—	172	22.5
—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	100	22.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	110	22.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	105	23.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	107	24.1
—	—	(1)	—	—	—	—	—	(1)	—	(1)	—	(1)	—	—	—	—	—	—	—	—	106	23.4
(1)	—	—	—	—	—	—	—	—	(1)	—	(1)	(1)	—	(1)	—	—	—	—	—	—	102	22.8
(1)	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	109	22.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	111	22.4
5	6	1	9	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	37.9
1	3	1	1	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	11	38.6
15	27	41	46	37	27	23	3	6	(1)	—	(1)	—	(1)	—	—	—	—	—	—	—	235	39.1
6	10	24	24	21	24	11	2	3	—	—	—	—	—	—	—	—	—	—	—	—	127	39.4
—	—	—	—	—	1	—	10	24	39	35	45	29	23	17	7	3	—	—	—	—	233	46.7
—	—	—	—	—	1	1	6	9	13	22	20	11	10	6	1	—	—	—	—	—	100	46.4
—	—	—	1	—	—	7	13	24	44	47	51	48	44	17	12	2	1	—	—	—	311	46.8
—	—	—	—	—	1	3	18	15	21	26	20	22	11	9	6	3	—	—	—	—	155	46.4
—	—	—	—	1	2	1	9	13	21	16	16	18	9	3	3	3	2	—	—	—	117	46.4
(1)	(1)	—	—	1	2	3	5	10	17	13	22	12	14	4	4	1	2	—	—	—	110	46.6
—	(1)	—	—	—	1	4	7	8	18	21	13	20	11	10	4	1	—	—	—	—	118	46.6
(1)	—	—	—	1	—	1	4	10	11	22	19	12	11	2	5	1	1	—	—	—	100	46.7
(1)	—	1	—	1	—	5	6	9	11	22	17	18	5	6	2	3	2	—	—	—	108	46.5
—	—	1	—	1	—	2	6	14	19	14	18	12	9	3	3	—	1	—	—	—	103	46.2
—	—	—	—	—	—	1	5	8	18	19	17	18	5	12	3	2	—	—	—	—	108	46.8

Fig. 9. Lake Siljan and the growth rates of its four coregonine species (*cf.* Table 8).

There are two further populations in Lake Vojmsjön apart from the sparsely-rakered whitefish. A real dwarfed planktonsik, which was not known to the local people, was discovered by Eric Fabricius in the 1940s. It has a terminal mouth and 38—39 gill rakers. Its ultimate size is only 10—12 cm. It is pelagic and plankton-feeding. The aspsik of the lake is some 20 cm and has 46—47 gill rakers (Table 7). The ecology of the Vojmsjön whitefish was discussed in some detail by Lindström and Nilsson (1962) and Lindström (1970).

The aspsik of Vojmsjön is pelagic and planktophagous and it does not take surface food, so far as is known at present. Lindström and Nilsson commented upon the diet difference between the aspsik of Vojmsjön and that of the Arjeplog lakes (to be presented later). Their conclusion of interactive segregation (due to the presence of another species) as the main explanation of the food difference found must now be revised. Genetic differences arising from local introgression to other species have certainly contributed to the different diets of the two aspsik stocks.

The small size, pelagic habits, non-association to running waters and the relatively few gill rakers all indicate that the Vojmsjön aspsik is evolutionarily modified by introgression. In a graded scale, where the Storvindeln deme of aspsik is the least introgressed, those of Vojmsjön and Storuman are the most modified.

Blue whitefish — the sixth and most competitive species

The blue whitefish or blåsik has a moderate number of gill rakers, more than 30 but less than 40. The mouth is terminal in dwarfed populations. These may have large eyes. Ecologically blåsik live in shoals and feed on plankton in summer, though they may also take benthic food, such as chironomid larvae. The species may spawn in running waters, early in autumn, or very deep on firm sediments late in high winter (February). Generally it is very abundant. Stream-spawning stocks have often been traditionally taken with pole nets in great numbers. Social gatherings of fishermen at the shore occur in the fishing season. Formerly the blåsik were sometimes transported alive to tarns or small lakes to grow up to larger specimens.

Because of its competitive edge, the blåsik may be the only species in a lake. This situation prevails in relatively small and shallow lakes of the lower regions of the bigger rivers of northern Sweden. Lake Vettasjärvi (area 1,000 hectares, altitude 352 m, depth 19 m) in the Ängesån river, tributary of the Kalix river may be selected as a typical case. The lake was surveyed several times because of legislation on mesh sizes of gill nets:

Rakers Sample	27	28	29	30	31	32	33	34	35	36	37	n	x̄
1928	1	—	1	3	2	2	1	—	—	—	—	10	30.5
1942—57	1	2	4	12	15	10	6	3	2	—	—	55	31.2
1977	1	9	14	21	44	27	25	5	6	2	1	155	31.3

Table 8. *Gill rakers of spawning whitefish and cisco in Lake Siljan.*

Rakers / Sample	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	n	x̄
Alderäng	—	1	—	4	11	12	20	9	7	5	1	6	8	2	3	6	7	8	10	9	10	5	4	1	1	—	—	—	—	—	—	—	—	150	—
Dynggrav	—	1	3	4	7	14	11	9	4	5	3	7	11	9	9	22	19	33	39	44	29	21	19	8	1	—	—	—	—	—	—	—	—	311	—
Vinäs	1	—	2	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	19.9
Ryssån	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	5	5	11	15	9	9	6	1	—	1	—	—	—	—	—	—	—	65	35.1
Fuån	—	—	1	5	6	6	3	3	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	21.0
Sollerön	—	—	—	—	—	—	1	—	2	2	6	6	14	11	6	7	5	13	12	9	14	4	9	3	1	—	—	—	—	—	—	—	—	125	—
Limån	—	—	—	1	—	2	2	—	2	3	10	6	12	7	8	12	12	24	26	47	24	24	14	6	3	—	—	—	—	—	—	—	—	245	—
Olsnäsviken	—	—	—	1	—	—	—	5	1	5	10	20	25	18	22	15	14	11	20	15	15	10	1	3	—	—	—	—	—	—	—	—	—	211	—
Österviken	—	—	—	—	—	—	—	4	6	6	16	17	28	28	22	12	8	7	7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	162	28.7
Insjön	—	—	—	—	—	—	—	2	3	10	21	44	46	47	28	24	15	7	5	4	—	2	—	—	—	—	—	—	—	—	—	—	—	258	28.8
Gråda	—	—	—	—	—	—	—	1	3	4	8	—	2	3	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	27.3
Siklöja (cisco)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	8	17	14	19	15	15	6	6	101	43.9

Table 9. *Gill rakers of whitefish in some lakes within the Ångermanälven river system.*

Rakers / Sample	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	n	x̄
Lake Tåsjön																																
planktonsik	—	—	—	—	—	—	—	—	—	—	3	—	—	1	—	1	1	4	12	17	43	78	75	58	27	31	11	4	1	2	369	41.8
blåsik	—	—	—	—	—	—	—	—	—	4	4	5	9	7	5	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	42	32.4
mixed catch	—	—	—	—	—	—	—	—	—	4	6	3	6	11	9	8	5	3	2	2	1	2	1	4	2	—	—	—	—	—	70	34.9
Lake Ormsjön																																
planktonsik	—	—	—	—	—	—	—	—	—	1	1	4	4	12	10	16	26	19	18	20	17	8	4	1	1	—	—	—	—	—	152	36.8
blåsik	—	—	—	—	1	—	—	1	4	10	14	22	26	28	24	19	16	5	4	7	4	—	1	—	—	—	—	—	—	—	186	33.2
Lake Flåsjön																																
blåsik	—	—	—	1	1	2	—	10	24	27	38	33	25	15	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	179	30.1
sandsik	1	6	18	58	50	55	52	21	4	2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	270	24.6
Lake Hotingsjön																																
blåsik	—	—	—	—	—	1	—	—	—	1	1	2	2	1	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	31.8

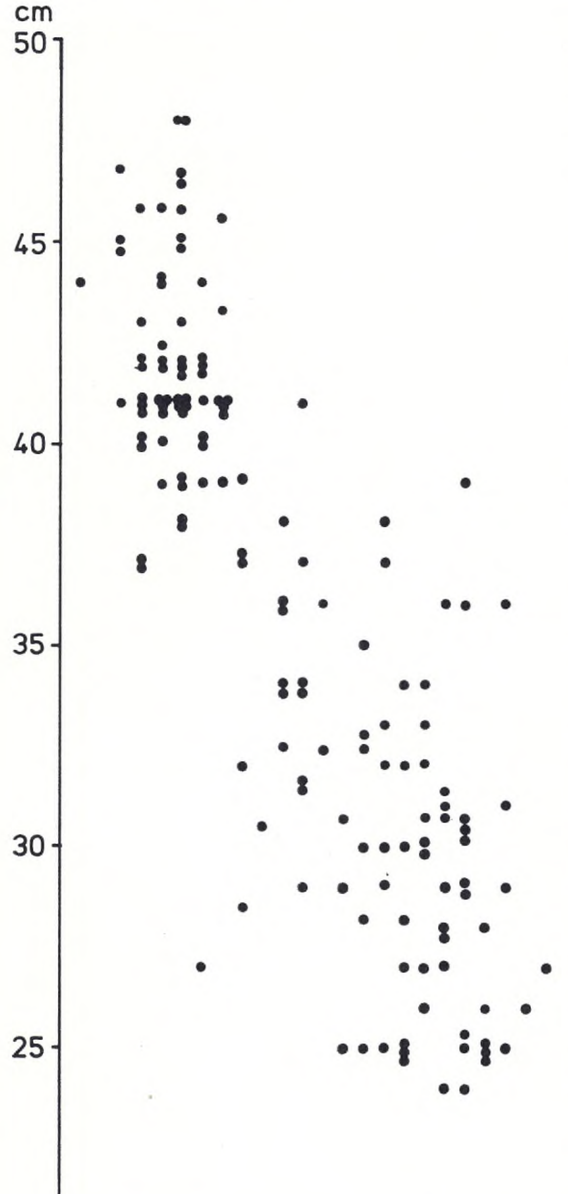


Fig. 10. At Alderäng, the inlet of River Dalälven into Lake Siljan, two species of whitefish spawn close together and produce hybrids (*cf*. Table 8).

Olofsson made the investigation of 1928 in the field, which gives fewer rakers. He cited fishermen who reported the existence of a second species in the lake, producing specimens of 3—5 kg every year. One fishermen told Olofsson that he had caught a whitefish of 7 kg and older reports ran up to 9 kg. This second species, probably a storsik or an älvsik, seems to have vanished now. Mr Filipsson, who fished Lake Vettasjärvi in 1977, got no specimen and the local people had not seen any large fish for years. The abundance of the Vettasjärvi blåsik was proved by the first night's catch on Filipsson's standard set of gill nets; it amounted to 700 specimens, and was the largest he ever got.

Lakes in the River Dalälven

Lake Siljan is by far the largest lake of the Dalälven river. Its area is 29,000 hectares, its altitude 161 m and its greatest depth 120 m (Fig. 9). Lake Siljan is inhabited by four coregonines, one of which is the cisco. Siljeström-Larsson (1730), Lundberg and Wahlberg (1892) and Arwidsson (1913) have described the four populations.

Siljeström-Larsson thought two of the forms were rather peculiar for the lake, *viz*. the "blickta" and the "ryssing". Linnaeus, however, when he visited the lake 1734 found the "blickta" to be a normal, though small-sized, cisco and he critized the quality of the picture given by Siljeström-Larsson. The "ryssing" was not commented upon by Linnaeus, who merely reiterated the fish list published four years earlier. Linnaeus in fact seems to have known whitefish only superficially. In his zoological lectures of 1748—52 at Uppsala (Lönnberg 1913) he presented the whitefish (sik) as fish that "live in lakes, mostly in Finland from where we got them salted". At least this is what the students noted from the lectures in their private writings At this time, however, whitefish was a staple food for large segments of the population of northern Sweden.

The "ryssing" is first mentioned in a court verdict of 1440 (courtesy Dr. Allan Rostvik). The name circulates in different versions (rössing, rysling, risling) in the Swedish provinces of Dalarna and Härjedalen and in neighbouring parts of Norway and means "small whitefish".

There are "ryssing" or blåsik spawning grounds in several streams around Siljan. Best known is the Ryssån river mouth, where ARWIDSSON (1913) found that the 18—24 cm fish spawned with a maximum around October 10—15. Traditionally they were caught in the night, with pole nets and a lamp. The river name Ryssån is known since 1663 but may not be primarily associated to the "ryssing" since it was at first spelled "Rijsåen" (courtesy A. ROSTVIK).

The blåsik or blue whitefish of Lake Siljan has about 35 gill rakers, as judged from the Ryssån population, where it spawns with no admixture from other forms. Otherwise (Table 8) the abundant blåsik intrudes on the spawning grounds of the large sparsely-rakered whitefish (storsik) of northern Siljan and the river whitefish (älvsik) of the southern part of the lake. Scatter diagrams (Figs. 10 and 11) clearly suggest both admixture and probable gene flow between the large-sized forms and the smaller, abundant blåsik.

There is no identifiable separate population of the planktonsik left in Lake Siljan. This species has probably been swamped by the blåsik, which in turn gets a somewhat higher number of gill rakers than it "should" have.

The process of ousting the planktonsik by the blåsik can, however, be observed in Lake Venjan, belonging to the western branch of the Dalälven river:

Rakers Sample	29	30	31	32	33	34	35	36	37	38	39	40	41	42	n	$\bar{x}$
Planktonsik	—	—	1	1	1	3	9	7	14	6	5	6	1	1	55	36.9
Blåsik	1	5	5	8	12	10	4	2	1	1	—	2	—	—	51	33.2

The two whitefish populations of Lake Venjan have long been known (AROSENIUS 1865). The local names refer to the size of spawning specimens. The blåsik is the largest, 20 cm or more, while the planktonsik is shorter than 20 cm. In recent times they have become still smaller, since their competition is harsher after the introduction of the cisco into the lake.

More sheltered from the blåsik has been the planktonsik population of Lake Amungen, of the same Dalälven branch as Lake Venjan. It was sampled in 1977:

Rakers Sample	35	36	37	38	39	40	41	42	43	44	n	$\bar{x}$
Planktonsik	4	2	5	15	28	24	19	13	6	1	117	39.7

The Venjan-Amungen trend of blåsik introgressing into the planktonsik, and finally ousting it, will be observed in many other lakes described in this and later sections.

Lake Storsjön

The Storsjön (area 456 km², altitude 292 m, greatest depth 74 m) is the largest lake of the Indalsälven river. The whitefish populations of the lake were discussed in some detail by SVÄRDSON (1953). Since that time, the älvsik of the lake has been proved to be of the Sällsjön stock and thus not native. A further species, the sandsik, is also found in Lake Storsjön (southern part) as well as in Lake Ockesjön just upstream of Storsjön and separated from it only by a broad, short stream.

The growth studies (*op.cit.*) proved the blåsik of Lake Storsjön to be a real dwarf. It never attained 20 cm, while the planktonsik was slightly larger. Both species grade into each other, the blåsik dominating the southern part of the lake and the planktonsik the northern and eastern, closer to the outlet.

It has also been recognized that the formal description of *Coregonus megalops* (WIDEGREN 1862) refers to the blåsik of Lake Storsjön. LILLJEBORG (1891) mentioned (p. 743) that one of the paratypes, then in the collections at Uppsala, was a ripe female only 150 mm in length. Unfortunately WIDEGREN's collections cannot now be traced. It seems clear, however, that *C. megalops* refer to the blåsik. It happens that this is the oldest blåsik description from Scandinavia (Fig. 12).

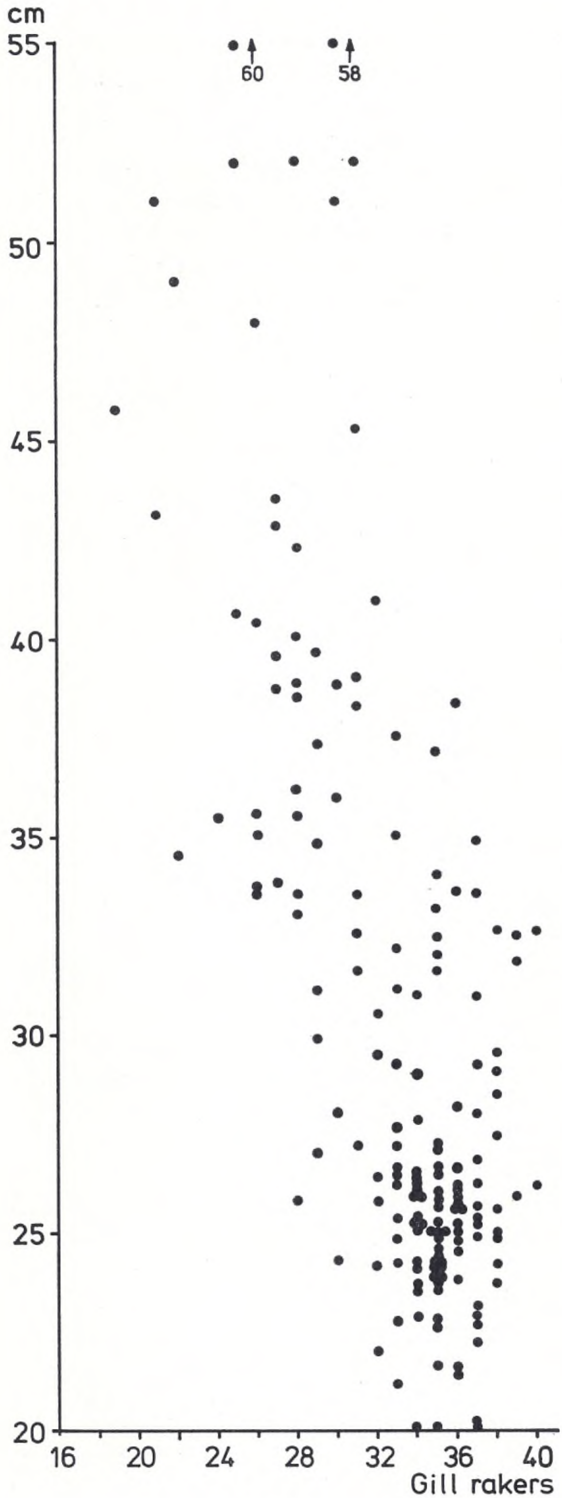


Fig. 11.

Lakes within the Ångermanälven system

Lake Tåsjön (area 450 hectares, altitude 248 m, greatest depth 80 m) is inhabited by two whitefish species, both of which are small. The larger one has 32 gill rakers and is a blåsik while the smaller has 42 rakers and is a planktonsik (Table 9, Fig. 13). It is not known which species is the more abundant.

Lake Ormsjön (area 2,500 hectares, altitude 264 m) has the same two species, but introgression has advanced. The planktonsik, again the smaller, has some 37 rakers while the blåsik has 33 (Table 9). There is also a sparsely-rakered population in the lake, presumably of the sandsik species.

The sandsik is fairly abundant in Lake Flåsjön (area 11,160 hectares, altitude 266 m) where gill-raker counts give 24—25 as the average. The blåsik population of the lake is abundant and has only 30 rakers. Introgression between the sandsik and blåsik seems to have taken place. No remnants of the planktonsik is available among the *c.* 450 specimens investigated.

In the small and shallow Lake Hotingsjön (Fig. 13) from which only a few specimens have been investigated, the blåsik dominates. One specimen may indicate the existence of a sandsik population also. The situation of Hotingsjön is typical of the smaller lakes of the region, of which Lomsjön, Nappsjön and Rissjön were among those dealt with by OLOFSSON (1933, 1934). He described the series of famous transplantations of the stunted Lomsjön whitefish (32—33 rakers) in the late 1920s, the first to be properly described in the literature. Lakes Nappsjön, Rissjön and others were devoid of whitefish and the Lomsjön spawners produced daughter populations, the first generation of which were much larger fish than their parents. Later they gradually became stunted like the parent population. OLOFSSON pointed out that although the growth rate was found to be highly modifiable, the gill-raker numbers and the spawning periods did not change. Later experiments have, of course, strongly confirmed these first conclusions by OLOFSSON.

Fig. 11. At the mouth of the Limån stream, in the southern part of Siljan, the blåsik (locally "ryssing") intergrades into the large-sized land-locked älvsik (cf. Table 8).

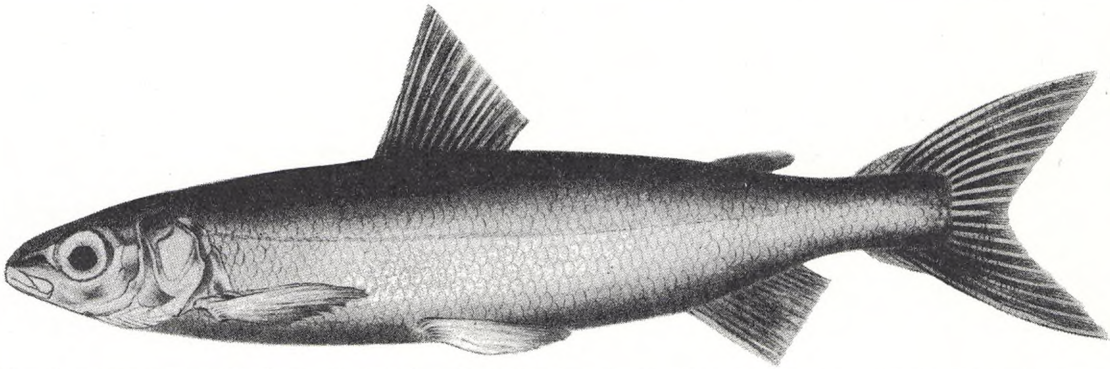


Fig. 12. *Coregonus megalops*, the blåsik of Lake Storsjön, Indalsälven river, as described by WIDEGREN (1862).

In the first general review (SVÄRDSON 1957) the älvsik and the blåsik were united to constitute a single species, mainly because of their similar gill raker numbers and the poor knowledge then existing of cases where the two species lived sympatrically. It has now been proved that such cases exist. The extreme variation then thought to cover the presumed species has obviously disappeared and both have their own, rather distinct, specific characters.

Six Coregonus species of the Göta river drainage

Vänern is the third largest lake in Europe. The lake area is 5,500 km² and the total drainage area is 47,300 km². The Göta river drains into the Kattegatt. The river originally had some magnificent waterfalls at Trollhättan but it is now navigable through sluices. The lake is dammed for hydroelectric purposes.

The surface of Vänern has an altitude of 43—45 m, its maximum depth is 102 m and considerable parts of the lake are 50—80 m deep. The lake is oligotrophic but has been somewhat affected by waste from paper-mill industries, communities and agriculture.

The fish fauna comprises 35 species, six of which are coregonines. The fish fauna was early described by LLOYD (1854) and WIDEGREN (1863). The coregonines have been treated by GÜNTHER (1866), FREIDENFELT (1928, 1933, 1936), SVÄRDSON (1957), SVÄRDSON and FREIDENFELT (1974). The fish fauna and the fisheries were surveyed by ALMER and LARSSON (1974) and ALMER (1978, 1979), the pelagic food web of the fish community by NILSSON (1974, 1979).

The average annual commercial catch in the period 1973—77 was 550 tons. Of this some 150 tons were ciscoes. Whitefish, despite their five

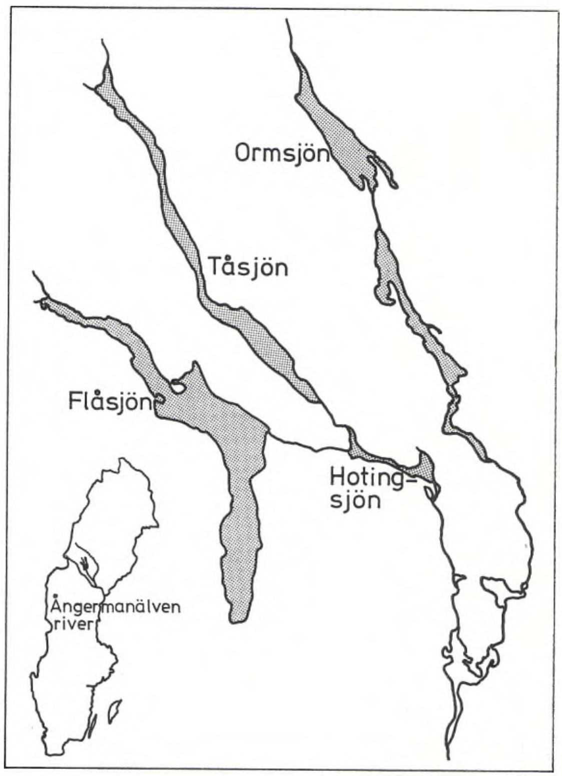
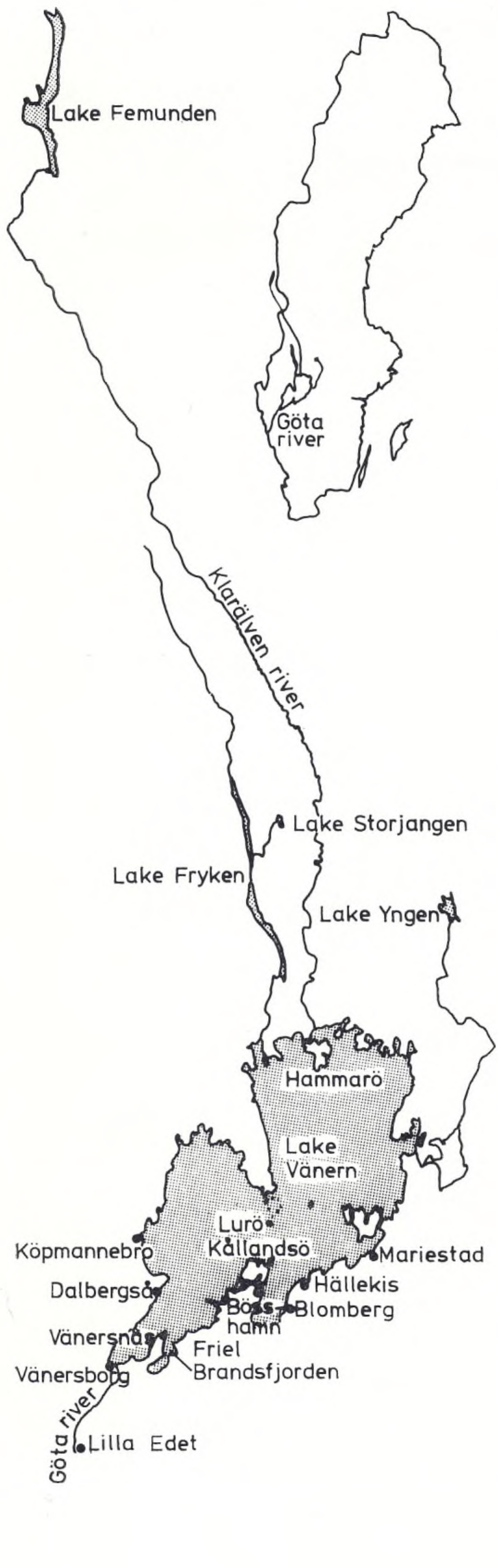


Fig. 13. The lakes of the Ångermanälven river, where the blåsik and the planktonsik are the most numerous whitefish species (*cf.* Table 9).



species, now amount to only 50 tons. The cisco has increased lately, whereas whitefish has decreased. Cisco eggs are sold as caviar and command a high price.

The cisco is quite dominant economically but from a systematic point of view the species is of less interest. It lives in a huge but normal population with an individual total length of 15—20 cm, age 4—5 years; the gill-raker number is 38—50 with an average of about 44.

There are no indications of growth-rate differences in various parts of the lake, or of the existence of a second, spring-spawning population of cisco in Lake Vänern.

The history of the identification of the five sympatric whitefish species is long and confused. The details of this history are dealt with elsewhere.

The five species are presented below in order of abundance in the lake.

Blue whitefish

The blåsik is locally called "gråsik" (grey whitefish), "helgamäss-sik" or "mårtenssik" according to the date of its main spawning. It is seldom heavier than 0.5 kg and is not very highly esteemed as food. Nilsson (1974, 1979) found it to be a pelagic plankton-feeder, in high summer heavily utilizing the large cladoceran *Bythotrephes cederstroemi*. In November 1975 it was found to be a predator on 0+ smelt. The blåsik spawns over gravel or sand at a depth of 2—5 m in late November or December, around the whole lake. The species is most abundant in the northern part of the lake. A cooperative investigation of Vänern by several agencies was performed in the period 1972—77 and many whitefish were then more closely studied. Table 10 presents the gill-raker numbers of some 850 blåsik of the Vänern stock, from localities all over the lake and experimental trawling in mid-lake. It can be seen that the average number of rakers is 31—33. There can be no doubt that introgression occurs and some of the trawl catches include specimens of other species, which, however, could not be sorted out by any objective criterion. The fishermen are unanimous that what they call "half-beaks"

Fig. 14. Lake Vänern and some of the feeding rivers, with associated lakes (*cf.* Tables 10—12).

Table 10. *Gill rakers of blåsik and älvsik from Lake Vänern.*

Rakers / Sample	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	n	x̄
Blåsik																										
Freidenfelt 1919—31 various localities	—	—	—	—	—	—	—	—	1	3	5	6	13	14	5	3	11	—	—	1	—	—	—	—	62	32.9
Eken, 1951	—	—	—	—	—	—	1	1	2	6	6	4	7	6	4	3	3	1	—	—	—	—	—	—	44	31.7
Hammarö, 1954	—	—	—	—	—	1	—	1	3	4	8	8	14	14	19	12	13	6	5	4	1	—	—	—	113	33.6
Hällekis, 1971	—	—	—	—	—	—	1	1	1	5	4	9	6	3	3	2	2	—	—	—	—	—	—	—	37	31.4
Trawl, 1972	—	—	—	—	1	3	2	5	9	11	14	26	36	36	48	31	24	19	13	5	2	—	1	1	287	33.3
Mariestad, 1973	—	—	—	—	—	—	—	2	9	10	2	3	9	5	5	2	3	2	1	—	—	—	—	—	53	31.4
Trawl, 1973	—	—	—	—	—	—	1	—	3	4	9	3	6	10	6	5	4	2	2	—	—	1	—	—	56	32.6
Kållandsö, 1973	—	—	—	—	—	—	—	—	1	4	1	8	6	6	4	—	—	—	2	1	—	—	—	—	33	32.2
Friel, 1974	—	—	—	—	—	—	—	—	—	—	1	3	4	4	4	9	2	—	—	—	—	—	—	—	27	33.6
Lurö, 1975	—	—	—	—	—	—	2	1	2	8	8	4	5	4	4	4	5	—	—	1	—	—	—	—	48	31.6
Trawl, 1975	—	—	—	—	—	—	—	—	—	2	1	7	9	8	4	3	1	3	1	—	—	—	—	—	39	32.9
Köpmannebro, 1975	—	—	—	—	—	—	—	—	2	1	2	2	2	5	7	3	1	3	2	1	2	1	2	—	36	34.6
Brandsfjorden, 1976	—	—	—	—	—	—	—	—	—	—	3	1	5	5	3	3	—	1	—	—	—	—	—	—	21	32.8
C. humilis Günther 1866 Brit. Mus. (Nat.Hist.) London	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	1	—	—	—	—	—	—	3	33.7
Älvsik																										
Vänern, 1850—70 Swed. Nat. Mus. Smitt, 1886	—	1	1	—	1	1	2	2	1	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	11	26.3
Freidenfelt 1918—34 various localities	1	1	2	9	10	20	19	10	5	7	2	1	—	—	—	—	—	—	—	—	—	—	—	—	87	25.6
Kållandsö, 1950—51	—	1	1	3	12	6	7	8	2	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	43	25.4
Friel, 1972—73	—	—	1	4	8	14	6	12	10	4	1	3	1	—	—	—	—	—	—	—	—	—	—	—	64	26.4
Dalbergsån, 1972	—	—	—	—	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	26.0
Köpmannebro, 1975	—	—	—	—	2	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	25.0

Table 11. *Gill rakers of storsik, planktonsik and sandsik from Lake Vänern and the Göta river. Some of the*

Rakers Sample	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Storsik																
Freidenfelt 1918—28 various localities	—	—	—	—	—	1	2	3	5	16	14	7	7	5	—	—
Kållandsö, 1951	—	—	—	—	—	—	—	2	1	1	5	3	4	2	1	3
Friel, 1972	—	—	—	—	—	—	1	—	—	1	1	—	1	—	—	—
Vänersnäs, 1973—75	—	—	—	—	—	—	—	—	2	2	1	5	5	1	1	1
Mariestad, 1973	—	—	—	—	—	3	7	11	12	24	27	20	15	10	5	1
Planktonsik																
Köpmannebro, 1923—24	—	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—
Kållandsö, 1951	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Köpmannebro, Röda ön, 1974	—	—	—	—	—	—	—	—	—	—	1	—	—	1	3	4
Köpmannebro, Gutvik, 1974	—	—	—	—	—	—	—	—	—	—	1	—	3	1	2	4
„ „ 1975	—	—	—	—	—	—	—	—	—	—	2	1	3	—	1	—
Sandsik																
Blomberg; Bösshamn, Freidenfelt 1920—24	—	—	1	2	12	8	20	19	14	16	9	6	2	—	4	1
Bösshamn, 1975	—	2	1	1	2	1	4	5	5	4	—	1	—	—	—	—
Vänersborg Bay, 1976	1	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—
Halleberg, 1978	1	1	4	8	8	6	4	4	1	2	4	2	—	2	—	—
Lilla Edet, Göta river, 1952	1	1	2	—	4	6	2	2	—	—	—	—	—	—	—	—
Archipelago, off Göta river, 1850—1920	—	1	1	4	6	4	2	1	—	—	—	—	—	—	—	—

(hybrids between the blåsik and the long-snouted form) have become more common in later decades. It seems reasonable to suppose that such hybrids were produced unintentionally by the fish culturists working on the lake from the 1920s to the 1940s.

Through the courtesy of the British Museum (Natural History), London, three paratypes of *Coregonus humilis*, GÜNTHER 1866 could be studied. Their gill rakers, as well as other characters, fit into the blåsik span of variation (*cf.* Table 10).

River whitefish

The älvsik (locally called "näbbsik") is represented by the long-snouted form. The length of the snout, however, can vary considerably and may be related to the fatness of the fish, as suggested by WIDEGREN (1863) and LILLJEBORG (1891). The last-mentioned author states that this form is the fattest of all Swedish stocks and is deserving of its second name "fetsik". It is generally regarded as the most valuable whitefish.

The älvsik is a bottom-feeder, mainly on relict crustaceans, molluscs or big insect larvae. In summertime it lives very deep, is fished at a depth of *c.* 50 m and becomes bloated when lifted to the surface. Its average size is 0.5—1.5 kg, maximum about 5 kg.

The älvsik spawns in November, at exposed coast areas, over firm bottoms at a depth of 8—20 m. Spawning grounds are known on all coasts. One stock also spawns in running water. This stock in the lower Gullspångsälven was widely known in the 1860s. It had a shorter snout than the others. It has now disappeared as a local deme.

Table 10 gives the raker counts. The Vänern älvsik has few rakers, with an average of 25—26.

WIDEGREN identified the älvsik stock as *C. oxyrhynchus*. So have most later authors. GÜNTHER, however, called it *C. lloydii.* FREIDENFELT (1933) found the Gullspångsälven stock sufficiently different to describe it as *C. amnipetens*. This stock was the one introduced in Lake Sällsjön in 1870 (p. 16).

Large sparsely-rakered whitefish

The storsik of Lake Vänern is identified by the fishermen from its large eyes. The local names *samples are clearly mixed or introgressed.*

36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	n	x̄
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	29.8
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	31.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	29.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	31.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	135	29.8
—	—	—	—	1	—	1	3	2	—	—	1	2	—	—	—	—	—	—	—	14	40.6
—	—	2	—	1	—	—	1	1	—	—	1	1	—	—	—	—	—	—	—	7	42.6
1	1	4	4	1	—	1	1	—	1	—	—	—	—	—	—	—	—	—	—	23	37.2
1	—	1	1	4	5	3	6	1	1	4	1	—	—	—	—	—	—	—	—	39	39.7
1	3	—	2	3	5	—	3	5	1	2	1	1	—	1	—	—	—	—	1	36	40.5
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	115	27.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	26.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	22.8
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	25.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	24.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	24.1

"blegsik", "glomsik" or "glyssik" refer to this character and the commercial fishermen think that the fish uses its big eyes to avoid their nets. In old times, this species was mostly caught on long lines, baited with cisco or smelt. FREIDENFELT (1933) once saw a specimen 40 cm long with seven ciscoes of average size in its stomach. The storsik also feeds on *Mysis*, *Pontoporeia*, molluscs and trichopteran larvae. The oldest specimen so far aged was 16 years old. The average size is about 1 kg, maximum *c.* 5 kg.

The storsik is an early spawner, it starts spawning already in October. A further name, "lövsik", refers to the spawning period, when leaves are falling. The spawning depth is 1—3 m, the bottom is stony. According to the fishermen, places where there is bog iron ore are selected. There might also be a sparse vegetation of *Isoetes*, *Scirpus* or *Potamogeton*. The spawning grounds are located in the southern part of the lake, mainly around Kållandsö and the Mariestad area.

Table 11 gives the gill-raker counts. The storsik of Vänern has more rakers, 29—31, than have conspecific stocks of most other Swedish lakes. This seems to be due to introgression mainly from the abundant blåsik, which spawns later, but partly over the same shallow waters.

WIDEGREN identified the Vänern population as *C. fera* (JURINE), while FREIDENFELT found it conspecific to *C. maraena*, (BLOCH). GÜNTHER thought it merited a special name, *viz. C. maxillaris.*

Lesser sparsely-rakered whitefish

It has taken a long time to identify this stock as a separate entity in Vänern. The species is mainly concentrated in the southern part of the northern basin and the southernmost part of the southern basin. The sandsik has acquired its national name from the Vänern stock. The fishermen recognize it by its small size, brownish colour and short nose. FREIDENFELT, in his posthumous manuscripts, which were recently edited and published with new material added (SVÄRDSON and FREIDENFELT 1974), was puzzled by the combination of few gill rakers, early maturity and small average size, since he thought the *oxyrhynchus*-form was the only one that had few rakers. The sandsik has 23—26 rakers (Table 11) in recent samples. Its food habits are not known but it is most probably a benthos-feeder. Spawning in November has been proved. The sandsik not only dominates the southernmost end of Lake Vänern but also lives in the Göta river and is sparsely caught in the archipelago off Gothenburg. In 1863 A. W. MALM, then the director of the Biological Museum, Gothenburg, took some whitefish from the Göta river to Mr GÜNTHER at the British Museum (Natural History). MALM considered these fish to be a nice series that neatly illustrated the variation of the *C. lavaretus*, which MALM thought was only one species, comprising all described forms except the cisco. However, GÜNTHER identified one of the specimens as a new species, *C. gracilis*. When MALM asked why he did so, GÜNTHER replied as follows in a letter: "*Coregonus gracilis* unterscheidet sich von *C. lavaretus* und *C. widegreni* durch seine auffallner schlanke Gestalt, welcher weder vom Alter noch Geschlecht abhängig ist, da dieser Character durch eine kleine Vermehrung der Schuppenzahl und namentlich durch den schlanken Schwanz, dessen Höhe weit geringer ist als die Länge der Mandibeln, sich ausdrückt. Ueberdem reicht in *C. widegreni* der Oberkiefer bis an's Auge selbst" (MALM 1877, p. 674).

It is true that *gracilis* is close to *widegreni*, as described by MALMGREN (1863) from Ladoga, the Gulf of Finland and Lake Vättern. Introgression by the *oxyrhynchus* in Vänern may have modified the *gracilis* in the direction mentioned by GÜNTHER.

Oxyrhynchus-genes seem to dominate in the sparse, fast-growing and fairly long-snouted population roaming the Viskan river mouth, some 50 km south of Gothenburg. A sample of 26 specimens from 1979 had 22—30, average 26.0 gill rakers.

Southern densely-rakered whitefish

This last species of Vänern is very rare and is found mainly in the vicinity of Köpmannebro on the western shore of the lake (Fig. 14). In Table 11 the gill-raker numbers are presented. Recent samples of spawners secured by Mr BRODDE ALMER from Gutvik display an average of 40 rakers. Blåsik, however, is clearly admixed in the samples and the true densely-rakered whitefish of Lake Vänern may have 40—50 rakers. Already FREIDENFELT was aware of a densely-rakered form, spawning at Köpmannebro, but he published only a popular note on it. Spawning takes place in late November and the spawning grounds are exposed to waves and are hard to fish. The feeding habits are not known at present.

The pattern of blåsik ousting the planktonsik in Lake Vänern conforms to the situation of many other lakes, as described in the presentation of the blåsik species.

The Vänern planktonsik was the only one of the five sympatric species that was not given a separate scientific name by GÜNTHER.

Lakes draining into Vänern

Lake Yngen (Fig. 14) had been studied by Mr JACOB SJÖSTEDT for more than 60 years, when, in 1854, he wrote about the lake in a letter to FRANZ von SCHÉELE (not published until 1977). The whitefish was the latest fish spawner of the lake, at November 20—25, and the fishery was very rewarding, though dangerous to the health, SJÖSTEDT says. Later on, the density and the average size of this whitefish are known to have been negatively correlated in their fluctuations (STENBERG, pers. comm.). The Yngen stock is a sandsik and it is the only species of its genus in the lake (Table 12). The gill-raker numbers have not changed during a century of investigation.

Lake Storjangen has a whitefish which is most probably an introgressed planktonsik (Table 12).

Lake Fryken, which is very deep (120 m), has a relict population of the four-horned sculpin from the time when the lake was connected to the Ancylus Lake. In the lake there also lives a population of introgressed planktonsik with numerous gill rakers, average 43—44.

The main feeder of Lake Vänern is the River Klarälven, which drains a large northern area, including some parts of south-eastern Norway. One of the headwaters is the large Norwegian Lake Femunden (area 200 km², altitude 673 m, depth 130 m). The lake was investigated in 1954 by the Drottningholm Institute. Its abundant whitefish was found to comprise several stocks. As the catch was taken in summertime, no biological separation of spawning shoals had taken place.

Table 12. *Samples of sandsik, blåsik and planktonsik in lakes, flowing to Lake Vänern*

Rakers / Sample	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	n	x̄
Lake Yngen, 1863[1]	—	—	—	2	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	23.3
„ „ 1956	2	1	9	16	26	17	17	18	12	9	1	1	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	135	24.6
„ „ 1977	—	1	1	2	3	5	5	5	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	24.4
Lake Femunden, <400 mm	—	—	—	—	—	3	3	13	20	23	14	21	15	3	9	5	11	17	6	10	—	—	3	2	3	2	4	2	—	1	1	—	—	191	32.1
„ „ >400 mm	—	—	—	—	—	1	1	—	—	3	10	3	7	8	30	29	42	39	42	21	6	8	2	7	19	19	16	16	14	7	3	—	1	354	37.9
Lake Storjangen	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	4	7	6	3	5	2	1	—	—	—	—	—	—	—	—	—	30	37.9
Lake Fryken, 1922	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3	3	1	2	—	—	1	—	—	12	44.2
„ „ 1956	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	2	2	1	8	5	2	3	4	2	1	—	1	—	33	43.0

[1] Smitt (1886).

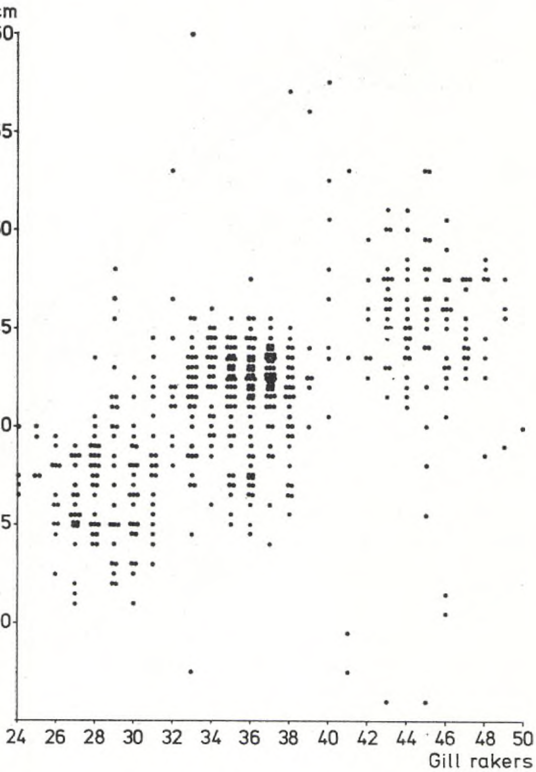


Fig. 15. Gill-raker numbers and size of Lake Femunden whitefish suggest three sympatric species (*cf.* Table 12).

It is, however, fairly clear from the scatter diagram (Fig. 15) that the lake is inhabited by a small-sized sandsik of 26—29 rakers and by a large-sized planktonsik with 43—47 rakers as well as by a third intermediate group of specimens (33—37 rakers) which no doubt is blåsik. Älvsik and storsik are probably not present in the lake; this fits into the general picture, where älvsik has seldom colonized upstream lakes and the storsik is often swamped by the sandsik.

The reason why the densely-rakered population of the Vänern basin is assigned to the southern planktonsik species and not to the northern aspsik is the proximity to the Jutland and the Bolmen, Hjälmaren or Åländern densely-rakered stocks (see below) and the wide distribution gap up to the aspsik populations of the Lakes Storlögdan, Storvindeln and Storlaisan (*cf.* Fig. 5). The final evidence that there are two independent densely-rakered species is presented in the next chapter.

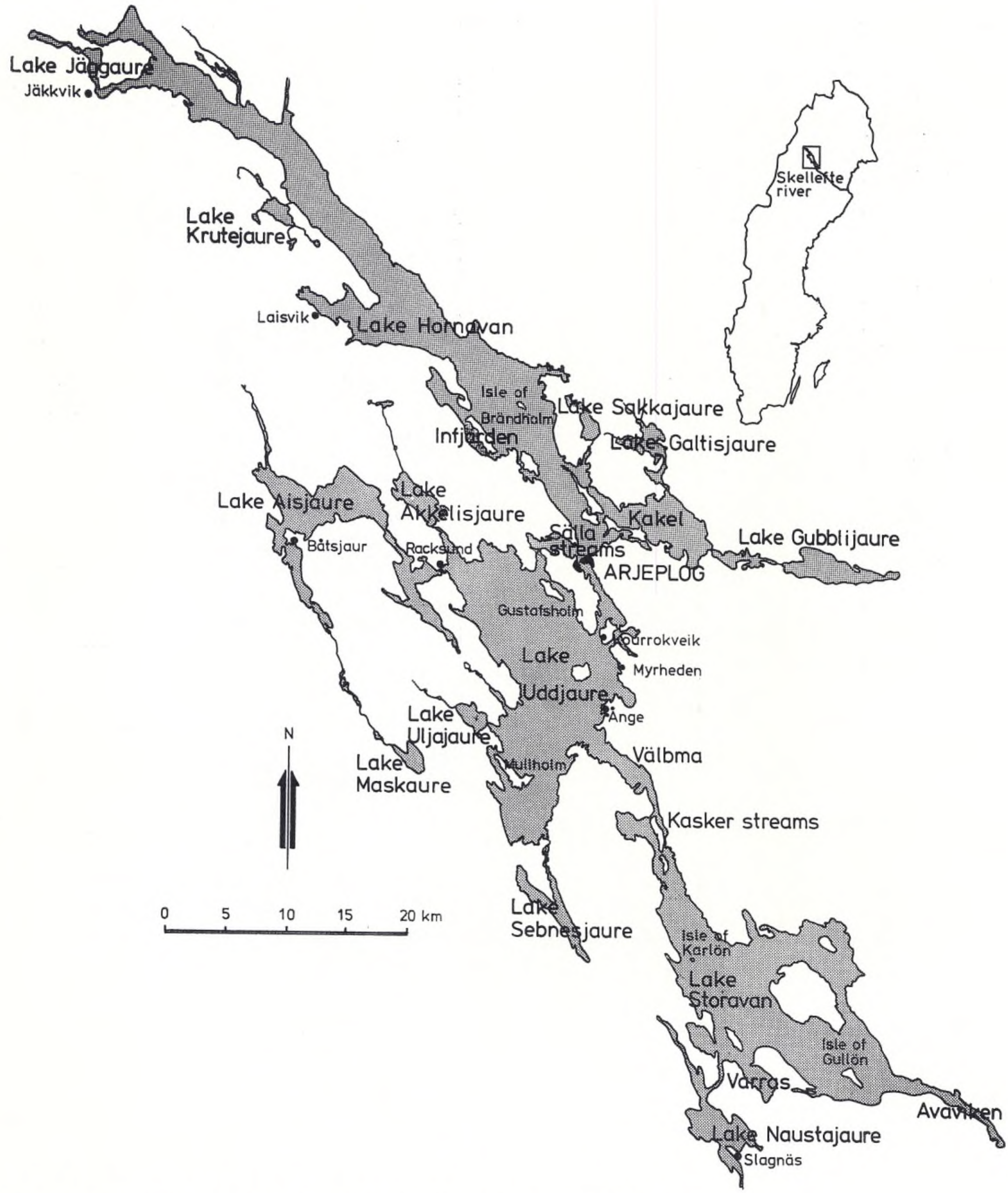


Fig. 16. The classical Arjeplog lakes of the Skellefte river system (*cf.* Tables 13—15).

The classical Arjeplog lakes

The large Arjeplog lakes of the upper Skellefte river are classic in coregonid research, because of the abundant whitefish and the fishermen's interest in them. At a very early stage the lakes were visited in autumn by people living at the Bothnian coast. Later, when colonization occurred, whitefish became of paramount importance for human survival in this area of severe climate.

The main lakes, with some of the smaller

Table 13. *Gill rakers of blåsik and planktonsik samples from the Arjeplog lakes (cf. Fig. 16).*

Rakers / Sample	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	n	x̄
Blåsik																						
Sakkajaure	—	—	—	—	—	—	2	1	1	1	3	4	2	1	1	—	—	—	—	—	16	35.1
Akkelisjaure	—	—	—	—	1	3	9	5	11	14	12	6	3	7	2	—	—	—	—	—	73	34.1
Hornavan																						
Infjärden	—	2	1	1	2	1	6	11	16	24	32	28	22	16	6	1	2	—	—	—	171	35.0
Kakel	—	—	1	—	1	11	16	27	39	36	26	20	12	6	3	1	—	—	—	—	199	33.7
Uddjaur																						
Racksund	—	—	—	—	—	—	—	5	7	8	14	17	15	13	4	—	—	—	—	—	83	35.8
Ånge	—	—	—	—	—	—	—	—	1	2	2	2	1	—	—	—	—	—	—	—	8	35.0
Kasker	—	—	—	—	—	3	6	10	10	26	13	11	4	4	1	2	—	—	—	—	90	34.2
Myrheden	—	—	—	—	1	—	3	6	8	7	14	6	5	4	2	—	—	—	—	—	56	34.6
Mullholm	—	—	—	—	—	—	3	5	7	9	3	5	3	2	—	—	—	—	—	—	37	34.1
Storavan																						
Karlön	—	—	1	1	2	3	9	7	12	17	10	8	2	1	—	—	—	—	—	—	63	33.2
Gullön	1	3	3	5	10	21	39	66	75	64	56	34	20	8	5	—	—	—	—	—	410	33.3
Avaviken	—	—	—	1	—	3	2	5	4	7	3	5	1	—	—	—	—	—	—	—	31	33.3
Planktonsik																						
Hornavan																						
Brändholm	—	—	—	—	—	—	—	—	3	7	10	25	23	42	39	32	8	1	—	—	190	37.9
Jutis	—	—	—	—	—	1	1	3	6	1	1	4	4	1	3	5	1	1	—	—	32	36.1

surrounding ones, are shown in Fig 16. Some data for the three big ones are given below:

Lake	Area	Altitude	Length	Depth
Hornavan	251 km²	425 m	67 km	240 m
Uddjaur	238 „	419 „	29 „	25 „
Storavan	172 „	418 „	30 „	25 „

Lake Hornavan is almost ten times as deep in its central parts as the two other lakes. Streams, bays and islands add to the great variety of habitats in the area. No ciscoes occur in the lakes but five whitefish species exist there. A rumour of a sixth form of whitefish persisted for more than a century but was never confirmed. Nowadays a sixth species (älvsik) has been released as millions of fry, blurring the evidence not only for the five indigenous species but also for the possible spontaneous sixth species.

Widegren (1866) and Olofsson (1915) were the leading Swedish whitefish specialists of their time and both studied the Arjeplog lakes. Olofsson, moreover, wrote his voluminous fieldnotes from numerous visits to the settlements of the area and in 1944 advised the present writer to concentrate on the many sympatric species of the lakes. Svärdson (1949, 1953, 1963) described four of the five species, Lindström and Nilsson (1962) and Lindström (1970) discussed whitefish food habits and competition. Vestermark (1908) presented the fisheries of the area.

Blue whitefish

The blåsik is by far the most abundant species in all lakes. It very seldom attains 20 cm in total length. Spawning fish are usually a mere 12—18 cm long. Its local name is "sellack" (small herring) with some prefix such as "små" (for very small ones) or "skarp" (skarp = with spawning tubercles). Lindström and Nilsson (1962) found that the blåsik turned over from a 100 % *Bosmina* diet in fish sizes below 14 cm to a more mixed diet and predominantly benthic food in fish specimens 16—17 cm long. There is no doubt seasonal and local variation of this July 1954 pattern, but the switch in diet with age and size characterizes the blåsik and is part of its competitive power. A seine catch in Aisjaur in July 1938 gave 175

Table 14. *Gill rakers of sandsik, storsik, and aspsik samples from the Arjeplog lakes (cf. Fig. 16).*

Rakers / Sample	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Sandsik																		
Jutis 1949—54	—	3	8	19	33	31	26	20	8	1	1	—	—	—	—	—	—	—
„ 1973—75	—	1	6	13	18	9	13	15	8	2	2	1	3	1	—	—	—	—
Gubbijaur	—	—	—	—	—	3	4	9	10	8	8	12	8	5	1	—	—	—
Storavan	—	—	—	1	2	2	1	1	2	1	1	—	—	—	—	—	—	—
Storsik																		
Hornavan																		
Arjeplog	—	1	—	9	13	8	8	9	3	1	1	1	1	—	—	—	—	—
Uddjaur																		
Gustafsholm	—	2	1	12	9	12	2	1	—	—	—	—	—	—	—	—	—	—
Myrheden	—	2	4	9	16	11	5	6	—	—	—	—	—	—	—	—	—	—
Kurrekvejk	—	2	—	3	3	3	1	1	1	1	—	—	—	—	—	—	—	—
Storavan																		
Gullön	1	5	8	12	28	30	12	9	6	6	10	3	1	4	4	—	—	—
Aspsik																		
Sälla streams	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kasker streams	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Aisjaur	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

blåsik and 22 whitefish of other species, as reported by Olofsson, who considered this ratio to be typical for the relative abundance of the forms.

The blåsik spawns in December or even in January along the shores, on firm bottom, not deeper than 5—10 m. The concentration of spawners was exploited by the local settlers, who salted the catch for the winter. The knowledge of spawning grounds for different local stocks has always been very good.

Morphologically, the blåsik is characterized by a terminal mouth and *c*. 33—36 gill rakers (Table 13). Relatively big eyes and head are negatively allometric and thus are found in small fish generally.

Southern densely-rakered whitefish

The planktonsik is sparse, as could easily be foreseen, since the blåsik is so abundant. It lives only in the deepest parts of Lake Hornavan, where the species is slightly larger than the blåsik. It is recognized by the fishermen as a separate stock, which they call "grå-sellack" (grey small herring). Like most deep-living forms it has large eyes. Another consequence of the habitat is the late spawning period, February to mid-March.

The planktonsik has more gill rakers than the blåsik, about 38. There is a cline of introgression blåsik-planktonsik from the shore to the deep area off Laisvik. The shore-spawning blåsik are extremely small, probably from food competition, and have relatively numerous gill rakers for the species. They grade all the way down to deep-spawning planktonsik, at 60—70 fathoms, with typical "gråsellack" characters.

The "gråsellack" had some economic importance in the 1930s and 1940s but nowadays it is not fished when spawning. Olofsson tells of a fisherman taking 1,400 "gråsellack" from his nets at —30°C, when the ice was very thick and covered by snow. Such awesome feats are no longer attempted.

Lesser sparsely-rakered whitefish

The sandsik is not abundant, as again could be foreseen because of the dense blåsik stocks. It is a benthos-feeder, and Olofsson found *Asellus*, *Gammarus*, *Pisidium*, chironomid larvae, and

33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	n	x̄
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	150	19.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	92	20.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	68	24.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	21.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	55	20.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	39	19.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	19.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	19.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	139	20.8
—	—	—	—	—	—	1	1	2	6	3	10	4	5	9	6	—	2	4	—	53	45.4
—	—	—	—	—	—	—	1	1	5	9	21	18	13	20	12	12	7	—	1	120	46.0
—	—	—	—	—	—	2	—	—	—	1	4	1	2	—	—	1	—	—	—	11	43.9

— more seldom — cladocerans in the stomachs. Obviously its diet overlaps that of the blåsik.

The sandsik is rather small, about 15—25 cm. Its distribution is concentrated in the western parts of the lake system. Its stronghold is in Lake Jutis (with probably no blåsik) where it is abundant. Svärdson (1953) thought the small-sized sandsik of Jutis to be a dwarfed storsik. This was before the discovery of the sandsik as an independent twin species with few rakers.

According to Olofsson's field-notes the sandsik is found in Lakes Jutis, Laisaure, Siebnesjaur, Uljajaur, Aisjaur (part of Uddjaur), Naustajaure (part of Storavan) and Varras (bay of Storavan). Sympatric occurrence with the blåsik exists in Aisjaure, Naustajaure and Varras.

The sandsik has about 20 gill rakers. The local people, because of its few rakers, call it "sik-sellack", indicating that it has the same number of gill rakers as the storsik. Other names are "Varras-sellack" (from the locality), "glansfisk", "tjerifisk" or "getjokk" (the Lappish name for a reindeer calf in its second year). The spawning is poorly known, except for stream-spawning in October in some places.

Large sparsely-rakered whitefish

Probably because of the sparseness of the sandsik, the storsik has managed to survive in a comparatively dense stock. The species is important for the fishery, especially at the well-known spawning ground at the isle of Gullön in Lake Storavan. Spawning takes place in December at a depth of 2—8 m.

The food is benthic; *Asellus*, *Gammarus*, trichopteran and chironomid larvae, *Pisidium* and other molluscs. Olofsson documented this diet in his fieldnotes and Lindström and Nilsson (1962) verified and stressed the rigid diet pattern of the species.

The storsik matures late, grows for many years and may attain a great size. The record weights are 5.2 kg from the large lakes, 3 kg from Galtisjaure and 2.5 kg in Jutis. It may be 0.3 kg before it spawns for the first time.

The gill rakers are few, 19—21 in different samples (Table 14).

Northern densely-rakered whitefish

The aspsik of the Arjeplog lakes is a large, well-known fish. Smitt (1882, 1886), though he did not say so, very probably got his material of *C. aspius* from the lakes. The locality was referred to as the "Pite lappmark", which implies a large area, including the upper Skellefte and Pite rivers. The type locality for SMITT's *aspius* should be restricted to Lake Hornavan, since SMITT referred to LAESTADIUS (*cf.* p. 18).

The numerous gill rakers, 44—46 as an average of different samples (Table 14), have been noted by all whitefish experts and local people ever since LAESTADIUS's time. Even the colour of the gills (bluish red) is said to be diagnostic in fresh fish. The present writer once saw an old fisherman rapidly sort a pile of whitefish into two different lots, one being storsik, the other aspsik. Later careful investigation showed that all of the fish had been correctly identified, although they were the same size and rather similar in appearance.

The diet of the aspsik was dealt with by LINDSTRÖM and NILSSON (1962), who stressed the surface-feeding habits in high summer. Some aspsik have been observed to be predators on the small nine-spined stickleback. The food value is rated as low and the aspsik is said to be deteriorating very rapidly.

Small immature aspsik are known to cause swirls of the water surface in the summer evenings when they feed on terrestrial insects. They have been given a special name; "påll-sellack", where "påll" means the water swirl.

Spawning is also diagnostic, since it is restricted to rapids of the main river, at the Sälla and Kasker streams (Fig. 16). The spawning period is in November. OLOFSSON told of the old-fashioned fishery at Kasker. It took place during 20 days, and 60—70 gill nets were used. The average annual yield on this spawning ground was 15,000 specimens, each weighing some 600—700 g. The largest aspsik ever observed was 1.6 kg.

It is significant that blåsik, planktonsik and aspsik are sympatric in Lake Hornavan. This fact proves that the three planktophagous whitefish are independent species. As far as is known at present this situation has no counterpart in Europe.

"Albask"

The sixth sort of whitefish in the Arjeplog lakes has been talked about ever since LAESTADIUS's time. WIDEGREN (1866) and OLOFSSON (1915) tried to identify it, as did OLOFSSON later and also the present writer. A few specimens have been presented. They were large fish with some 30 gill rakers and could not be securely identified either as hybrids storsik x aspsik or as the missing species älvsik.

The existence of the spontaneous population of älvsik is by no means impossible, since that species has colonized other large lakes, though only the Torne river to such an altitude. The "albask" is said to be large (record size 3 kg), less grey in colour than the aspsik and with a redder gill colour like the storsik. It should have black spots on the gill cover. Spawning is reported to be in streams earlier than the aspsik. This seems to fit the älvsik very well, but unfortunately no spawning sample has ever been found by a scientist. In the 1940s fry of the true älvsik from Råne river mouth at the Baltic coast was released in the lakes and the possibility of exploring the "albask" has thus gone.

Experimental hybrids

Stray specimens of storsik were found among spawning aspsik in the Sälla stream when this study began in 1944. The possibility of natural hybrids was thus proved. The "albask" obviously might have been such hybrids. If so, the observation of alleged pure schools of "albask", as well as their spawning before that of aspsik, is probably incorrect.

A first experiment on Arjeplog whitefish was concerned with the influence of new environment. It was found (SVÄRDSON 1950) that the morphology of aspsik and storsik was modified by growth-rate changes in small lakes, while the gill rakers were not altered.

A second experiment started in 1953, with the aim of elucidating the real background of the "albask" story. Aspsik males from the Kasker streams were kept alive until storsik females at Gullön were ripe. The hybrid fry was hatched at Kälarne research station and the fingerlings were released into Norra Stensjön, a lake which had no whitefish population of its own.

By aging the fish from the scales, rich samples of F_1 and F_2 fish could later be studied (SVÄRDSON 1965). Later on, the annual samples from the lake could not be identified as F_3 generation or

Table 15. *The Arjeplog hybrid whitefish. The milt from 26 aspsik males (40—50 gill rakers, average 45.7) was used in December 1953 to fertilize the eggs from 17 storsik females (16—21 rakers, average 18.8). The fingerlings were released in Lake Norra Stensjön in September 1954 and F_1 and F_2 specimens were identified later on the age of their scales. From 1965 onwards the F-generations or backcrossings could no longer be separated. Note the increased gill-raker variation from the F_2-generation. The trend towards slightly higher raker numbers in later years might be due to "the human factor" when counting (cf. Methods).*

Rakers / Sample	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	n	$\bar{x}$	St.dev.
F_1	—	—	—	1	1	1	1	3	18	53	86	89	80	62	34	17	9	1	—	—	—	—	—	456	29.3	1.99
F_2	—	—	—	2	3	5	17	29	32	49	50	45	56	55	34	25	12	9	3	2	1	1	—	430	29.1	3.03
F_n (1965—68)	1	—	2	2	4	9	18	24	29	55	54	48	54	71	49	28	24	12	7	1	—	—	—	492	29.3	3.17
F_n (1969—72)	—	1	1	4	4	5	9	22	20	32	43	49	52	62	32	23	30	12	5	3	1	—	—	410	29.6	3.22
F_n (1973—77)	—	—	—	1	1	7	13	21	23	42	46	55	64	60	49	51	39	21	9	—	—	—	—	502	30.0	3.05

backcrossings but had to be referred to as F_n fish. A summary is given in Table 15.

It is clear that the F_1 generation was intermediate between the parent species, as far as gill rakers were concerned. Likewise, the variation within the F_2 became much greater, because of general genetic principles. Up to now, the variation has not decreased, suggesting a low pressure of natural selection for rakers. The slight tendency towards more rakers in later years is not significant, when allowance is made for the "human factor" of progressively closer scrutinity in the counting technique. This factor was dealt with in the introductory section on Methods.

The enigma of the "albask" will never be solved. What the observant fishermen saw might well have been hybrids. But indirectly, the "albask" created the Lake Norra Stensjön population of hybrids, which should be most valuable as a test stock for future, more powerful protein analyses. If these hybrids could be shown to be storsik/aspsik intermediates, then the method concerned will certainly be a powerful one in *Coregonus* research.

The Motalaström and Norrström river systems

The Motalaström river drains a considerable part of south-east Sweden to the Baltic Sea (Fig. 17). The outlet is at Norrköping in the narrow Bråviken bay. The river drainage covers several lakes, including Vättern, which is the second largest lake in the country.

The Norrström river has its outlet at Stockholm and the system comprises Lakes Mälaren and Hjälmaren, the third and fourth largest in Sweden.

The two river systems have many eutrophic lakes, where coregonines do not live. Other lakes, however, are inhabited by arctic char, whitefish and cisco, and illustrate the dominance of whitefish over char and, again, the dominance of cisco over whitefish (Svärdson 1976).

Vättern

The surface area is 1,899 km², the altitude 88 m and the maximum depth 128 m. The lake is oligotrophic and a trend towards eutrophication has recently been checked by sewage plants. The fish fauna and the yield were presented by Grimås *et al.* (1972). The first study of the lake was by Widegren (1862, 1863) who identified its two whitefish species as *C. oxyrhynchus* and *C. fera*. Malmgren (1863) suggested that his own new species *C. widegreni* (described from Ladoga) was the second whitefish in Lake Vättern, alongside *oxyrhynchus*. Ekman (1916) supplied more information about the long-nosed whitefish and compared it with the corresponding population of Lake Vänern. Finally Thienemann (1921) suggested new names for both populations, *viz. C. lavaretus vaetterensis* for the long-nosed form and *C. holsatus suecica* for the second whitefish species.

All writers agree that there are two separate populations of whitefish in Vättern. The älvsik — or *oxyrhynchus* — has a restricted spawning site, in a small bay at Kråk on the western shore

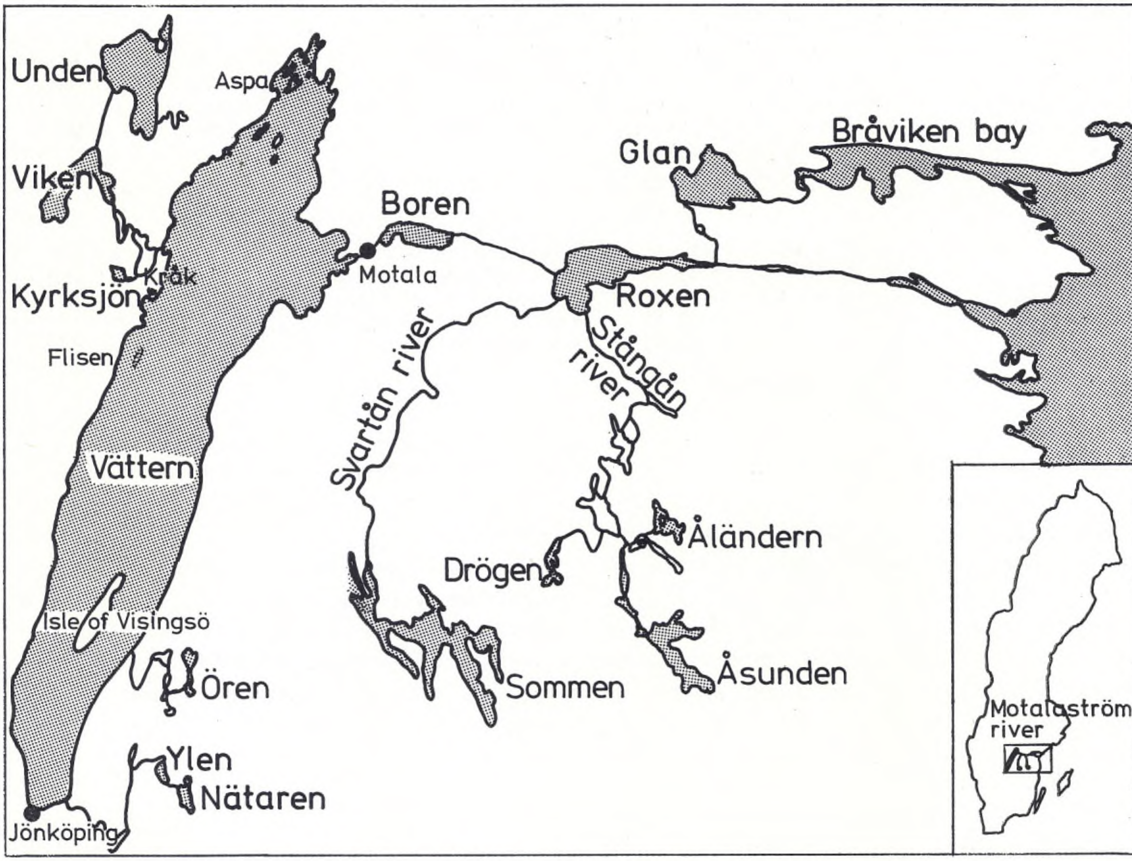


Fig. 17. Lakes of the Motalaström river (*cf.* Table 16).

(Fig. 17). The spawning takes place early, in the last half of October, before that of the other species. The Kråk population has an average of 29—30 gill rakers (Table 16) and a clearly protruding snout. It is a benthos-feeder, which gorges on crustaceans such as *Mysis*, *Pallasea*, and *Gammaracanthus*, develops considerable fatness and roams about widely in deep waters. The high quality of the älvsik together with its mobility, which makes it vulnerable to gill nets, gives this species commercial importance. How much of the annual yield of whitefish (150 tons) is accounted for by the älvsik is not known, but the share of that fish is higher than its concentrated spawning locality might indicate.

The second whitefish of Vättern spawns at many places, at the shore or on the steep slope down to deeper waters. Around the isle of Visingsö this species is known to spawn in December at 20 metres depth or deeper. It is bloated when lifted, hence its local name "kulsik" (ball-whitefish). These fish have 24—25 rakers (Table 16). It is at the southern tip of the lake, at the town of Jönköping, where the lake is eutrophic from waste discharges, that the whitefish grows most rapidly. Spawners in this area have 26 rakers. At Motala, on the eastern shore, the spawning population has some 24—25 rakers; SMITT (1886) found the same number at this locality. On a well-known spawning ground some way out from the shore, at Flisen, rather close to Kråk, there is some introgression to the long-nosed species. This can be seen not only on the nose but also from the rakers, which average 26. At the northern tip of the lake, at Aspa, another well-known spawning population has some 25 rakers. The fishermen

Table 16. *Gill rakers of whitefish samples from the Motalaström and Norrström rivers.*

Rakers / Sample	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	n	x̄
Unden	—	—	—	—	—	—	—	—	—	—	—	3	6	14	28	36	42	40	15	10	7	2	—	—	—	—	—	—	—	—	—	—	203	31.8
”	—	—	—	2	2	5	9	10	9	11	12	11	4	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	80	24.6
Kyrksjön	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	3	5	5	7	6	—	—	—	—	—	—	—	—	—	30	35.8
Vättern																																		
Kråk	—	—	—	—	—	—	—	—	4	9	11	38	27	56	47	45	34	19	12	5	1	—	—	—	—	—	—	—	—	—	—	—	308	29.7
Aspa	—	—	—	—	—	1	1	5	8	7	10	5	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	25.1
Flisen	—	—	—	—	—	1	7	11	25	43	41	33	14	18	13	4	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	214	26.2
Motala	—	—	—	1	3	5	21	28	46	43	31	17	10	6	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	212	24.6
Visingsö	—	—	—	—	2	5	15	23	36	39	36	11	13	1	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	186	24.8
Jönköping	—	—	—	—	—	—	—	2	6	4	7	7	4	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	37	26.4
Nätaren	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	2	2	1	4	4	3	—	—	1	—	—	—	20	38.1
Ylen	—	—	—	—	—	—	—	—	—	1	—	3	2	4	5	4	9	6	9	2	7	8	5	4	3	1	—	4	—	—	—	—	77	34.3
Ören	—	2	—	1	8	4	2	7	1	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	21.0
Sommen	1	—	5	13	31	39	37	25	8	2	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	161	21.3
Drögen	—	—	1	2	4	4	6	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	21.2
”	—	—	—	—	—	—	—	—	—	2	13	14	18	21	24	28	19	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	145	29.5
Åländern	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	5	5	12	7	4	2	1	39	43.0
Hjälmaren	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3	23	20	19	14	8	2	1	1	—	94	40.6
Mälaren	—	—	—	—	—	—	—	—	—	—	1	—	8	15	31	23	22	14	9	1	3	1	2	—	—	(4)	—	—	—	—	—	—	130	31.2

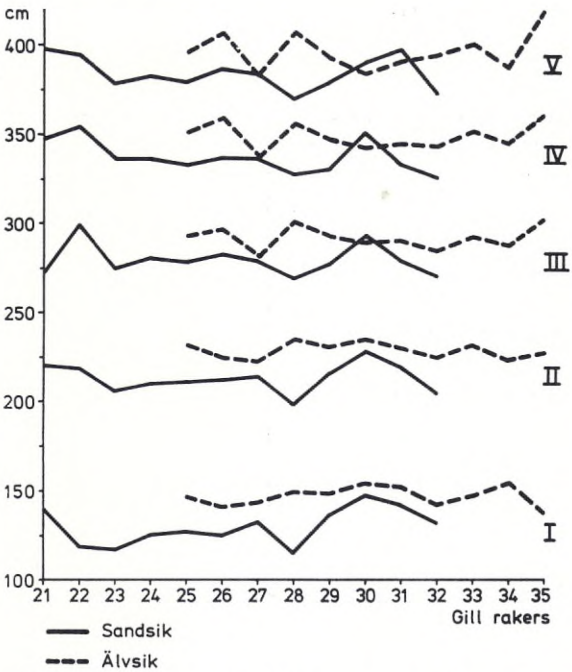


Fig. 18. Total length at different ages of spawning sandsik and älvsik within Lake Vättern. The rich material was broken down into gill-raker classes. Note the more rapid growth of the älvsik.

use several names for these populations, referring to the depth of spawning. However, the populations all seem to belong to the sandsik, *i.e.* the lesser sparsely-rakered whitefish. Whether the storsik, *i.e.* large sparsely-rakered whitefish, occurs in Vättern cannot be ascertained at present. However, the finding, in September 1974 of one specimen weighing 8.5 kg, aged 18 or 19, indicates population remnants of this larger and long-living species. The commercial catch mostly produces whitefish of 300—600 g. The sandsik is a benthos-feeder, but is generally not so fat as the long-nosed species. The growth rate of the sandsik is slightly inferior to that of the älvsik (Fig. 18).

Lake Vättern is also inhabited by a cisco with 44—48 rakers in different samples (SVÄRDSON 1957). No evidence of two sympatric cisco species has been found in Vättern. The cisco spawns very deep, 50 m or more, on the eastern shore, in December. In summer it feeds mostly on the slope of the western shore (WIDEGREN 1863). The size of the Vättern cisco is known to have fluctuated, 15—25 cm, during the last 150 years.

Unden

This lake has a surface area of 9,540 hectares, an altitude of 117 m and a maximum depth of 93 m. It had a dense smelt population, which prompted a human introduction of char from Vättern. There is no cisco. Instead, a similar-sized blåsik, with 32 rakers, is found. Besides this, there is a larger form, with 24—25 rakers, which no doubt is identical with the corresponding Vättern stock. An experienced fisherman, who exploits the spawning crowd of this sandsik, maintains there is also a larger sort in the lake, with few rakers. Two specimens of this presumed storsik were found to have a slightly better growth rate but the gill rakers were within the sandsik range. As in Lake Vättern it is conceivable that a storsik population does survive.

Kyrksjön

The small-sized whitefish of this lake (with no cisco) has 35—36 rakers. It may, however, have been introduced and is thus of limited interest.

Ören

Area 960 hectares, altitude 196 m, maximum depth 39 m. The lake drains into Vättern by a small stream. The fish fauna, comprising *inter alia* char, smelt, a sparsely-rakered whitefish and two cisco species, is most interesting.

The sparsely-rakered whitefish of Ören has only 21 rakers. Whether it should be termed sandsik or storsik is impossible to judge from its appearance. The largest known specimens are 2—3 kg.

The morphological difference between the two ciscoes is small and is a consequence of the spring-spawning habit and the dominance of the autumn-spawning normal form. The spring-spawner lives deeper, with a slightly slower growth rate. No diet analyses have been performed, because of the difficulty of identifying the two species in the feeding period. The spring-spawning cisco is formally described as a new species in a later section (p. 71).

In Table 16 one fish from Ören with 31 rakers is included. It is most probably a spontaneous hybrid between whitefish and cisco, since it had partly pigmented rakers, intermediate between the unpigmented rakers of the whitefish and the pigmented ones of the cisco. In most populations this specific difference can be observed.

Sommen

Area 13,220 hectares, altitude 146 m, maximum depth 53 m. This oligotrophic lake must have acquired its fish fauna very soon after Lake Ören, and from the same direction — the east. The lake has been searched for spring-spawning cisco, so far with negative results. The normal autumn-spawning cisco is abundant, as is also the smelt, The lake is best known for its sparse but very large char. The whitefish is the same sparsely-rakered species as in Lake Ören, with only 21 rakers. In Table 16 again one specimen with 32 rakers is recorded, which may be a whitefish x cisco hybrid. LILLJEBORG (1891) in his fauna most surprisingly reports "specimens from Lake Sommen with 30—33 gill rakers". This may indicate a blåsik population which has now disappeared, or, alternatively, a higher frequency of hybrids at that time.

Drögen

Area 1,040 hectares, altitude 155 m, maximum depth 36 m. The case for the first of the alternatives, just mentioned in connection with Lake Sommen, is strengthened by the situation of Lake Drögen. This lake was presumably also populated at roughly the same time as Sommen and it has the same sparsely-rakered whitefish as Ören and Sommen but also a blåsik with 29—30 rakers. There is no spontaneously occurring cisco in Drögen but it has recently been introduced.

Åländern

Area 1,000 hectares, altitude 90 m, maximum depth 26 m. This lake, known for its relict population of the four-horned sculpin, must have been colonized later than the Ören-Sommen-Drögen chain of lakes and after the Baltic Ice Lake was drained.

The level of the Ice Lake was, just before the drainage, some 140 m in the region of Åländern (AGRELL 1976). This means that Åländern, as an independent lake, was created much later. This is significant since it shows that the planktonsik of the lake (43 rakers) may have come from the west (via the Vänern basin and during the transition from Yoldia Sea to Lake Ancylus). There is no cisco in Lake Åländern.

Nätaren-Ylen

Nätaren is the larger of these two lakes, having an area of 1,160 hectares, its altitude is 251 m, and its maximum depth 27 m. Ylen just downstream is smaller, and shallower. These lakes are drained by the Huskvarnaån river into Vättern (Fig. 16). The whitefish of Nätaren has now gone because of too strong eutrophication. The sample is from 1951. It indicates the presence of a planktonsik, while Ylen seems to have a blåsik stock (Table 16). The presence of cisco in Ylen was reported by the fisherman to TRYBOM (1892) and has later been verified.

In view of the high altitude of the Lakes Nätaren-Ylen, the presence of planktonsik, blåsik and cisco is enigmatic. It could be explained either by drainage to the south-west (Kattegatt) in an early glacial period (NILSSON 1968) or by drainage to the Baltic in the east before the heavy tongue of glacier in southern Baltic vanished. When this barrier was removed two cisco species, a sparsely-rakered whitefish, char and smelt spread from the east as will be discussed in connection with the dispersal of the spring-spawning cisco (p. 75).

Boren, Roxen, Glan

Boren, Roxen and Glan lie downstream of Vättern and are not inhabited by whitefish but by cisco. Other lakes of the Motalaström drainage (Fig. 16) also have only ciscoes.

Hjälmaren

Hjälmaren, area 480 km^2, altitude 22 m, maximum depth 25 m, is the fourth largest lake in Sweden. It is eutrophic, and is very rich in smelt and sander (SVÄRDSON and MOLIN 1973, SVÄRDSON 1976). The lake has no cisco, but there is a whitefish stock. This is a planktonsik with 40—41 rakers, a rapid growth rate and a fairly large size (1 kg).

Mälaren

Mälaren, area 1,162 km², altitude 0.5 m, maximum depth 64 m, is Sweden's third largest lake. It is rather eutrophic, and has a huge cisco population. There is also a sparse whitefish stock of älvsik (31 rakers). The highest recorded weight is 5 kg. Some planktonsik from Hjälmaren can be found, either coming from natural spread downstream or from fry introductions which are known to have taken place. Lake Mälaren was isolated from the Baltic Sea rather recently and 1,000 years ago was essentially a bay with brackish water in its eastern part. The whitefish of the Baltic archipelago off Stockholm has almost the same number of rakers.

The cisco dominance is more obvious in relation to the blåsik and planktonsik than to the sparsely-rakered sandsik and älvsik. The lakes of Motalaström and Norrström can be arranged as follows:

Cisco only	Sympatric cisco and älvsik/sandsik	No cisco but some blåsik/planktonsik
Boren	Mälaren	Hjälmaren
Roxen	Vättern	Unden
Glan	Sommen	Åländern
Åsunden	Ören	Drögen

It seems natural that the more densely-rakered whitefish species are more inclined to feed on plankton and therefore to be more obligate competitors with cisco than are the benthos-feeding, sparsely-rakered whitefish species.

The two river systems are certainly inhabited by four of the six Scandinavian whitefish species. A fifth, the storsik, may occur sympatrically with sandsik in Lakes Vättern and Unden and actually be the only species in Lakes Ören, Sommen and Drögen.

The two whitefish species of the Baltic Sea

MÖRNER *et al.* (1977) described the deglaciation of the Baltic basin. The huge Scandinavian glacier melted more rapidly on the western side of Sweden than on the eastern. The north-western part of the province of Skåne (Scania) could probably be colonized by whitefish and cisco some time after the Lower Baltic stadial (13,100—12,700 yr BP). At the same time the first proglacial lakes opened out at the glacier's front in northern Germany and the present Poland.

For a long time a heavy tongue of the Baltic glacier persisted in the area Bornholm—German coast, blocking the penetration eastwards of brackish water around Skåne. Two ice lakes in the south were instead drained to the east, to the Karelian Sea, a bay of the Arctic. In Older Dryas (11,900—11,750 yr BP) the two ice lakes united to form the Baltic Ice Sea, connected with the Arctic in the north-east. The glacier was still blocking passage from the west.

In the Allerød period (11,750—10,950 yr BP) the Baltic Ice Sea was rapidly enlarged by the melting away of the glacier tongue up to a line Öland/Gotska Sandön/Ösel/mouth of Gulf of Finland. The uplifting of the land transformed the sea into a lake in Younger Dryas (10,950—10,000 yr BP). This Baltic Ice Lake was drained southwest to the Öresund area but later sank 26 m in the year 8,213 BC (CALDENIUS 1944) down to the world sea level, when the glacier withdrew from Mount Billingen, just west of Lake Vättern.

After that dramatic change the melting of the glacier was speeded up. The Yoldia Sea formed, flooding central Sweden's lowland and the ice-free part of the Baltic. This marine stage persisted for probably less than 1,000 years. The uplifting of land again transformed the Yoldia Sea into the huge Ancylus Lake, while the rest of the glacier melted away in the mountains of northern Sweden.

Again the continuous upwarping, especially of the Gulf of Bothnia area, tilted the whole Ancylus Lake to the south, inundating large areas of land between Gotland and the German coast. The Ancylus Lake found an outlet in the Öresund area, instead of over the Vänern basin.

The general world sea level was rising because of the amelioration of the world climate and the shrinking of glaciers. The Ancylus outlet was subsequently widened and sea water entered the basin after the lacustrine stage of some 1,500 years. The huge lake was transformed into the Littorina Sea, which was at its maximum about 5,500 yr BP.

Finally, when the world climate again became colder, the straits of Öresund became shallower, and the water of the Littorina Sea more brackish, as it is nowadays. The last 2,000 years of the Baltic's history are sometimes called the Limnaea stage.

To sum up, parts of the whole Baltic basin have been filled three times by fresh water (two periods of Baltic Ice lakes and the Ancylus stage) and also three times by salt water (Baltic Ice Sea, Yoldia Sea, Littorina Sea up to the present). Drainage has been to the east in two early stages, later to the west or south-west. Maps illustrating the more important stages are given by MÖRNER *et al.* (1977) and FLINT (1971, p. 351).

It seems clear that whitefish and cisco may have colonized the Baltic basin (and later northern Sweden) from the west-south-west as well as the east-north-east. Moreover, postglacial uplifting of the Gulf of Bothnia area 250 m higher than the White Sea basin has tilted river systems to the east (Fig. 19). Through this tilting and headwater transfer fish could have traversed northern Finland from the Baltic to the east but also, by river-system transfer in a N—S direction, from White Sea drainage to Baltic rivers. In fact many avenues of postglacial colonization exist.

At the maximum of the Ancylus Lake, six whitefish species and one cisco probably lived there. At the Littorina maximum, some 4,000 years later, no cisco and only two whitefish species could possibly exist, the whitefish only in sheltered brackish bays or as anadromous forms.

At present, cisco can live only in the eastern part of Gulf of Finland and the northern part of the Gulf of Bothnia, where the salinity is only 2—3 per mille.

Whitefish, however, are more widely spread and they exist along all the coasts. They are rare in the Belt area and along the German coast where the salinity is highest.

The two whitefish species of the present Baltic Sea are the älvsik and the sandsik. The älvsik has been presented in a special section, where it was pointed out that it is principally an anadromous species, running the larger northern rivers for spawning and roaming about widely in southern feeding migrations. It was also pointed out that

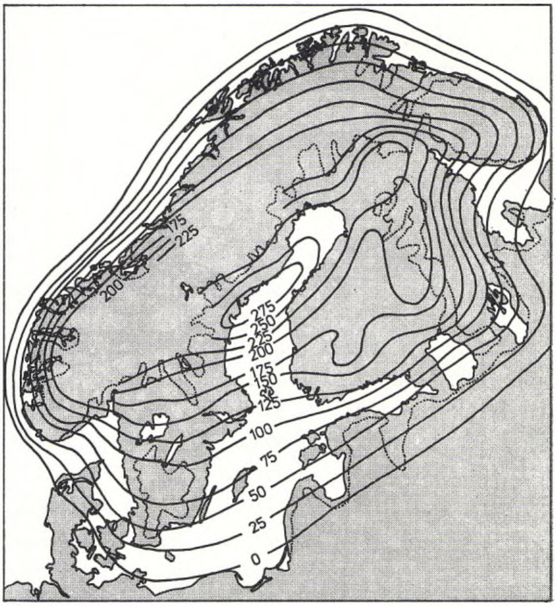


Fig. 19. The postglacial isostatic uplifting of the Baltic basin (in metres). Dotted lines mark the highest shores of the sea or the Baltic freshwater stages.

älvsik is the species described by LINNAEUS 1758 as *Salmo lavaretus*.

Along the Swedish coast, from Stockholm southwards, samples of the älvsik demonstrate a slightly falling trend in number of gill rakers (Table 17). The ecology was discussed by DAHR (1947).

There is no evidence of two sympatric species along this stretch of the coast. The whitefish are no longer anadromous, as they are along the northern coast, and the rivers are rather small. The Västervik population has a tendency to move for spawning towards a local stream and the Kristianstad population, which happens to be the most southerly one known at the Swedish Baltic coast, runs into the small Skräbeån river.

Most interestingly, the whitefish around Gotland, in the central part of the Baltic Sea, clearly belong to the second species:

Rakers	19	20	21	22	23	24	25	26	27	28	n	$\bar{x}$
Specimens	2	4	12	24	36	33	29	19	7	3	169	23.7

It should be observed that Gotland has only small brooks and no rivers and that the surroun-

Table 17. *Gillrakers of whitefish from the Swedish Baltic coast south of Stockholm.*

Rakers / Sample	23	24	25	26	27	28	29	30	31	32	33	34	35	36	n	x̄
Off Stockholm	—	—	2	5	5	14	15	11	8	6	1	2	—	1	70	29.3
„ Oxelösund	—	—	1	1	6	5	4	4	4	—	—	—	—	—	25	28.5
„ Arkösund	—	—	2	2	3	4	6	8	3	1	—	—	—	—	29	28.8
„ Valdemarsvik	—	—	1	1	2	10	4	6	1	1	—	—	—	—	26	28.6
„ Västervik	—	—	6	7	12	24	25	20	10	6	3	1	—	—	114	28.8
„ Borgholm	—	1	—	1	5	3	2	1	—	—	—	—	—	—	13	27.5
„ Kristianstad	1	2	2	2	8	7	4	—	—	—	—	—	—	—	26	27.0

ding sea has a higher salinity than exists along the Swedish mainland coast, because of the Coriolis force that carries salt water northwards along the Baltic Soviet coast.

Along the Swedish Baltic coast the sandsik lives allopatrically only around the isle of Gotland, but it occurs sympatrically with älvsik along the Bothnian coast, from Sundsvall Bay northwards. The sandsik becomes progressively more common to the north and it strongly dominates the commercial fishery (Table 18).

The älvsik is sold as class I (> 0.5 kg) or II while class IV fish are predominantly sandsik as are also class III though slightly less so. The commercial fishery takes place outside the spawning season when the two species are mixed.

Valtonen (1974, 1976) discussed the same problem on the Finnish side. The sandsik is already sexually mature below 25 cm size, while the älvsik does not mature until much later. The fishery should therefore exploit the sandsik but save the young specimens of the more valuable älvsik. The sandsik feed more heavily on *Pontoporeia* which gives a higher infestation of acantocephalan parasites, while the young älvsik lives closer to the shore and prey on gastropods. On the Swedish side of the Gulf of Bothnia, Petersson (1971) found the sandsik to be more infested by *Triaenophorus*, indicating a copepod diet. Finally Karlsson and Larsson (1969) discovered only cisco eggs in the stomachs of trawl-taken sandsik in October at a depth of 15—17 m.

The sandsik spawn at the shores of the archipelago but the species may also run the rivers. In his field notes from the 1920s, Olofsson described the runs of both älvsik and sandsik in the Torne river. The älvsik with 29—31 rakers, weighing 0.5—1.5 kg, ran up to the Kukkola rapids, 20 km from the mouth, where they spawned around October 6th. The sandsik with 23—25 gill rakers, locally called "sapakka" (=the small one) ran later, up to Vojakkala, 10 km from the river mouth, to spawn at the end of October. The average weight of the "sapakka" was 150—300 g.

The first author to mention the smaller whitefish species of the Gulf of Bothnia was Widegren (1867). The fishermen, of course, were aware of it long before that. When Malmgren (1863) presented the fish fauna of Finland he described two species of whitefish in Lake Ladoga as well as in the Gulf of Finland. The "walaamka" of northern Ladoga was characterized as a relatively small whitefish, living very deep, being

Table 18. *Gill rakers of whitefish in the trawl fishery off Luleå, in the Gulf of Bothnia.*

Class	Weight	Sample	Rakers															x̄
			21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
I and II	> 0.3 kg	84	—	—	—	—	1	3	6	7	18	19	14	6	7	3	—	29.5
III	0.3—0.15	402	7	8	23	36	50	55	51	44	37	39	28	16	3	2	3	27.1
IV	< 0.15	342	1	9	34	42	61	60	41	32	26	15	8	5	4	3	1	26.3

bloated when lifted. It was named *C. widegreni*, in honour of the Swedish authority of that time. MALMGREN stated that he had also seen the *widegreni* species from the Gulf of Finland and he was sure that it was conspecific with the population of Lake Vättern, which WIDEGREN, one year earlier, had identified as *C. fera*, (JURINE).

The two Baltic whitefish names having priority are thus *C. lavaretus* (LINNAEUS 1758) and *C. widegreni*, MALMGREN 1863.

In the southern Baltic, THIENEMANN (1922, 1935, 1937) found the Schnäpel of the River Schlei (Schleswig-Holstein) to be anadromous and to have 30—31 gill rakers. Thienemann thought it had a shorter snout than the *oxyrhynchus* of the North Sea (formerly running in French, Belgian, Dutch, German and Danish rivers) having the same number of gill rakers. He called the Schnäpel *C. lavaretus baltica*. This whitefish is rare and sporadic along the German Baltic coast but was found also in Vorpommern (THIENEMANN 1935).

Further east it lives along the Polish and Lithuanian coasts and sympatrically with the *widegreni* species. The latter was called *C. lavaretus polonica* by KULMATYCKI (1927). The *lavaretus* has 33 (WIESE 1938) or 31—32 rakers (GAYGALAS 1972) and *widegreni* only 20 rakers (KULMATYCKI most probably undercounted them). A land-locked population of *lavaretus* in Madüsee was named *Salmo maraena* (BLOCH 1783) but was identified with *lavaretus* by NÜSSLIN (1882) and THIENEMANN (1922) as having 32—33 rakers. The gill rakers might equally well indicate that the *C. maraena* was a population of blue whitefish, but BLOCH's (*op.cit.*) fish were large, 60—70 cm, 2.5 kg or more, and very fat and they fed on molluscs. This strongly suggests that the Madü whitefish is a land-locked älvsik and consequently that the *C. maraena* is synonymous with *C. lavaretus*.

Land-locked populations of *widegreni* in Poland may not all be native but some may have been introduced (STAFF and WILMAN 1936).

The same two species also occur along the Latvian coast (MANNSFELD 1930). MANNSFELD found them to have 31—38 (average 33.9) and 18—25 (average 23) rakers respectively. A third species, a densely rakered one with 40 rakers, drifted downstream to the Gulf of Riga when introduced into Lake Burtneck (from Lake Chudskoye or Lake Peipus).

In the Gulf of Finland the two species obviously introgress and a third — a densely-rakered one — again appears drifting down from the Salis (Lake Chudskoye) or the Neva (from Ladoga). Leaving aside this densely-rakered species since it never spawns in the Baltic and does not really belong to its whitefish fauna, the two real Baltic species were sampled by PRAWDIN (1931) and were found to have 22—31 rakers, average 25 and by PIROZHNIKOV (1971) as a more long-nosed form with 29 rakers.

It seems as if only the *widegreni* species actually runs the Neva. PRAWDIN (1931) gives a sample from the Neva of 22—29 rakers, average 25. BERG (1916—1948) identified this anadromous form as the *C. lavaretus* and the observation by MANNSFELD (1930) that BERG's identification was at variance with that of *lavaretus* elsewhere within the Baltic Sea seem to have been ignored.

Lake Ladoga (THIENEMANN 1926, 1929, PRAWDIN 1931, 1954, SHAPOSHNIKOVA 1973) is inhabited by two or possibly three whitefish species with few gill rakers. The "valaamka" or "valantka" form is the one described by MALMGREN as *widegreni*. According to SHAPOSHNIKOVA it has 23—28, average 25 gill rakers. Its head is longer, the snout deeper than those of the "lake form" which has slightly fewer gill rakers (21—29, average 23.8). This second larger form was called "walkea" or "white whitefish" by MALMGREN and the Finnish experts serving THIENEMANN with data and material. It is also called "luutokka" (bottom whitefish) or "nuotta" (seine whitefish). This is a *lavaretus* population, in spite of the few rakers.

JÄÄSKELÄINEN (1927) discussed the *widegreni* population of Ladoga. He stressed the deepwater habit with spawning at 50—100 m depth in the northern part of the lake in late December, its small size of 650—700 g, the diet on *Pontoporeia* in the 25—50 m layer, and the fatness that makes it commercially important.

In spite of the considerable efforts made by SHAPOSHNIKOVA (1973), it is not possible to identify the four or five whitefish species of Ladoga with certainty to those of Lake Vänern. Both lakes are big and were inundated by the sea in the Littorina period. It appears that the sandsik of both lakes has taken over the outlet stream and the estuary while it has introgressed intensively

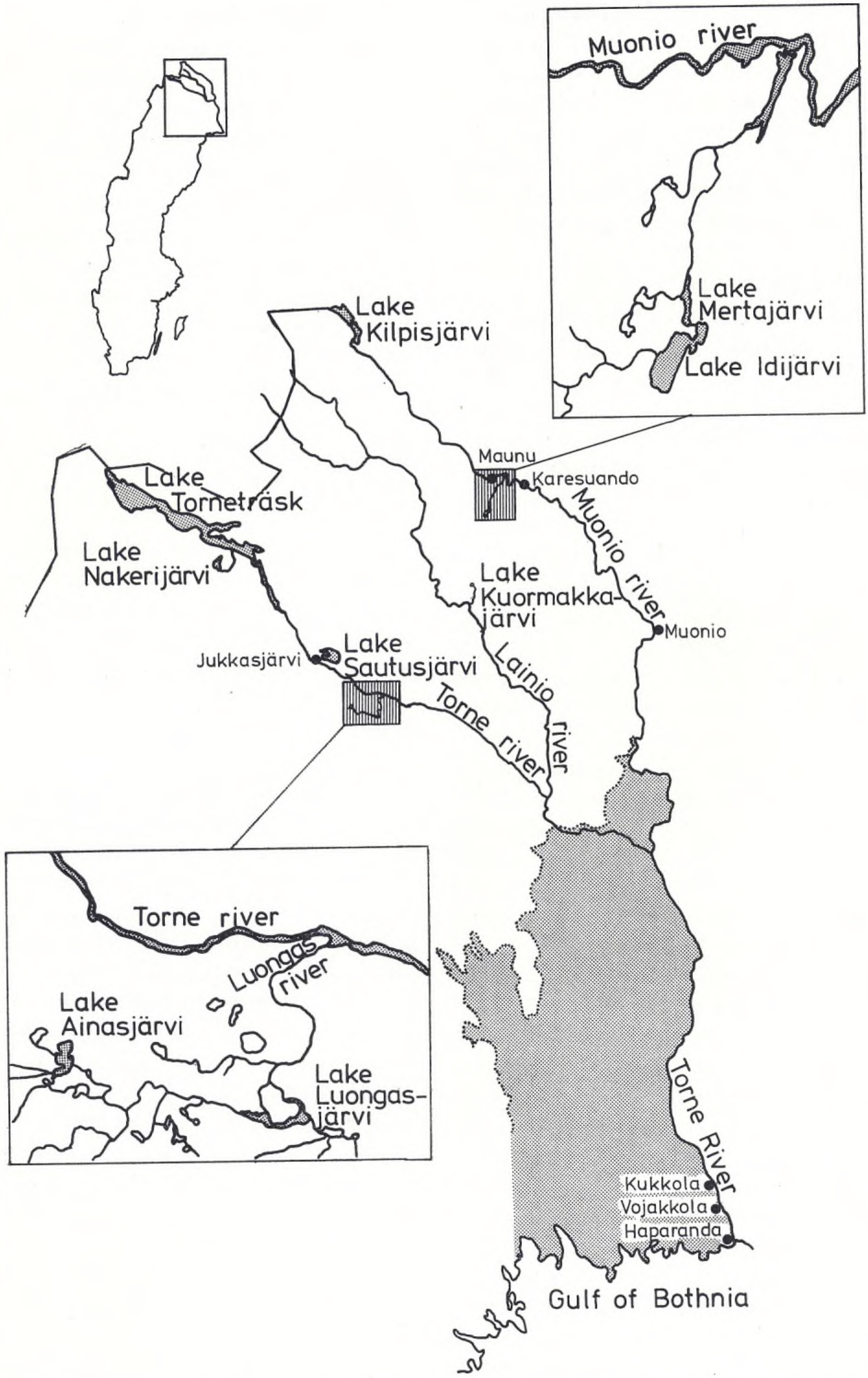


Fig. 20. Lakes of the Torne river system. Grey markings show the drainage area covered by the highest shores of the Ancylus stage of the Baltic (*cf.* Table 19).

to the land-locked älvsik and caused the gill rakers of the älvsik to become exceptionally few. In both lakes a blåsik and a densely-rakered whitefish live as the third and fourth species. The main uncertainty is whether the storsik, the *C. maxillaris* of Vänern, also exists in Ladoga.

However, the names given to the whitefish populations in Lake Ladoga have relevance to the Baltic populations only as far as the *widegreni* is concerned. MALMGREN's name *widegreni* from 1863 also refers to the Gulf of Finland, as stated by the author. Generally the names *C. baeri*, KESSLER 1864, and *C. ludoga*, Poljakow 1874, are significant only if it can be shown that *baeri* refers to the storsik. In that case it is two years older than *C. maxillaris*, GÜNTHER from Vänern.

To sum up, the Baltic is inhabited by two whitefish species, the *lavaretus* and the *widegreni*. The latter is most abundant in the Gulf of Bothnia but it occurs also along the south-eastern Baltic coast, including Gotland.

The Torne river drainage

The Torne river, with the tributaries the Muonio and Könkämä rivers, constitutes the political boundary between Sweden and Finland. The highest Baltic shores, from the Ancylus stage, lie at a present altitude of 180 m. Although this is much lower than the highest shores further south in Sweden, the flatness of the terrain and the sparsity of rapids or (small) waterfalls suggest that the colonizing whitefish had an easy access to a large part of the drainage area (Fig. 20).

As was explained in detail in the last section, both älvsik and sandsik run the lower part of the river, upstream to Kukkola and Vojakkola. Since the sandsik is normally more often land-locked than the älvsik, the former species should dominate the lakes of the river. The third sparsely-rakered species, the storsik, should be rare since it is less competitive.

These hypotheses, based on the experience from other rivers, are only partly confirmed by the actual populations. It seems that the älvsik is more lacustrine in the Torne river than elsewhere.

Through the courtesy of Dr P. TUUNAINEN, Helsinki, who is the head of a Finnish field

Table 19. *Gill rakers of whitefish samples from the Torne river drainage (cf. Fig. 20).*

Rakers / Sample	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	n	x̄
Kilpisjärvi 1974—75 [1]	5	4	15	40	75	76	121	78	77	32	16	6	7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	475	20.7
,, 1977	—	—	—	—	—	—	1	6	11	13	8	6	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	46	24.0
,, 1974, 1977	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	21.3
Maunu 1875 [2]	—	—	—	—	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	22.0
Idijärvi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	6	19	11	13	11	4	1	1	2	—	—	—	—	—	70	33.4
Mertajärvi	—	—	—	—	—	—	—	—	—	—	1	—	4	13	6	8	10	9	6	2	2	—	—	—	—	—	—	—	—	—	61	30.2
Kuormakkajärvi	—	—	—	—	—	—	—	—	3	12	13	3	7	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	25.1
Torneträsk 1921—54	—	—	—	—	—	—	—	1	8	17	30	64	65	49	34	31	11	6	1	—	—	—	—	—	—	—	—	—	—	—	317	27.2
Nakerijärvi	—	—	—	—	—	1	—	1	5	1	7	6	10	10	12	10	10	7	9	4	5	4	—	2	2	—	—	—	—	—	106	—
Vieksalahti	—	—	—	—	—	—	—	—	—	1	9	8	9	5	5	2	3	1	2	2	2	6	9	17	13	13	8	7	1	1	124	—
Jukkasjärvi	—	—	—	—	—	—	—	1	1	4	11	10	14	12	14	5	5	3	2	1	—	1	4	4	3	—	—	—	—	—	95	—
Sautusjärvi	—	—	2	3	1	1	1	—	—	2	3	6	2	15	18	9	2	1	—	2	—	—	—	—	—	—	—	—	—	—	68	—
Ainasjärvi [3]	—	—	—	2	25	22	31	45	21	2	3	2	5	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	163	21.6
Luongasjärvi [3]	—	—	—	1	7	3	6	19	5	23	18	47	18	11	19	3	—	2	—	—	—	—	—	—	—	—	—	—	—	—	182	25.2

[1] Courtesy P. Tuunainen, Helsingfors.
[2] From Lilljeborg 1891.
[3] Courtesy G. Lithner, Stockholm.

station at Lake Kilpisjärvi, it is known that this lake is inhabited by a dense whitefish population. The fish are rather small-sized and have few rakers. According to the Finnish staff, 475 whitefish specimens had an average of 20.7 gill rakers. A sample kindly brought to the Drottningholm Institute proved, however, that the counting techniques applied were obviously different from ours, as we found 24 rakers (Table 19).

Lake Kilpisjärvi is the headwater of the Könkämä river. Dr Tuunainen also stated that stray specimens of a larger whitefish are sometimes caught in the lake. Three such specimens were identified from the scales by the Drottningholm staff. On the basis of a comparison with other lakes (Locknesjön, Storvindeln, Skikkisjaure, etc.) these larger fish could be storsik. Their gill rakers were within the range of the more abundant species.

At Maunu, downstream the river, where its name changes to the Muonio river, and close to the village of Karesuando, Lilljeborg (1891) had in 1875 found some large whitefish specimens, more than 40 cm, with few rakers. At Muonio, still further downstream, Olofsson in his field notes recorded specimens up to 60 cm and 2.5 kg. Günther (1866) described other large fish from the same locality as *C. lapponicus*. Dr A. Wheeler of the British Museum (Natural History) kindly investigated three syntypes of *C. lapponicus*. He found 26 rakers in two specimens and 27 in the third (Wheeler in litt.). This count suggests that *C. lapponicus* is synonymous with *C. lavaretus*, *i.e.* the älvsik.

The Idijokki tributary, running north to the Muonio river roughly at Karesuando, is full of small lakes. All of them are densely populated by small-sized blåsik. These shallow lakes are comparatively warm and are inhabited by roach, perch and ruffe. Svärdson (1976) summarized experiments to reduce the whitefish populations in a series of these lakes. Two of them, Lakes Mertajärvi and Idijärvi, are included in Table 19. The blåsik of the lakes have 30—33 gill rakers, *i.e.* quite normal counts.

The Torne river proper is inhabited by two whitefish species with few gill rakers. A clear-cut sympatric occurrence is found only in Lake Sautusjärvi, close to the village of Jukkasjärvi. Olofsson studied the two forms and found one to be slightly smaller than the other and much more abundant. It had only 18—20 gill rakers whereas the second species had 28—29 (Table 19). It seems that the smaller is a sandsik, the larger an älvsik.

The small Luongas tributary (Fig. 20) is populated by a population of 21—22 rakers in the headwater Ainasjärvi but by a population of 26 gill rakers in Lake Luongasjärvi, further downstream. This situation suggests a sandsik in the upper region of the river and a penetrating älvsik further downstream.

Lake Torneträsk, with an area of 322 km^2, altitude 342 m, maximum depth 168 m, is the headwater of the Torne river. Ekman (1912) described its whitefish as large (average 1 kg, maximum 4 kg). Nowadays the whitefish in this lake is smaller and more abundant than it was formerly. No introduction by man is recorded and, if whitefish was ever so introduced, this must have been done more than 150 years ago (Tuolja pers. comm.). The gill rakers of the Torneträsk whitefish number about 27. The span of variation is small and suggests a species not introgressed to other forms.

Introductions in smaller lakes around the Torneträsk are, however, known to have taken place in this century. Such a lake is Nakerijärvi. The eggs are said to have been secured at Vieksalahti, just south of the Torneträsk, or at Jukkasjärvi further downstream. At both places there are two whitefish species in the river, the larger älvsik and a small-sized planktonsik with 38—40 gill rakers. It appears from the sample from Nakerijärvi that probably both species were involved in the egg collection. At Jukkasjärvi the älvsik has 26—29 rakers and at Vieksalahti mostly 25—27.

Through the courtesy of Dr Magnus Berg, then at Tromsø, Norway, whitefish heads from Lake Stuorajavre were secured in 1953 and 1954 and later investigated at Drottningholm (Svärdson 1957, p. 318). These whitefish mostly had 24—27 rakers but two specimens with 32 and 34 suggest a second blåsik population. It should be remembered that Lake Stuorajavre belongs to the Kautokeino river, which is a tributary to the

Alta river, running to the Alta Fjord in northernmost Norway. The parts of the Kautokeino river furthest upstream lie just beside the headwaters of the Lätäsäno river, which runs south through north-western Finland to Enontekis, where the Könkämä river changes its name and becomes the Muonio river. Because of the uplift difference that has occurred, whitefish from the Baltic might easily have spread from the Torne over to the Alta river, or *vice versa*, though the latter is a trifle less probable.

The interpretation of the Torne river whitefish species is uncertain. The occurrence of both blåsik and planktonsik are documented but these fish are noticeably not so frequent in the various lakes as they are in most other river systems. Storsik may occur in Lake Kilpisjärvi as a rare population; elsewhere it is not recorded. Two sparsely-rakered species dominate the whole Torne river system and the larger, or älvsik, is more common nowadays than in any other river but the Indalsälven, where it was introduced by man into a headwater, Sällsjön, in 1870.

There are three possible explanations for the Torne river deviation. First, a human introduction may actually have occurred, albeit at a time before records were kept. Second, the river valley was more easily colonized by the älvsik than is usually the case, because the terrain is flat and the Baltic shores ran far inland. Third, the similarity to the whitefish fauna of the rivers of Norway and the Kola peninsula of the U.S.S.R. running to the Arctic suggests a connection and is related to the status of the sparsely-rakered whitefish in those rivers. This problem will be dealt with further in a later section.

Some southern rivers: Lagan, Rönne and Mörrumsån

In southern Sweden, whitefish are less abundant than they are in the northern parts of the country. The eutrophic status of the lakes and the dense populations of other fish species, notably cyprinids, are mainly responsible for this situation. The cisco is also relatively more common here, as this coregonine is better adapted to eutrophic lakes than are all whitefish species except planktonsik. No anadromous whitefish live in the lower parts of the rivers here discussed.

The Lagan river

Bolmen is the largest lake of the river drainage. Its area is 180 km², its altitude 143 m and its maximum depth 37 m. There are one cisco and two whitefish species in the lake. The whitefish have the local names "lövsik" (=spawning when leaves are falling) and "djupsik" (=deep-spawning). Kösen is a small lake close to Bolmen (Fig. 21, Table 20) inhabited by one of the two Bolmen whitefish.

The gill rakers prove the two species to be blåsik and planktonsik with some 34 and 41 gill rakers respectively. The Bolmen stock of blåsik was named *C. lavaretus bolmeniensis* by MALM (1877). A short description was also given by SMITT (1882).

The general relation between these two species is well documented. The blåsik tends to swamp the planktonsik. Possibly because of the eutrophic status of the lakes, the planktonsik has resisted this competition better within the southern river systems than in most other lakes. In the Lakes Kösen, Vidöstern, Flåren and Rusken the planktonsik seems to be allopatric, though the gill raker numbers (42—40—39—38) suggest some earlier introgression. In the small lakes around the limnological research centre of Aneboda, the planktonsik has few gill rakers (38—37) while the blåsik has about 30. The small-sized Allgunnen planktonsik is a documented planktonfeeder. The blåsik stock has a slightly varied diet. The Allgunnen blåsik was widely spread by the fish-culture activities of the Aneboda station in the early part of this century. It has been possible to trace a number of established transplanted whitefish populations from data in archives and the paper by MELANDER (1945). In Table 20 four such lakes have been sampled (Lakes Assjön, Mien, Yttre Hallången and Stengårdshultsjön). All of these now have allopatric whitefish populations with the same number of gill rakers as the Allgunnen parent stock. This is further evidence of the general rule that gill rakers do not change in a new environment.

THIENEMANN (1921), in a short paper on

Table 20. *Gill rakers of whitefish samples from the Lagan lakes and the transplanted Allgunnen stocks.*

Rakers / Sample	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	n	x̄
Övringen	—	—	—	—	—	—	—	—	1	2	—	—	1	3	4	8	13	9	4	9	—	1	—	—	—	—	—	—	55	37.0
Allgunnen																														
"landsik"	—	—	—	—	2	3	2	5	5	8	5	1	2	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	37	29.6
"djupsik"	—	—	—	—	—	—	—	—	—	—	—	—	1	5	9	10	25	12	4	9	—	1	—	—	—	—	—	—	76	37.1
Rusken	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	3	4	6	3	4	2	1	1	—	—	—	—	28	39.0
Flåren	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	4	5	4	4	3	—	—	—	—	—	—	—	25	38.3
Hindsen	3	6	8	6	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	23.3
Vidöstern	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	3	39.7
Bolmen																														
"lövsik"	—	—	—	—	—	—	—	1	1	4	2	6	14	11	11	9	3	3	2	—	1	—	—	—	—	—	—	—	68	34.1
"sik"	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	2	1	1	2	1	—	—	—	9	41.7
Kösen	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	1	5	15	17	26	36	29	21	24	20	7	3	1	208	41.6
Introductions of Allgunnen "landsik"																														
Assjön, Emån river introd. 1905, sample 1951—54	—	—	—	—	1	4	4	17	21	16	12	16	8	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	101	29.9
Mien, Mieån river introd. 1902, sample 1951	—	—	—	—	1	3	5	9	8	12	9	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	52	29.3
Yttre Hallången, Nissan river introd. 1914, sample 1951—54	—	—	—	—	2	12	12	14	27	21	14	13	12	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	130	29.5
Stengårdshultsjön, Nissan river, introd. 1928, sample 1951	—	—	—	—	2	5	4	8	5	3	2	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	32	28.4

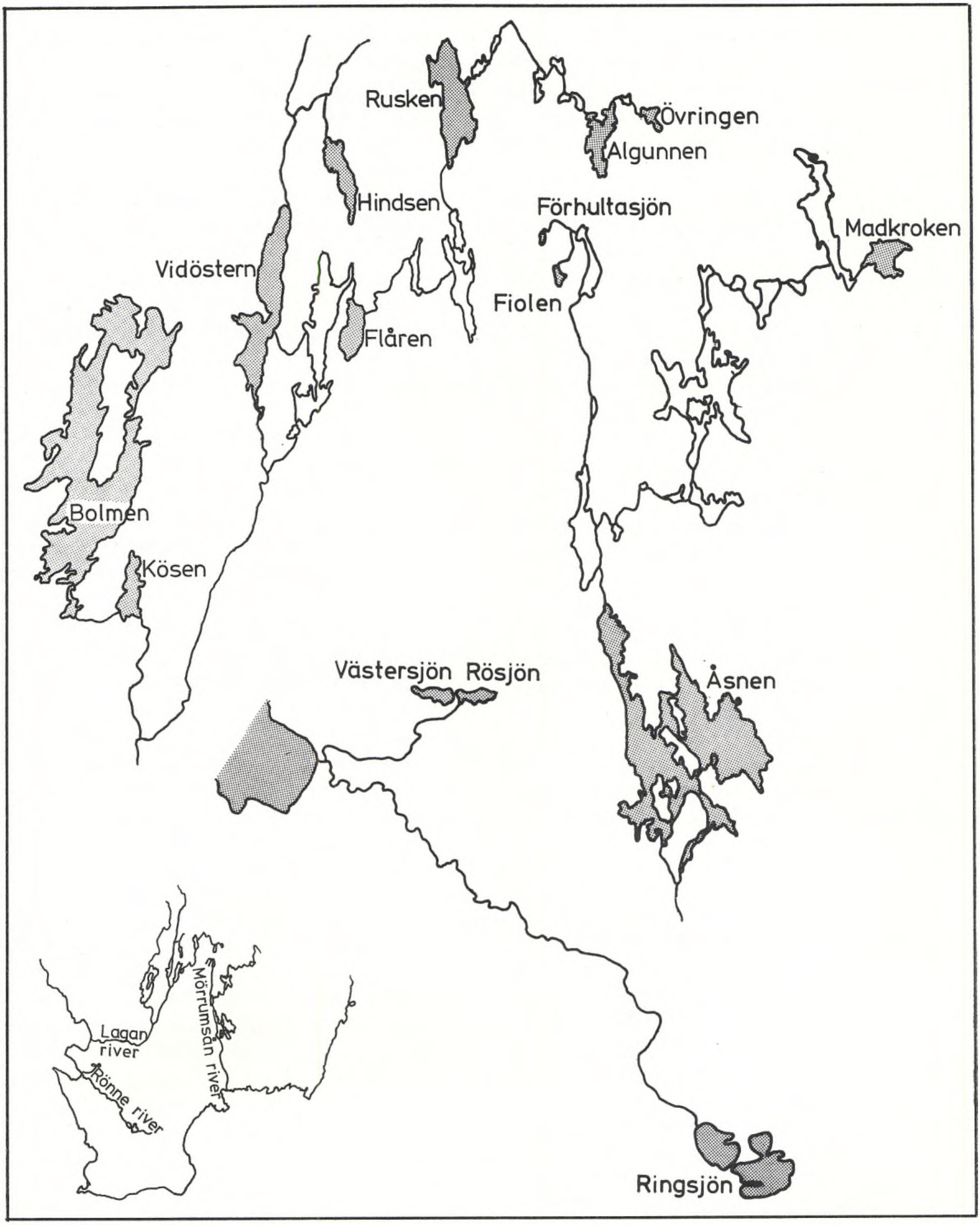


Fig. 21. Lakes of the Lagan, Rönne and Mörrumsån rivers (*cf.* Tables 20—21).

Swedish coregonine fish, called the Allgunnen blåsik *C. lavaretus lavaretus* and judged it to be typical. The planktonsik, with its terminal mouth, was mistaken by THIENEMANN for a cisco. The poor quality of the sample available to him prompted his remark on there being few rakers for a cisco.

Within the Lagan valley only one lake is known to have a sparsely-rakered whitefish. The Lake Hindsen whitefish, with 23 gill rakers, are of average size and are most probably a sandsik stock. This stock is of zoogeographical interest since the sandsik could have colonized the lake very early, from the Laholm Bay of the Kattegatt. The sandsik of Hindsen, together with similar stocks in Schleswig-Holstein, and possibly those of the Stavanger area in Norway, suggest a northward dispersal of a sandsik stock in the glacial refugium of lakes of the present North Sea floor.

The evidence is even stronger that the planktonsik has spread along the same route. The abundant occurrence of the planktonsik within the Lagan valley, the dense gill rakers of the Kösen and Bolmen stocks and the still higher gill-raker counts of stocks within the parallel Göta river drainage (*cf.* p. 35) strongly suggest evolutionary relations with the planktonsik demes of western Jutland. The Danish stocks in turn can have arrived in their present lakes from nowhere else than fresh water refugia on the North Sea floor, since they cannot tolerate the marine environment.

The Rönne river

The Ringsjön (area 4,500 hectares, altitude 54 m, maximum depth 18 m) has a well-known whitefish stock. In all faunas they are called Ringsjön blåsik, but this is at variance with the terminology of this paper, where the name blåsik is restricted to another species. It was studied by Professor SVEN NILSSON of Lund University, who took some specimens to VALENCIENNES. They were subsequently described by VALENCIENNES as the new species *C. nilssoni* in 1848. NILSSON himself acknowledged this honour and used the name in his fish fauna of 1855. THIENEMANN (1921) pointed out that the description by VALENCIENNES was ambiguous but that NILSSON seven years later was the first to use the name, which therefore was valid. It could be added that most old descriptions of coregonids are ambiguous and few stocks can be identified from the text, most having to be identified by the locality or other circumstances.

The gill rakers of the Ringsjön stock prove it to be a planktonsik (Table 21). Samples of almost century-old museum specimens, investigated in the early 1950s, and a fresh sample in 1952, gave 37.2 and 37.5 as gill-raker counts (SVÄRDSON 1957), whereas more recent samples from the 1970s consistently produce higher counts (39.1—39.2). This difference is an illustration of the human factor mentioned in the section on Methods. There is no evidence and only a very small probability that the allopatric stock has changed lately.

The Ringsjön planktonsik must be one of the oldest whitefish demes within the country. This part of Skåne (Scania) was early covered by a glacial lake. The whitefish must certainly have arrived from the northern part of the present Öresund Straits and thus is related to other planktonsik stocks, spreading from the North Sea floor. The name *C. nilssoni*, VALENCIENNES 1848 is therefore attached to the planktonsik species and there seems to be no other planktonsik stock named within Scandinavia.

Ecologically the planktonsik is outstanding for being eurythermic, *i.e.* enduring warm eutrophic lakes (Ringsjön is also known as the best bream lake in Sweden) as well as cold, oligotrophic ones.

It seems to have been the first postglacial colonist in many river valleys.

Two small lakes on the top of the Hallandsås ridge also belong to the Rönne river system (Fig. 21). The Västersjön (450 hectares, altitude 66 m, maximum depth 13 m) and Rössjön (240 hectares, altitude 66 m, maximum depth 24 m) are inhabited by ciscoes. From what is known about early deglaciation history (MÖRNER *et al.* 1977) these high lakes must have got their ciscoes very early. If a colonization by ciscoes from the west has ever occurred in southern Sweden, the populations of the two Hallandsås lakes certainly belong to this category (Table 21).

The Mörrumsån river

The largest lake within the drainage is Åsnen (area 15,000 hectares, altitude 138 m, maximum

Table 21. *Gill rakers of whitefish and cisco in lakes of the Rönne and Mörrumsån rivers as well as the lake Åsnen hybrids whitefish x cisco.*

Rakers Sample	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	n	x̄	St.dev.
Rönne river																										
Ringsjön 1872—82	—	—	—	—	—	—	1	1	5	9	6	10	4	3	—	1	—	—	—	—	—	—	—	40	37.2	—
„ 1952	—	—	—	—	—	—	—	1	3	5	6	8	2	3	1	1	—	—	—	—	—	—	—	30	37.5	—
„ 1974	—	—	—	—	—	—	—	—	—	3	7	9	16	9	7	5	2	—	—	—	—	—	—	58	39.2	—
„ 1977	—	—	—	—	—	—	—	—	1	1	6	17	14	10	8	2	2	—	—	—	—	—	—	61	39.1	—
„ 1978	—	—	—	—	—	—	—	—	1	6	13	13	23	16	15	5	4	—	—	—	—	—	—	96	39.2	—
Cisco, Rössjön 1979	—	—	—	—	—	—	—	—	—	—	—	1	1	1	6	7	4	1	—	1	—	—	—	22	41.8	—
Mörrumsån river																										
Förhultasjön 1975	—	—	—	—	—	—	—	1	2	2	1	2	1	2	—	1	—	1	—	—	—	—	—	13	38.0	—
Fiolen 1975	2	1	4	1	4	4	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	30.7	—
Madkroken 1977	—	—	—	4	1	8	2	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	32.3	—
Åsnen 1951	—	—	—	—	—	1	4	5	9	20	10	6	2	1	—	—	—	—	—	—	—	—	—	58	36.0	1.62
„ 1977	—	—	—	—	—	10	17	31	51	61	59	52	29	18	7	12	3	2	—	—	—	—	—	352	36.7	2.38
„ cisco 1951	—	—	—	—	—	—	—	—	—	—	—	2	1	1	5	8	10	12	6	3	2	1	—	51	43.3	2.23
„ „ 1977	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10	16	44	54	31	27	6	4	1	197	44.0	1.67
F_1-hybrids (Gravtjärn 1952—58)	—	—	—	—	—	1	1	5	16	20	53	50	43	23	22	17	8	4	4	2	—	—	—	269	38.6	2.44
F_2 (Öratjärn 1958—63)	—	—	—	—	2	5	12	23	41	59	50	35	22	7	6	4	—	—	—	—	—	—	—	266	36.4	2.05
F_2 (S. Stensjön 1959—63)	—	—	1	2	4	12	19	34	49	61	80	58	21	17	6	2	—	1	—	—	—	—	—	367	36.3	2.21
F_3 (Öratjärn 1961—64)	—	—	—	—	—	2	10	12	26	45	57	48	31	19	6	2	—	—	—	—	—	—	—	258	37.1	1.93
F_3 (S. Stensjön 1962—64)	—	—	—	1	1	4	2	11	19	31	39	20	13	6	5	1	—	—	—	—	—	—	—	153	36.7	2.04
F_n (Öratjärn 1965—75)	—	—	1	—	1	6	21	48	131	230	251	226	147	74	28	10	3	1	—	—	—	—	—	1,178	37.1	1.86
F_n (S. Stensjön 1965—75)	—	—	—	—	1	5	13	47	95	121	138	125	91	57	28	3	1	—	—	—	—	—	—	725	37.1	1.98

depth 14 m). The lake is inhabited by a small-sized whitefish with terminal mouth, locally called "ranning", and a sympatric cisco population. Since the two species have overlapping spawning periods in November, this lake was used in the early 1950s to produce whitefish x cisco hybrids. This experiment was performed at the Kälarne research station, some 700 km north of Åsnen and was summarized by SVÄRDSON (1965).

The "ranning" population has some 36—37 gill rakers, while the cisco has 43—44. Recent samples from 1977 have slightly higher averages than the 1951 samples (*cf.* Ringsjön above). The F_1 hybrids had 38.6 rakers and a span of variation (32—46) which was larger (Table 21) than that of the whitefish or the cisco. The F_1 fish were grown to maturity in a small tarn, Gravtjärn, close to the Kälarne field station.

The F_2 fish were raised in two different small lakes, Öratjärn and Södra Stensjön, south of Kälarne. The two samples, summarized from 5 and 6 years' fishing, had 36.4 and 36.3 gill rakers. The mouth characters of the cisco were scarcely observed at all in the F_1 fish (except tendencies in some specimens) and were even less evident in the F_2 fish. The F_3 fish and later generations of these now self-reproducing stocks are presented in Table 21. FERGUSON *et al.* (1978) found them to be of whitefish character with no discernible protein genes from the cisco, an observation that fits the morphological appearance.

Unfortunately the gill raker difference between the planktonsik and the cisco was small, compared with that of the hybrids from the Arjeplog lakes (*cf.* p. 43). The apparent similarity of the F_n fish to the whitefish parent may mask a persisting hybrid gene pool like that of the Arjeplog hybrids. On the other hand, the sudden drop of gill-raker numbers from F_1 to F_2 generation in the whitefish x cisco hybrids suggests a selection against the cisco genes. The standard deviation is lower in F_2 than in F_1 suggesting elimination of the most extreme gene combinations. In later generations the standard deviation is not changed significantly.

This experiment is of great interest for the interpretation of the evolution and taxonomy of coregonine fish. Two well-defined sympatric species of Lake Åsnen, undoubtedly cohabiting for about ten thousand years without producing more than stray hybrids, have not developed a barrier of sterility but can be hybridized by man. If and when the environment changes, as in Lake Orrevann in Norway (PETHON 1974), the two species may start producing mass hybrids, and the genes of one species may invade the gene pool of the other and be selected for or against. Conceivably, some genes from one species may be incorporated in the genome of the other and create new combinations, which in turn may accelerate the adaptation to the environmental change. Introgression thus enters the evolutionary process and hastens local adaptation.

It is to be hoped that the F_n generations of whitefish x cisco hybrids can be saved for future studies and more penetrating protein analyses.

Apart from Lake Åsnen, Lakes Förhultasjön, Fiolen and Madkroken, in the uppermost part of the Mörrumsån river, have been sampled (Table 21). The gill rakers suggest the existence of planktonsik and blåsik but two specimens with 18 and 19 rakers from Lake Madkroken (not included in the table) show that the storsik or the sandsik also lives there. There is some evidence that large-sized whitefish with few rakers were earlier fished in the nearby Lakes Helgasjön and Innaren, but no recent samples have been studied.

Introgression and order of arrival in the upper Ljusnan

The Ljusnan river traverses central Sweden from the Norwegian border to the Baltic Sea. In the lower part the anadromous älvsik runs the river (Table 3). There are no large lakes within the river system. Since the älvsik might be land-locked only in lowland large lakes and the aspsik is restricted to more northerly rivers, there are four species of whitefish that could have colonized the river valley from the Ancylus stage of the Baltic, *viz.* storsik, sandsik, blåsik and planktonsik.

The upper part of the river system is split up into four streams with whitefish lakes, *viz.* the Mysklan and Ljusnan proper, the Särvån tributary from the north and the Härjeån tributary from the south (Fig. 22).

The Särvån tributary

Lake Övre Särvsjön, 800 hectares, altitude 650 m, is the headwater of the Särvån stream. The lake

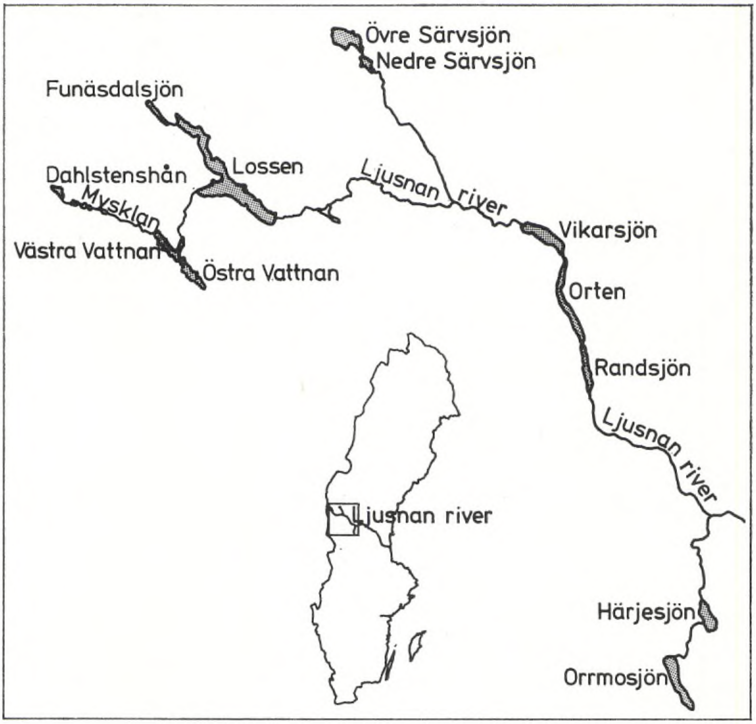


Fig. 22. Lakes of the upper Ljusnan river (*cf.* Table 22).

was treated with rotenone in October 1974 in order to get rid of the whitefish (and pike, perch and burbot) before the lake was, for hydroelectrical purposes, artificially connected by a tunnel to a char lake in another stream at a lower altitude.

Samples of the whitefish, killed by the rotenone, fell into three categories, also known by the local people to exist in the lake. The large fish had 22 gill rakers and were identified as storsik (Table 22, Fig. 23). Surprisingly the medium-sized and small fish both had the same number of gill rakers (37—38). Their growth rate, however, was different, and the medium-sized fish were rare as compared with the small ones.

Some rotenone also spread to Lake Nedre Särvsjön, which is smaller and has an altitude of 630 m. SVÄRDSON (1957) already had some material from the lake but the rotenone-killed sample was considerably larger (Table 22, Fig. 24). Now, it was evident that the corresponding medium-sized and small fish of Nedre Särvsjön had different numbers of gill rakers and thus were certainly genetically distinct stocks. The identification of the smaller as planktonsik left the medium-sized as blåsik. The sparse, medium-sized fish of the upper lake were thus most probably blåsik that had managed to climb the stream to Övre Särvsjön and there maintained themselves as a more fast-growing fraction, although introgression had increased their gill rakers.

The Mysklan and Ljusnan rivers

In the Mysklan stream the whitefish have climbed to altitudes not met with in other parts of Scandinavia. In a wider part of the stream, called Dahlstenshån, at 814 m, there is a self-reproducing native stock of whitefish (GUSTAFSON pers.comm.). According to reports to the Drottningholm Institute by anglers these whitefish are large, about 1 kg and strike the fly to produce excellent angling. No raker counts have been made so far on the fish from Dahlstenshån, but the evidence downstream the Mysklan suggests that these large fish are storsik with few rakers.

The evidence comes from Lake Östra Vattnan. Intensive fishing in the winter of 1977—78 by Mr GUSTAV OLOFSSON confirmed local statements

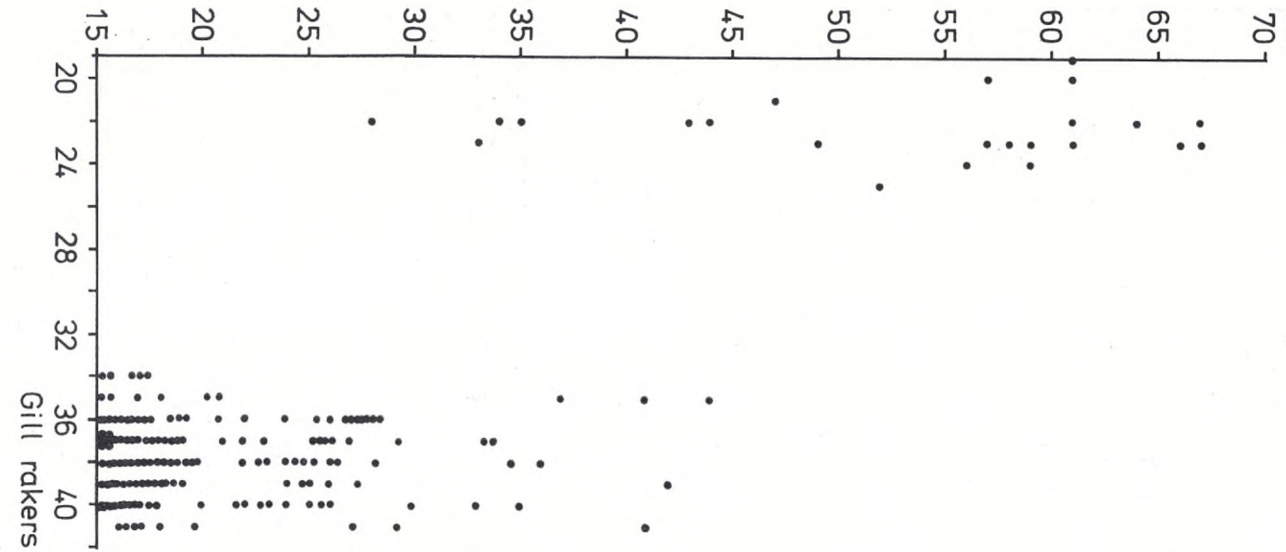
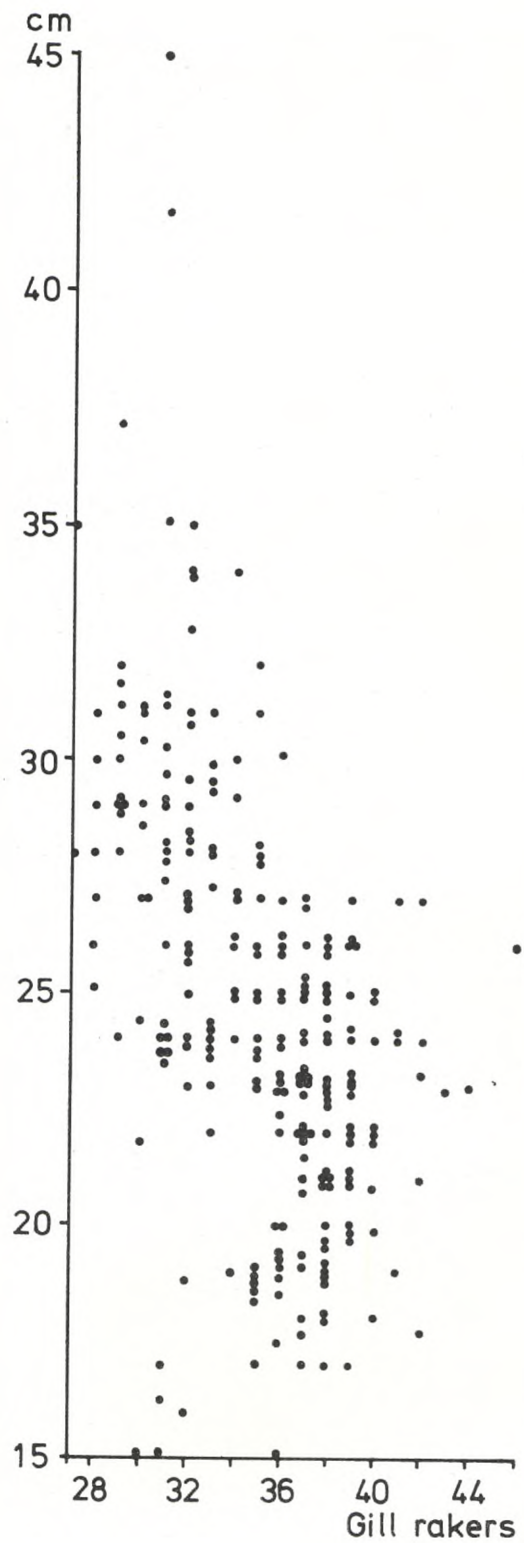


Fig. 23. Gill-raker numbers and size of whitefish sampled from those killed by rotenone in Lake Övre Särvsjön in 1974 (*cf.* Table 22).

Table 22. *Gill rakers of whitefish samples from lakes within the Ljusnan river (cf. Figs. 22—27).*

Rakers / Sample	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	n	x̄
Ö. Särvsjön, large	—	—	2	2	1	8	8	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	22.2
„ „ small	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	9	25	32	29	21	23	9	—	—	—	—	—	153	37.8
N. Särvsjön, all	—	—	1	—	—	—	—	1	—	—	2	7	12	10	23	23	14	11	21	24	30	31	20	9	4	5	1	1	—	1	251	—
Ö. Vattnan, all	—	3	3	8	20	42	45	28	13	4	6	2	4	4	4	3	3	3	1	—	—	—	—	—	—	—	—	—	—	—	196	—
Harrsicklingen	—	—	—	—	—	2	1	—	—	—	—	—	1	1	2	1	4	2	—	—	—	—	—	—	—	—	—	—	—	—	14	—
V. Vattnan	—	—	—	—	—	—	1	2	4	10	3	2	4	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	26.9
Funäsdalsjön	—	—	—	—	—	—	—	—	—	—	—	1	3	3	1	4	4	2	1	—	—	—	—	—	—	—	—	—	—	—	19	31.5
Trammarna [1]	—	—	—	—	—	—	1	2	1	7	16	26	34	28	17	11	9	3	—	—	—	—	—	—	—	—	—	—	—	—	155	29.3
Lossen, large	—	—	—	—	—	—	3	2	9	28	46	54	61	51	28	20	7	2	1	—	—	—	—	—	—	—	—	—	—	—	311	28.8
„ small	—	—	—	—	—	—	—	—	—	1	1	8	13	24	35	47	59	30	22	8	2	1	1	—	—	—	—	—	—	—	250	32.3
Vikarssjön, large	—	—	—	—	—	—	2	5	4	5	6	3	3	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	26.4
„ small	—	—	—	—	—	—	—	—	—	—	—	—	—	3	4	8	7	13	8	7	7	3	2	—	—	—	—	—	—	—	62	34.3
Orten-Randsjön, all	—	—	—	1	1	2	4	7	18	24	21	16	14	11	8	8	7	9	11	7	9	3	2	1	—	2	—	—	—	—	186	—
Orrmosjön, large	—	—	—	4	2	5	6	6	7	3	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36	23.6
„ small	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	6	6	9	7	8	6	2	2	2	—	51	39.8
Härjesjön, large	—	—	—	—	4	1	14	16	4	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	47	23.8
„ small	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	4	3	7	6	6	9	2	1	1	—	—	43	38.9

[1] Lake Trammarna is now part of Lake Lossen.



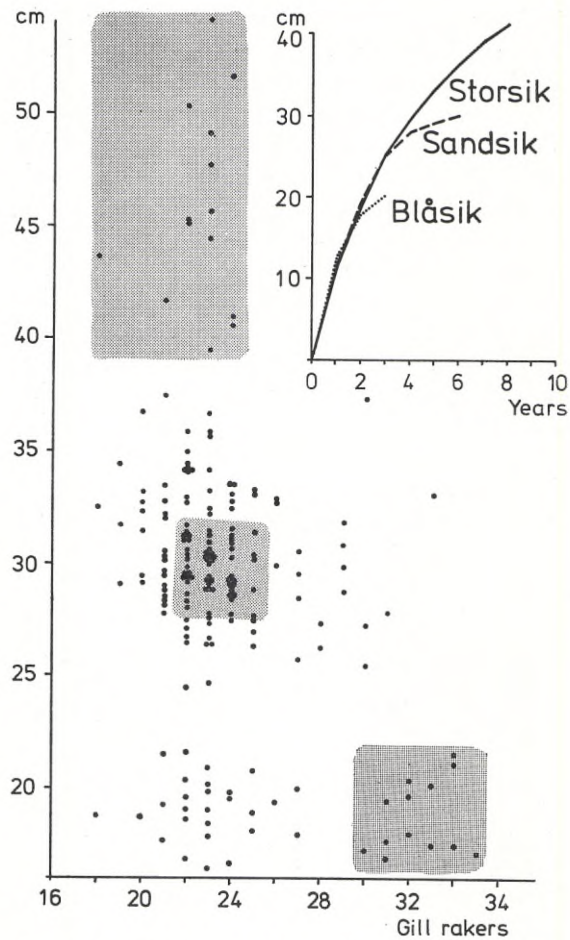


Fig. 25. Gill-raker numbers of whitefish in Lake Östra Vattnan. Subsamples (grey) were used for growth analyses, suggesting three sympatric species (*cf.* Table 22).

that a big whitefish had a special spawning ground, separated from those of two other populations. Because of the thick ice, gill nets could not be set on the shallow spawning ground but only about 50 m away, where straying storsik got caught. In all nearly two hundred fish were taken, the majority of which were the medium-sized sandsik with 21—25 rakers. A minority group consisted of blåsik under 20 cm with some 31—34 rakers (this population is known to be dense). The final minority group was made up of the large-

Fig. 24. Gill-raker numbers of small- and medium-sized whitefish in Lake Nedre Särvsjön (*cf.* Table 22).

sized storsik roaming about the spawning ground. They had 21—24 rakers and could be identified only by their growth rate (Fig. 25).

Lake Harrsicklingen between the two Vattnan lakes has a sandsik and a blåsik population. Lake Västra Vattnan seem to have a rather introgressed sandsik x blåsik stock.

Further downstream the Ljusnan river, the biggest lake is Lossen, populated by two whitefish stocks. The larger fish are sandsik and the smaller are blåsik. However, the gill-raker counts, 28—29 and 32, clearly indicate considerable introgression, though the growth rates keep the two populations apart so that they can easily be separated by the fishermen.

The local conditions for mutual gene flow are less favourable in Lake Vikarsjön, further downstream, where the sandsik has 26 and the blåsik 34 rakers. Still further downstream the Ljusnan the river widens to form the long lakes Orten-Randsjön. Some 180 fish from these lakes are broken down into size and raker categories in Fig. 26, from which it can be seen that there is still a storsik group, a sandsik majority group (25—28) and a small-sized blåsik group with 34—37 rakers.

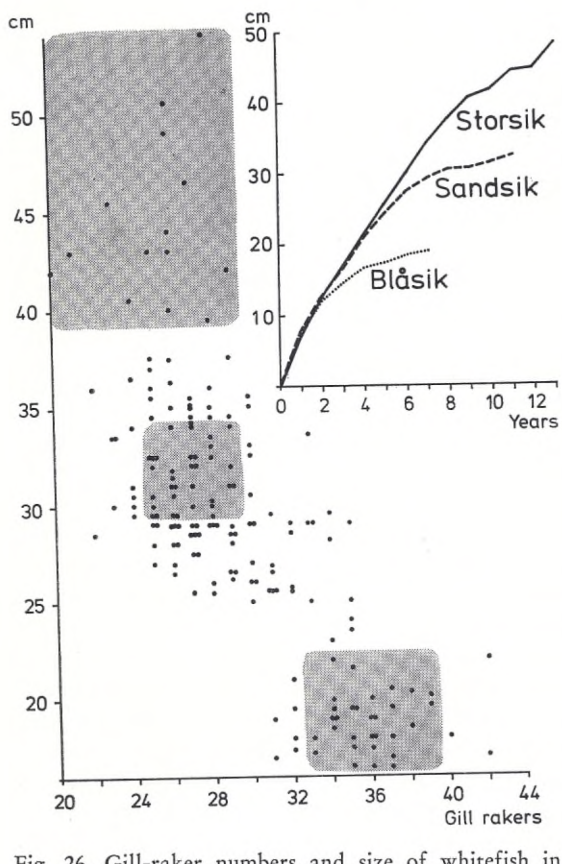


Fig. 26. Gill-raker numbers and size of whitefish in the lakes Orten-Randsjön, Ljusnan river. Subsamples, analysed for growth rates (grey) suggest three sympatric species (*cf.* Table 22).

The Härjeån stream

The general ousting process where blåsik swamps and eliminates the planktonsik is in full swing in the Särvån tributary, is over or has never occurred in the Ljusnan proper (*vide infra*) but conceivably has not started in the third tributary, the Härjeån. Waterfalls or rapids may be responsible for the sheltering of planktonsik in this stream. As proved by Lakes Härjesjön and Orrmosjön (altitude 433 m) the small planktonsik has 40 or 39 rakers (Table 22).

The sandsik is undoubtedly the main stock of sparsely-rakered whitefish in these lakes of the Härjeån tributary. But scales of the larger specimens again suggest the existence of storsik as a rare fraction. Fish of 40—45 cm total length were found to be either 13—15 years of age or only 5—9. This highly irregular growth pattern is the same as that found in several other lakes where the more abundant and competitive sandsik swamps the larger storsik, with its more long-lasting growth but slower generation turnover (Fig. 27).

The drainage of upper Ljusnan is a well-known site for decaying glaciers during the final stage of deglaciation. They have melted *in situ*, creating large areas of dead-ice landscape, with characteristically fringed mini-lakes. The distribution of the four whitefish species between the three rivers (Särvån, Ljusnan, Härjeån) suggests the order of colonization. The storsik and the planktonsik were probably the first arrivals, as can be deduced from upper lakes in several other big rivers. If the planktonsik was the very first, it could have climbed the Särvån and the Härjeån but not the Ljusnan proper (including the Mysklan), where the glaciers still blocked the passage. The storsik was next and could penetrate all three streams and climb close to the ice in the Mysklan because

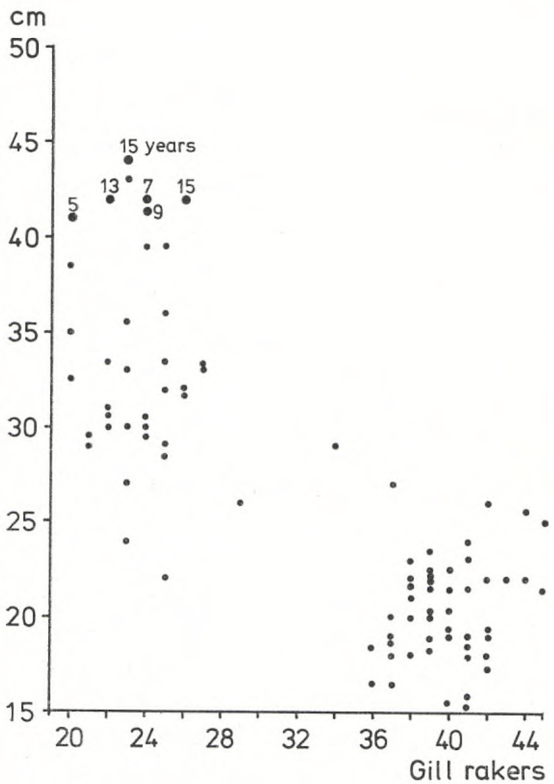


Fig. 27. The age variation of similar-sized sparsely-rakered whitefish of Lake Orrmosjön suggest two populations, living sympatrically with the small-sized planktonsik with 40 rakers (*cf.* Table 22).

of its general adaptation to cold conditions. Next came the sandsik and blåsik pair, of which the blåsik is known to run in streams for spawning and to force its way in rapids. The sandsik might have been the third species to arrive, since it climbed the steep Härjeån (from 350 to 430 m altitude) but not the Särvån (from 400 to 650 m). Finally came the blåsik, which was capable of forcing its way upstream the Särvån and even of sending an "advance party" into Lake Övre Särvsjön, while the Härjeån stream was definitively impassable because of new falls and rapids.

Introgression complexities of the Gimån lakes

The Gimån river is the largest tributary to the Ljungan river. Its headwater lake, Locknesjön, was the first to be presented in the series of selected whitefish lakes. The Gimån is populated by the four species storsik, sandsik, blåsik and planktonsik, just as is the upper Ljusnan river. All except the blåsik are native in Locknesjön and in this section the complexities that stem from the addition of the blåsik species will be discussed.

The Ljungån tributary

The Gimån river receives the Ljungån tributary from the north (Fig. 28). Within this tributary three lakes will be discussed, *viz.* Stora Övsjön, Sicksjön and Ansjön. The Kälarne field station is situated close to Lake Ansjön, and its ponds are fed by water from the outlet stream.

Lake Stora Övsjön is populated by a planktonsik deme with 41 gill rakers. Its altitude is not high (282 m) but the lake has obviously been hard to reach for penetrating fish, possibly because of a too narrow outlet stream. Arctic char survives here, which is a rare situation in the area (*cf.* Locknesjön). The occurrence of planktonsik with 41—42 rakers in the two headwaters Locknesjön and Stora Övsjön suggests that this species was the earliest colonist of the Gimån river valley, as was also the case in the upper Ljusnan lakes (as well as in lakes of the upper Hårkan tributary of the Indalsälven river).

The planktonsik of Stora Övsjön is known by the local people to be split into larger and smaller fish. When spawners above 305 mm size were separated from other spawning fish, of less than 300 mm, a slight gill-raker difference appeared (Table 23). Svärdson (1958, p. 235) commented upon this fact and suggested that a small-sized species with many rakers was just about to terminate a swamping process of another population with slightly fewer rakers.

There is, however, a striking similarity to the situation of the Särvsjön lakes in the upper Särvån, where an "advance party" of penetrating blåsik, from Nedre Särvsjön, have pushed upstream into Övre Särvsjön and are swamped, as far as gill rakers are concerned, but not as regards growth tendencies. The Övsjön might thus as well be looked upon as the very first step of an evolutionary process where the successful blåsik species enters a new lake, which will be taken over later if and when more colonists arrive.

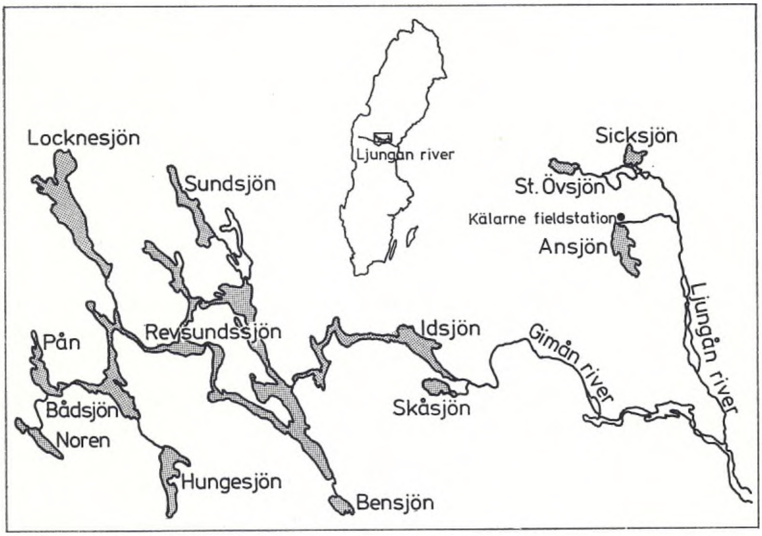


Fig. 28. Map of lakes within the Gimån river (*cf.* Tables 23—25).

More blåsik colonists have certainly arrived in Lake Sicksjön to enable the species to multiply in spawning crowds of its own. When their number is sufficiently high the situation becomes reversed, blåsik can now invade the spawning schools of planktonsik and start the genetic swamping. This process seems to be far advanced in Lake Sicksjön (Table 23), where the local people know only one kind of "smäling" (small whitefish), while the gill rakers of the samples indicate that there is an admixture of two groups of spawners or, alternatively, one single gene pool, derived from both blåsik and planktonsik.

In Lake Ansjön (Table 23) the blåsik and planktonsik have established a sort of compromise, where the larger fish, more than 25 cm long and with 33—34 rakers, have one or two spawning grounds of their own, while the more abundant, and smaller, fish with 36—37 rakers, have several spawning sites around the lake. Of more than 3,000 investigated specimens from Lake Ansjön, none had as many as 45 rakers while in Lake Sicksjön 5 specimens (out of 900) had that number or more. This fact suggests that more planktonsik genes remain in Lake Sicksjön but, judging from the relative frequency of the twin populations in the two lakes, the planktonsik of Ansjön is the more abundant.

The sparsely-rakered whitefish are non-existent in Lake Stora Övsjön and are rare and only sporadically caught in Lake Ansjön, but they have built up an exploitable population in Lake Sicksjön. Age and growth studies indicate that they are a deme of sandsik. The larger storsik species may never have colonized the Ljungån tributary or, alternatively, it has later been completely eliminated by competing species.

The Gimån proper

There are several clusters of lakes downstream of Locknesjön (Fig. 28) all of which have two or three sympatric whitefish species. No lake has a population of cisco, which has not penetrated the Gimån up to this altitude.

The Lakes Noren, Pån and Hungesjön all run into Lake Bådsjön. They all have a large, rare sparsely-rakered whitefish, which presumbly is a storsik. It has been sampled only in Bådsjön (Table 24) but is stated by the local people to exist in the other lakes as well. The abundant whitefish is small and has 31 rakers in Bådsjön and Hungesjön, 33 rakers in Pån and 37 in Noren (altitude 348 m as against 307 m for Bådsjön). This conforms to the general picture of blåsik (31—33) ousting the planktonsik (37).

The next group of lakes consists of Sundsjön and Bensjön which run into the large Lake Revsundssjön. Sundsjön has two populations, one

Table 23. *Gill rakers of whitefish samples from lakes within the Ljungån tributary.*

Rakers / Sample	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	n	x̄
River Ljungån																																			
St. Övsjön																																			
Jan. 1956 < 30 cm	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5	5	13	17	17	23	12	13	3	1	2	113	41.2
„ 1956 > 30.5 cm	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	2	2	9	7	12	7	8	8	3	—	—	—	61	40.0
Sicksjön																																			
Jan. 1950	—	—	—	—	—	—	—	—	—	—	—	—	1	3	2	9	12	9	12	11	14	6	4	4	2	2	1	2	—	—	1	—	—	94	33.6
Febr. 1951	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2	3	4	6	5	4	—	1	2	2	3	—	1	3	—	—	—	38	35.9
„ 1953	—	—	—	—	—	—	—	—	—	—	—	—	1	3	3	8	10	17	26	19	24	14	10	9	6	2	1	1	1	3	1	1	—	160	34.5
„ 1954	—	—	—	—	—	—	—	—	—	—	—	—	1	3	4	14	18	10	17	14	16	10	4	3	1	1	1	—	1	—	—	—	—	118	33.1
„ 1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	1	6	16	21	14	11	10	3	5	1	4	3	4	3	—	1	—	—	107	34.6
„ 1956	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	10	19	13	17	15	14	17	11	3	3	—	3	1	1	—	—	—	1	129	34.1
Jan. 1951	—	—	—	—	1	2	2	3	3	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	22.6
„ 1954	—	—	—	—	2	6	11	5	8	7	7	10	2	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	23.4
„ 1955	—	—	—	—	1	1	4	11	4	7	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	22.7
„ 1956	—	—	—	2	—	5	6	12	20	16	9	3	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	75	23.1
„ 1960	—	—	3	3	3	11	11	12	16	7	6	3	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	76	22.0
Ansjön																																			
Febr. 1951	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3	11	14	17	16	13	12	12	5	1	—	—	—	—	—	106	36.9
„ 1952	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	4	4	3	5	1	1	1	—	—	—	—	—	21	37.8
„ 1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	12	20	20	24	29	31	22	13	2	3	—	—	1	—	—	—	180	35.8
„ 1953 [1]	—	—	—	—	—	—	(1)	—	—	—	(1)	—	—	—	1	2	6	13	20	28	28	18	12	4	3	1	—	—	—	—	—	—	—	136	34.4
Jan 1954 [1]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5	6	9	13	21	19	5	5	3	2	1	—	—	—	—	—	—	—	91	33.9
Febr. 1955 [1]	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	2	6	9	7	8	11	8	6	1	—	1	—	—	—	—	—	—	—	63	33.7
„ 1955	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	4	3	10	17	18	36	38	41	26	21	7	2	2	1	—	—	—	—	228	36.0
„ 1956 [1]	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	5	8	8	21	10	6	12	2	1	2	—	—	—	—	—	—	—	—	78	33.4
„ 1956	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	8	3	11	16	24	18	9	16	5	2	—	—	—	—	—	—	—	115	35.2
„ 1958 [1]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	7	12	11	8	3	3	6	2	—	—	—	—	—	—	—	—	—	55	33.4
„ 1964	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	10	24	29	32	49	57	42	29	11	6	4	2	—	—	—	—	300	36.4
„ 1965	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	5	16	26	31	61	47	32	41	25	7	3	1	—	—	—	—	—	300	35.7
„ 1966	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3	4	8	22	35	47	44	46	36	31	14	3	4	—	1	—	—	—	300	36.2
„ 1967	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	7	14	21	27	43	37	34	48	30	18	13	—	—	—	—	—	—	300	36.4
„ 1968	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	5	14	19	27	45	46	47	35	31	16	11	4	1	—	—	—	—	304	36.3
„ 1969	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	2	8	12	27	37	51	45	42	38	22	7	2	1	1	—	—	—	299	36.7
„ 1970	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	4	7	11	21	25	34	46	43	48	26	19	5	2	1	—	—	—	—	292	36.3
„ 1972 [1]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5	3	2	1	—	—	—	—	—	—	—	—	—	—	13	34.6
Jan. 1973 [1]	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	4	—	2	2	1	1	—	—	1	—	—	—	—	—	—	—	11	34.5
„ 1974 [1]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	1	—	—	—	2	—	—	—	—	—	—	—	—	—	6	34.2

[1] Spawners larger than 25 cm.

Table 24. *Gill rakers of whitefish samples from lakes of the Gimån river.*

Rakers / Sample	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	n	x̄
Noren, Dec. 1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	7	7	19	17	16	6	5	1	1	1	—	—	—	—	—	82	37.0
Pån, Dec. 1955	—	—	—	—	—	—	—	—	—	—	—	1	2	8	8	12	17	14	14	14	8	6	2	1	1	—	—	—	—	—	—	—	—	108	33.0
Hungesjön, Jan. 1956	—	—	—	—	—	—	—	—	—	1	1	3	7	8	6	15	12	11	9	4	3	2	1	—	—	—	—	—	—	—	—	—	—	83	31.5
Bådsjön, Dec. 1955	—	—	1	—	3	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	20.9
,, ,, 1955	—	—	—	—	—	—	—	—	—	—	1	1	5	8	12	8	10	8	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	61	31.0
Bensjön, Jan. 1957	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	8	8	14	13	8	6	1	3	—	—	—	—	—	—	—	—	—	—	64	33.5
Sundsjön, Jan. 1951	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	2	4	10	9	7	6	4	1	3	—	—	—	—	—	—	50	37.2
,, ,, 1951	—	—	1	—	2	2	3	2	4	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	22.4
Revsundssjön, Oct. 1960	—	—	1	2	3	1	2	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	21.1
,, Febr. 1971	—	1	1	1	7	4	8	3	6	—	3	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	22.6
,, Jan. 1973	—	2	5	5	16	14	18	10	9	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	84	21.5
,, ,, 1974	—	—	2	5	8	21	17	11	13	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	83	22.0
,, ,, 1951	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	3	2	7	13	18	14	8	3	1	1	—	—	—	—	—	—	74	36.7
,, ,, 1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	2	11	12	16	14	19	7	4	—	2	2	—	—	—	—	—	93	36.6
,, ,, 1971	—	—	—	—	—	—	—	1	2	7	11	25	37	48	66	51	35	14	9	3	4	2	1	—	—	—	—	—	—	—	—	—	—	316	29.9
,, ,, 1974	—	—	—	—	—	—	—	—	—	1	8	8	10	13	16	14	6	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	80	29.3
Skåsjön, Jan. 1957	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	13	18	22	27	13	4	5	4	—	—	—	—	—	—	109	37.4
,, ,, 1971	—	—	—	—	2	9	7	8	7	10	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	23.3
,, ,, 1973	—	—	—	—	—	1	1	2	2	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	24.0

medium-sized with 22 rakers and one small-sized with 37, while Bensjön has one population of 33—34 rakers. Revsundssjön has been sampled more often and is known to be inhabited by three populations: one large-sized with 21—22 rakers, one medium-sized with 36—37 and one dwarf with 29—30 rakers and a terminal mouth.

Within this cluster of lakes, Sundsjön is the only one without blåsik and it is inhabited by sandsik. The tendency of blåsik to have a detrimental effect on sandsik is also seen elsewhere (the Dalälven river system, the Arjeplog lakes etc.). The Bensjön population of blåsik is more or less pure, while that of Revsundssjön may have included sandsik genes to give it its low average (29—30).

Further downstream lie Lakes Idsjön and Skåsjön (Fig. 28), of which Idsjön probably is the most often discussed of all Swedish whitefish lakes. The three populations of this lake were described in detail (SVÄRDSON 1953, 1970), although the now obsolete species names of the 1953 paper were exchanged for the letters A, B and C in the 1970 paper. Selection of extreme parent fish within the B species gave progenies with clearly different gill-rakers numbers (SVÄRDSON 1958). All samples available are summarized in Table 25 for Idsjön and Table 24 for Skåsjön.

The three Idsjön species have 20—21 rakers (large fish), 36—37 rakers (medium-sized) and 26—27 rakers (dwarfs), while those of Skåsjön have 23—24 rakers (medium-sized) and 37—38 rakers (small).

Again, as in Lake Sundsjön, the two species blåsik and sandsik are mutually exclusive in Skåsjön. The key interpretation is that the blåsik, for whatever reason, has not succeeded in colonizing Skåsjön. This fact in turn has enable the sandsik population to survive alongside the planktonsik population. Even the storsik actually still survives in Skåsjön where some stray large whitefish with few gill rakers are found, having a growth curve quite distinct from that of the sandsik (Fig. 29).

Lake Idsjön is inhabited by storsik, a deviating blåsik stock and a medium-sized river-spawning population of planktonsik; there is no sandsik. The dwarfed blåsik with a terminal mouth and only 26—27 gill rakers is outstanding for its few rakers. The missing sandsik and the exceptionally few gill rakers of the swamping blåsik are conceivably correlated, *i.e.* the genes from the sandsik have caused the exceptional low gill-raker count of the Idsjön blåsik deme. It is interesting to note that this blåsik is a *Bosmina*-feeder in summer and thus has no trace of the benthos-feeding habit of the sandsik. It is a river-spawner but does not run the Gimån more than 50—100 m from the lake, while the planktonsik is a more pronounced stream-spawner.

It seems tempting to suggest that the medium-

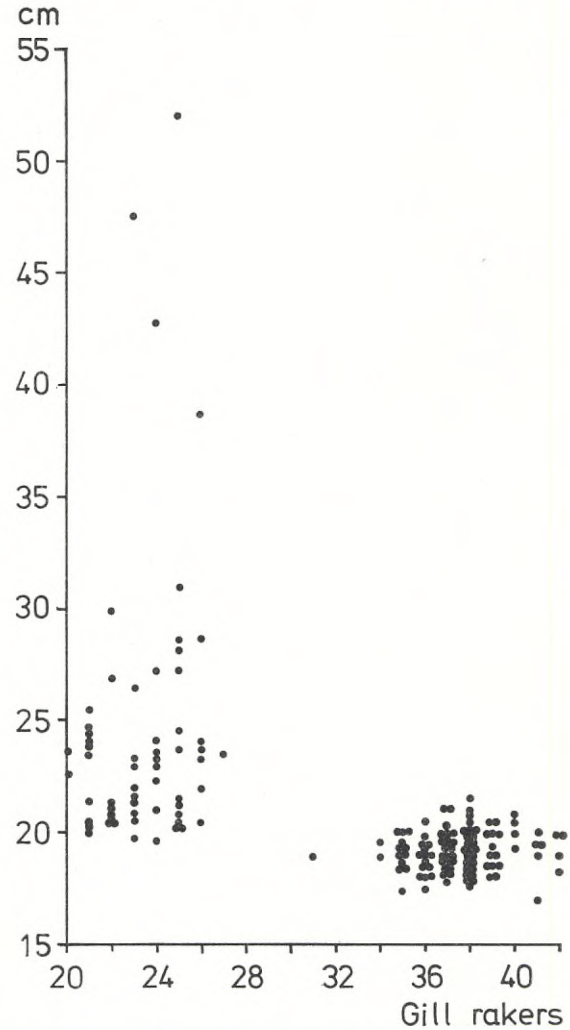


Fig. 29. Gill-raker numbers and size of whitefish in Lake Skåsjön suggest three species, one of which is a rare, large, sparsely-rakered whitefish (*cf.* Table 24).

Table 25. *Gill-raker counts on the three sympatric whitefish species of Lake Idsjön.*

Rakers Sample	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	n	x̄
Storsik																																				
„ 1953	—	—	—	—	—	4	3	3	—	—	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	22.5
„ 1956	—	—	1	4	6	8	6	2	2	2	2	1	—	—	2	—	—	—	—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	40	22.8
Jan. 1952	—	1	4	13	15	31	27	10	5	2	—	2	—	—	1	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	114	20.6
„ 1957	—	1	3	3	4	5	6	2	1	2	—	1	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	31	21.3
„ 1958	1	2	12	8	20	27	18	11	6	1	2	1	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	111	20.2
„ 1959	—	2	9	20	27	51	36	26	17	7	3	1	—	—	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	202	20.6
„ 1960	—	1	5	12	22	21	9	7	2	2	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	84	20.0
„ 1961	—	—	1	4	7	15	11	11	6	3	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	21.1
„ 1962	—	—	—	2	8	14	9	9	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	20.9
„ 1963	—	—	3	10	11	13	14	8	3	4	—	—	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	70	20.8
„ 1964	—	—	1	3	3	7	3	3	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	20.7
„ 1965	—	—	1	4	3	5	1	4	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	20.6
„ 1967	—	—	1	3	5	12	7	7	5	2	—	—	—	—	2	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	46	21.6
„ 1968	—	—	—	—	3	3	2	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	20.8
„ 1969	—	—	—	1	2	5	4	4	—	—	—	—	—	—	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	20	22.8
„ 1970	—	—	—	1	3	4	6	3	3	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	21.6
„ 1971	—	—	—	1	—	1	2	4	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	22.0
Nov. 1972	—	1	3	2	6	8	16	7	6	1	—	—	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	21.1
„ 1973	—	—	—	1	3	1	6	3	—	—	—	—	1	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	22.4
Planktonsik																																				
Nov. 1947	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	3	2	4	3	5	2	—	—	1	—	—	—	—	—	—	23	36.3
„ 1948	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	3	9	11	13	24	12	8	8	3	3	—	—	—	—	—	—	—	97	35.9
„ 1950	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	5	3	8	11	10	7	3	3	1	—	1	—	—	—	—	—	—	55	35.3
„ 1954	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	11	18	34	38	51	51	35	28	15	13	2	1	—	—	—	—	—	300	36.4
„ 1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	11	27	36	44	46	59	37	23	9	2	2	—	—	—	—	—	—	300	36.0
„ 1974	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	4	5	11	5	11	6	3	4	—	—	—	—	—	—	—	50	37.9
„ 1978	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	2	3	8	18	29	47	58	45	35	18	9	—	1	—	—	—	—	—	276	36.9
Blåsik																																				
Dec. 1950	—	—	—	—	—	—	1	3	4	6	12	11	8	4	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	52	25.5
„ 1952	—	—	—	—	—	—	—	2	4	15	24	21	18	13	5	7	1	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	114	26.4
„ 1954	—	—	—	—	—	—	5	13	28	34	66	55	49	31	13	7	2	2	—	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	308	25.8
„ 1955	—	—	—	—	1	1	2	10	21	50	55	61	42	31	15	5	4	2	—	2	1	2	1	—	—	—	—	—	—	—	—	—	—	—	306	25.9
„ 1956	—	—	—	—	—	—	5	11	28	42	62	79	51	35	22	10	8	3	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	358	26.0
„ 1970	—	—	—	—	—	—	3	9	14	49	60	55	55	53	22	20	12	4	3	1	2	1	—	2	—	—	—	—	—	—	—	—	—	—	365	26.6
„ 1971	—	—	—	—	—	—	2	—	6	23	15	27	36	38	18	27	17	16	10	3	1	1	1	—	—	—	—	—	—	—	—	—	—	—	241	28.0
„ 1974	—	—	—	—	—	—	1	3	14	22	30	28	36	29	16	9	4	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	198	26.5
„ 1975	—	—	—	—	—	—	—	6	15	22	33	34	42	34	28	17	11	2	3	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	251	27.0
„ 1976	—	—	—	—	—	—	3	4	5	24	38	50	48	27	20	16	7	7	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	250	26.7
„ 1977	—	—	—	—	—	—	—	1	7	18	21	23	29	21	18	20	7	3	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	172	27.2
„ 1978	—	—	—	—	1	2	1	6	14	26	42	45	57	42	20	15	11	9	4	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	296	26.8

sized planktonsik of the Gimån proper, which is fairly common in most of the lakes in spite of the fact that a modified blåsik lives sympatrically, is in fact a balanced hybrid of the two species. Of course, it might very well have happened that after the first colonization wave of pure planktonsik (41—42 gill rakers) up through both branches of the Gimån, there came a second, later wave of a stabilized hybrid with about 37 gill rakers. At the same time the blåsik introgressed to the sandsik, and swamped it, but got some of its genes incorporated in its pool and became a less formidable competitor. If so, the blåsik population of the Gimån proper came to be slightly different from that of the Ljungån tributary. Blåsik is larger than planktonsik (and has more than 30 rakers) within the Ljungån river, while blåsik is smaller than planktonsik (and may have fewer than 30 rakers) within the Gimån proper.

This interpretation is speculative and can be tested only by future methods of investigation. It seems a paradox, however, that the most studied lakes (Ansjön and Idsjön) have whitefish populations which are hard to fit into the specific framework.

The spring-spawning cisco, Coregonus trybomi sp.nov.

Svärdson (1957) knew the spring-spawning cisco from three Swedish lakes. It appeared that the species had colonized these lakes from the Baltic Ice Lake (Svärdson 1958) and thus must have come from the east. No other European localities for the species were then known. The cisco form *C. sardinella baunti*, Muchomediarow, from the Tsipikan river of Siberia was described as spring-spawning. The Swedish populations were thus provisionally classified as *baunti*, albeit with specific status, and it was suggested the distribution gap between Scandinavia and Siberia was not real (Svärdson 1957).

Later the spring-spawning cisco was found in some Finnish lakes, in the border zone to the U.S.S.R. (Airaksinen 1968 a, 1968 b). Recently it has been confirmed that no spring-spawning ciscoes are known from the Soviet Republic of Karelia (Y. Smirnov, 1978, pers. comm.). The Siberian *baunti* form has become better known since 1957 and is now found to be neither a cisco nor really a spring-spawner but to spawn in late winter. Shaposhnikova (1974) summarized the work of Anpilova and others to show that *baunti* should be considered a whitefish and ranged in the population series of *C. lavaretus*.

The supposed area of origin for the spring-spawning cisco can now be restricted to a preglacial lake isolation somewhere in the western part of the present U.S.S.R. The time has come to describe formally the spring-spawning cisco as an independent species. It is here given the name *Coregonus trybomi*, in honour of the prominent Swedish fisheries biologist Filip Trybom (1850—1913), who was the first to publish on its existence and to study its morphology (Trybom 1903).

Diagnosis

Similar to *Coregonus albula*, except for morphological consequences associated with rapid embryonic development in spring. These characters cannot be used for identification, except locally by comparison with the sympatric stock of the *albula* cisco. The only diagnostic feature is the linkage of spawning to increasing photoperiod, resulting in reproduction during the first half of May (exceptionally in late April). In the Swedish populated lakes, the ice has long gone when the spring-spawning cisco spawn at a depth of 15—20 m.

Holotype

Museum of Natural History, Stockholm No 798009 (Fig. 30). Ripe female, collected in Lake Ören on May 17, 1978, by Mr Tore Svensson.

Length: total 232 mm, caudal 210 mm, standard 196 mm. Rays: dorsal 11, pectoral 16 (left) and 17, ventral 12 (left) and 11, anal fin 15. Proportions, as per mille of total length: head 175, eye diameter 43, snout length 39, tip of snout to front of dorsal 387. Maxillary extends longer than front of eye.

Scales of lateral line 79, branchiostegals 12, gill rakers of first left arch 39.

Paratypes. Ripe males and females from the same spawning shoal as the holotype are in the collections of the Stockholm Museum No 798010-

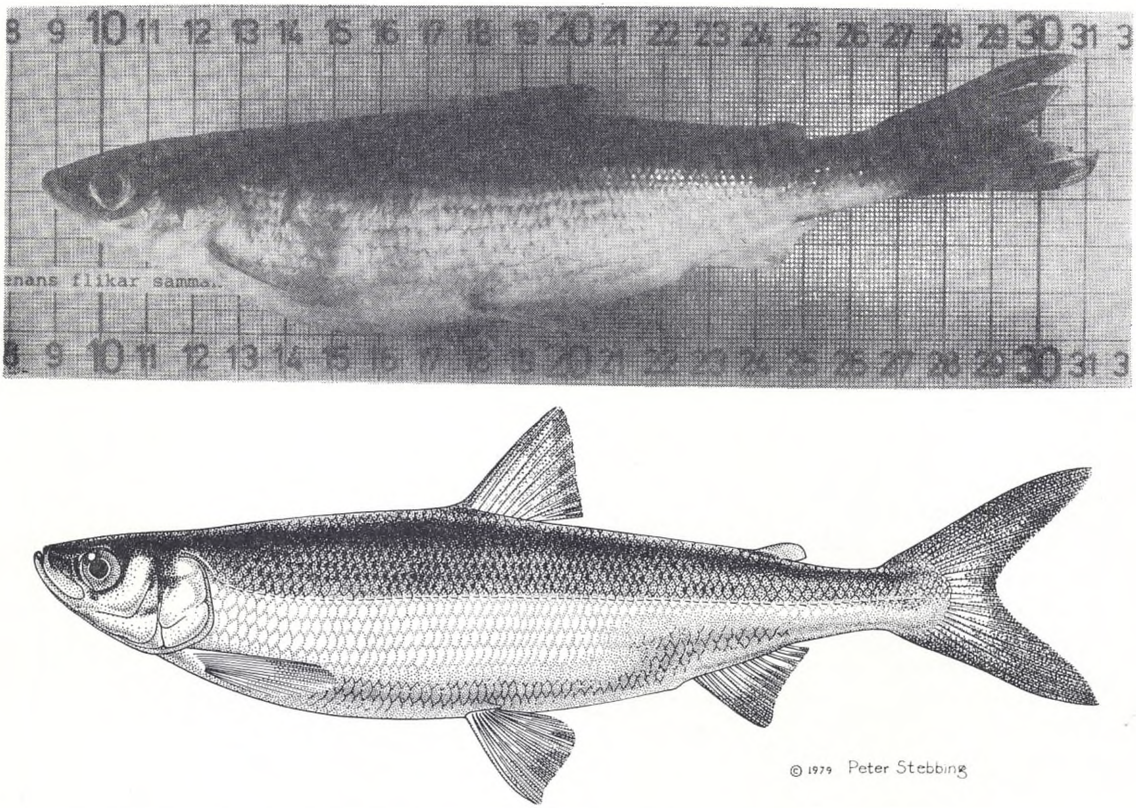


Fig. 30. *Coregonus trybomi, sp.nov.*, holotype (above) and paratype.

13 (females) and No 798014-22 (males). One further specimen was drawn by PETER STEBBING, London (Fig. 30).

Morphology, as population averages of four stocks

Some measurements of the stocks of spring-spawning as well as sympatric autumn-spawning ciscoes from Lakes Stora Hålsjön, Åsunden, Fegen and Ören are assembled in Table 26.

The following characters are specific for *trybomi* in all four lakes: fewer vertebrae, lateral line scales, gill rakers and dorsal rays. It is suggested that these characters are effects of a more rapid development in higher temperature. Vertebrae tend to be fewer in conditions of higher temperature, lower oxygen content of incubation water and lower amount of light penetration (YERMOKHIN 1974). KOELZ (1929) found some evidence of fewer vertebrae in *Coregonus* stocks from warm bays or lakes. The first zone of growth on the scales is narrower in *trybomi* than in sympatric *albula* because of the shorter season of growth. The Fegen stock is most easily separable from the sympatric *albula* by its large eyes and head.

Significance of eye size

Some *Coregonus* species have been named with reference to their strikingly large eye size, *e.g. C. megalops* or *C. macrophthalmus*. Even fishermen often identify a "sort" of whitefish by their eyes, *e.g.* in Lake Vänern. In the case of the spring-spawning cisco, however, only one of its four known Swedish populations is characterized by large eyes (Fig. 31). It appears that the eye size may be strongly influenced by some other factor than heredity. SVÄRDSON (1950) found in experiments that fast-growing progeny of Arje-

Table 26. *Morphological data on the sympatric ciscoes Coregonus albula and Coregonus trybomi, sp.n. in the four Swedish lakes in which they are known to exist.*

Lake	Stora Hålsjön				Åsunden			
Species	trybomi		albula		trybomi		albula	
Date and size of sample	April—May 1939 77 sp		Nov. 1940 62 sp. „ 1953 43 „ „ 1968 62 „		May 1956 9 sp.		Nov. 1968 89 sp.	
Average, st.dev.	x̄	St.dev.	x̄	St.dev.	x̄	St.dev.	x̄	St.dev.
Total length, mm [1]	247	12.4	284	15.5	230	11.9	174	8.0
Vertebrae	55.57	0.94	57.50	1.04	54.22	0.83	55.74	1.55
Number of gill rakers	42.00	1.95	45.25	1.74	44.00	1.87	44.33	1.24
Rays, dorsal fin	10.57	0.62	10.81	0.51	11.22	0.44	11.49	0.66
Rays, anal fin	13.66	0.62	13.11	0.73	13.67	1.00	14.45	0.75
Rays, pectoral fin	14.77	0.81	14.68	0.92	16.55	0.53	15.74	0.90
Eye diameter [2]	—	—	4.69	0.29	4.90	0.45	5.29	0.23
Length of head [2]	—	—	17.62	0.89	17.82	0.99	18.67	0.62
Distance snout—frout of dorsal fin [2]	—	—	38.77	1.87	38.94	2.09	38.81	1.18
Height of body [2]	—	—	19.17	1.55	18.46	1.69	17.98	0.81
Number of lateral line scales	—	—	81.03	3.46	75.00	2.78	79.57	3.95

Lake	Fegen				Ören			
Species	trybomi		albula		trybomi		albula	
Date and size of sample	May 1960 27 sp. „ 1967 10 „ „ 1969 8 „		Nov. 1968 100 sp.		April 1957 100 sp. May 1967 102 „		Nov 1967 75 sp. „ 1968 100 „	
Average, st.dev.	x̄	St.dev.	x̄	St.dev.	x̄	St.dev.	x̄	St.dev.
Total length, mm [1]	150	10.5	156	7.5	219	13.5	205	7.5
Vertebrae	53.24	1.28	56.52	1.26	54.55	1.03	55.19	1.32
Number of gill rakers	42.98	1.45	45.66	1.22	43.79	1.56	44.87	1.54
Rays, dorsal fin	10.96	0.60	11.78	0.63	10.99	0.69	11.58	0.70
Rays, anal fin	13.36	0.86	14.21	0.82	12.95	0.85	14.30	0.91
Rays, pectoral fin	15.62	0.81	16.20	1.26	16.66	0.82	15.71	0.89
Eye diameter [2]	6.73	0.45	5.45	0.30	4.80	0.37	5.12	0.25
Length of head [2]	20.04	1.11	18.99	0.69	17.92	0.64	18.84	0.74
Distance snout—frout of dorsal fin [2]	38.04	1.47	40.01	1.44	40.08	1.60	40.46	1.19
Height of body [2]	17.92	1.39	18.84	1.90	18.14	1.37	17.12	1.83
Number of lateral line scales	76.22	3.31	77.11	3.50	76.32	3.22	81.61	4.07

[1] Size fluctuates over the years. On the whole the two sympatric ciscoes are of equal size.
[2] % of total length.

plog whitefish had much smaller eyes than their more slow-growing parents. The progeny had grown in warmer and shallower water.

McLaren (1963) found for plankton (*cf.* Baker 1978) and Brett (1971) for fingerling sockeye that there were metabolic gains if the feeding took place in warmer, upper layers of water while the processing of food occurred in deep water of low temperature. A daily vertical migration should optimize the metabolism for growth and survival. The cisco has such a vertical diel movement in a pronounced degree.

Elliott (1975) studied the effects on growth of reduced food ration for brown trout kept in various temperatures. For smaller fish the energy budget became progressively more favourable for growth in lower temperature, when the ration was reduced. In nature the food ration should certainly

Fig. 31. *Coregonus trybomi* (below) from the large-eyed population of Lake Fegen, compared to the sympatric *albula*.

be reduced in a situation of competition between two species, one of which is dominated by the other (SVÄRDSON 1976). To stand this competition better, the dominated population can have a better energy budget if it withdraws to deeper and colder water. It appears that the spring-spawning cisco, or other pelagically living populations which are poor competitors, actually developed habits better suited to deep living, enlarged eyes being part of the general adaptation. The proximal factor for developing large eye size may be low light intensity, cold environments, reduced food ration, or a combination of these parameters. ELLIOTT (*op.cit.*) found larger trout to be less sensitive than small fish to the correlation between reduced food ration and better growth in low temperature. It is interesting to find that deep-living pelagic *Coregonus* populations generally tend to be dwarfed. This seems to be a further adaptation, the purpose being to save energy, not primarily for growth but for production of large and relatively numerous eggs.

History of discovery

On April 11, 1903 Mr MAURITZ STENBERG took three not quite ripe *trybomi* specimens from Stora Hålsjön to Dr TRYBOM. He knew the common cisco from elsewhere and was most surprised that Stora Hålsjön had two sympatric ciscoes, one of which spawned around May 1 and was intensively exploited by the local fishermen. In November of the same year he supplied TRYBOM with specimens of the sympatric autumn-spawning population.

TRYBOM could find no morphological difference between the two populations. He noted that there were no counterparts described in the literature (except in herring) and concluded that some unknown but unique hydrological regime might prevail in the lake. He refused to give the two ciscoes specific, as even subspecific status (TRYBOM 1903).

EKMAN (1909) mentioned in passing that Lake Ören, in which he studied the arctic char, had, according to the fishermen, two distinct ciscoes, one of which was spring-spawning. EKMAN mentioned the similarity to the Stora Hålsjön case but seems to have later ignored the problem in his famous zoogeographical book on the Scandinavian fauna (EKMAN 1922).

RUNNSTRÖM (1941) sampled both ciscoes in Lake Stora Hålsjön in 1939 and 1940 and obtained fertilized eggs from the fisheries consultant ELIS SKOGLUND. Three specimens were caught in Lake Åsunden in April 1939, at a depth of 30 m. RUNNSTRÖM described the differences in number of vertebrae and fin rays between the two — as he interpreted them — subspecies of cisco.

SVÄRDSON (1949) pointed out that the spring-spawning cisco was a biological species and could not have originated in the present localities but must have evolved elsewhere. RUNNSTRÖM and SVÄRDSON (1956) summarized further material and called for more local observations.

In 1960 it was proved that Lake Fegen, downstream the Åsunden, was also inhabited by *trybomi* (SVÄRDSON 1960). Since then, Mr GÖSTA MOLIN, fisheries consultant of the Drottningholm Institute, has performed exploratory fishing in fifteen different lakes of the area, searching in vain for the *trybomi*. So far only four lakes are known to be inhabited.

Lake Hålsjön belongs to the Viskan river system, Lakes Åsunden and Fegen to the Ätran river. The Viskan and Ätran rivers run to the Kattegatt. Lake Ören, however, belongs to the Motalaström river system, draining to the Baltic.

AIRAKSINEN (1968 a, 1968 b) reported twin cisco species of Lakes Änättijärvi, Sokojärvi and Kajoonjärvi in East Finland. The last-mentioned two lakes have a spring-spawning cisco, while Änättijärvi has a winter-spawning population alongside the normal autumn-spawning one. Other lakes of the area have allopatric winter-spawning ciscoes.

The Finnish populations are probably conspecific with the *trybomi* species but should be studied further in order to confirm the actual spawning periods.

Conservation

The *trybomi* stocks of Lakes Hålsjön and Åsunden are threatened by extinction because of pollution, while that of Fegen is sparse and the whole lake is becoming acid (LESSMARK 1976). Lake Ören seems to have the best prospects of conserving the *trybomi* species.

Postglacial spread

The *trybomi* cisco has such a restricted geographical distribution in Sweden that its postglacial dispersal can be fairly accurately outlined. In the Allerød period (11,750—10,950 yr BP) the threshold between Onega and the White Sea was probably lifted above sea level, creating the Baltic Ice Lake (MÖRNER *et al.* 1977). During the same period, a gigantic tongue of the Baltic glacier, extending from Gotland to Bornholm and the German coast, had vanished. Between the Taberg and Skövde stages, within the Younger Dryas period (10,950—10,000 yr BP), or roughly 10,700 yr BP, a local tongue of ice covered the Vättern basin, separating proglacial lakes east and west of the tongue (LUNDQVIST and NILSSON 1959). The former lakes drained to the Baltic Ice Lake, while the latter ran to the Kattegatt.

About 10,700 yr BP, when freshwater fish could first spread across the Baltic basin, one or several such proglacial lakes, running east, must have been colonized by a fish fauna comprising arctic char, a sparsely-rakered whitefish, two ciscoes and smelt. The char was probably the first to cross, as is indicated by its survival in Lake Mycklaflon (Emån river) where none of the other species followed.

Further downstream the Emån, a sparsely-rakered whitefish as well as autumn-spawning cisco colonized Lake Nömmen. Smelt, which is a very poor climber in river valleys and therefore a relict (EKMAN 1922) of ancient shores, managed to colonize Lakes Östra Lägern and Västra Lägern.

A modern remnant of the east-running proglacial lakes of this period is Lake Ören, where the char, smelt, sparsely-rakered whitefish and the twin cisco species have all survived. The altitude (196 m) is very high indeed for smelt and Ören, like the Lägern lakes (198 m) is an exception to the rule established by EKMAN of absence of smelt above the highest shores.

A crucial period came when the ice tongue of the southern Vättern basin had disappeared and the mighty glacier lay straight across the basin in the Skövde phase of Younger Dryas, 10,400 yr BP. Lake Ören was now isolated, but the local Vättern Ice Lake was higher than the present Vättern and some of its water and fish fauna spilled westwards when the glacier withdrew from some critical passpoint on the western shore of the basin. Then the fish slipped into local lakes, the headwater of the time for the rivers Ätran and Viskan and, possibly, there were more western drainages into what is now part of the Göta river system. Then the two ciscoes, the sparsely-rakered whitefish and the smelt could colonize Lake Stora Hålsjön, where smelt is again an exception to the EKMAN rule. The three *Coregonus* species, but not the smelt, spread downstream the Ätran river where they survive in Lakes Åsunden and Fegen (Fig. 32). The char certainly also spread west but has happened not to survive sympatrically with the whitefish and ciscoes but only allopatrically in Lake Östra Nedsjön and some other small lakes of this area.

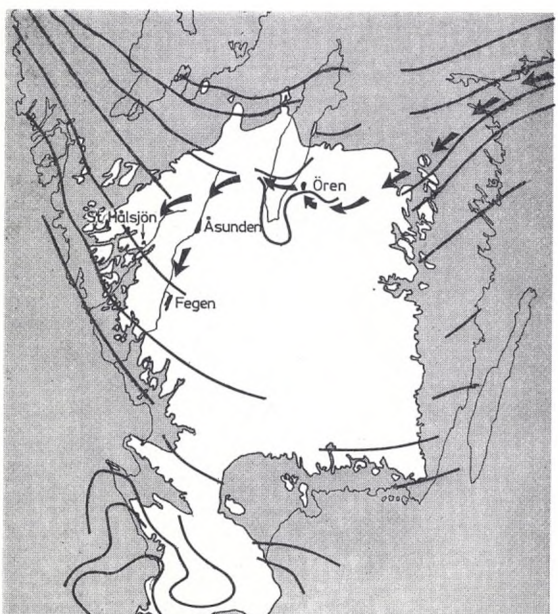


Fig. 32. The suggested route of dispersal when *Coregonus trybomi* arrived in its present lakes during the Younger Dryas period, *c.* 10,400 yr BP.

Probable origin

For freshwater fish that have to survive a long winter of partial starvation, the fingerling size of first autumn is critical. It follows that arctic or subarctic fish tend to spawn already in autumn or during winter to enable the fry to hatch at the earliest possible time and maximize the growing potential of the first summer (NORDQVIST 1903, EKMAN 1922). If, however, enough time is available for first summer growth, the drawbacks of a slow embryonic development during winter are overwhelming. Spring spawning is thus the rule for warm-water fish species.

Spring spawning is obviously exceptional for a cisco. It follows that the *trybomi* species must have evolved in a much warmer environment than is normally experienced by the cisco. Its forebears must certainly have been spawning in autumn or winter.

The Eem interglacial was warmer than the present one. According to the supposed distribution of land and sea of that time (FLINT 1971, p. 630) Scandinavia, including part of Finland, was then an island. The Eem Sea covered the Baltic basin and vast areas of present north-western U.S.S.R. Some large lakes, and presumably also small ones, existed south-east of the Eem Sea.

If ciscoes from the Arctic coast spread, after a pre-Eem glaciation, some of them may have been isolated in warm lakes during the Eem interglacial and then become transformed into spring-spawners by local selection. During the Weichsel period of glaciation some of these populations may have been selected back to at least winter spawning habits while others were able to retain their spring spawning. The local climate, predation, and the competition pressure from other planktophagous fish should have influenced the outcome of this evolution.

In the postglacial warming up during the Allerød period, the *trybomi* could have slipped from proglacial lakes somewhere in present west or northwest U.S.S.R. into the Baltic Ice Lake and later spread to Scandinavia. The secondary contact with *albula* might have been rather late, since the occurrence of only autumn-spawning ciscoes in the Emån river drainage could indicate that the *albula* cisco was the first to traverse the Baltic. At about the same time the Finnish lakes with *trybomi* became isolated as independent bodies of water.

V. DISCUSSION

What is a Coregonus species?

The theory of speciation is now well integrated into the general theoretical framework of the biological mechanisms of evolution. For bisexual vertebrates, speciation theory states that populations in geographical isolation evolve according to the selection enforced by the environment (biotope, climate, predators, competitors). Incipient isolating mechanisms evolve as part of the general diversification. This first step of speciation involves geographical subspecies. In the case of freshwater fish, where local isolation is often pronounced, a group of local demes, of similar characters sharing a common progenitor, together constitute one subspecies. The pollan populations of Ireland are a good example (Ferguson *et al.* 1978).

When formerly isolated populations meet secondarily, the incipient isolating mechanisms reduce the gene flow. Hybrid imbalance or sterility reinforce the isolating barriers in the zone of overlap, reducing the wastage of gametes that produce hybrids. This stage gives the population semispecies status (Ayala 1978).

In a final stage, the two populations can no longer produce fertile hybrids in nature. They are then fully-fledged species and their subsequent evolution is independent and irreversible.

When the speciation theory is applied to the genus *Coregonus*, there are some striking complications.

Whitefish and cisco have — since Linnaeus — been treated by all systematists as two clearly distinct species. Some writers have even been inclined to give them separate generic status. Except for some stray specimens they usually do not hybridize in sympatry. Sympatric populations, however, are fertile when artificially crossed, as is proved by the Lake Åsnen case (p. 60). The hybrid stock is capable of self-reproduction, though in later generations the cisco genes are selected against and seem to be weeded out. At any rate the gill rakers (p. 59) and some proteins indicate that such a process occurs (Ferguson *et al.* 1978). Gasowska (1958) also found fertile whitefish x cisco hybrids and she discussed their morphology at some length.

Sympatric whitefish and cisco of Lake Orrevann, Norway, began to hybridize when the environment of the lake was affected by agricultural pollution (Pethon 1974, Svärdson 1976). The gene pools of the whitefish and the cisco species are obviously not fully and irreversibly isolated. Strictly speaking, then, the two taxons are not full species but are only semispecies, albeit well-advanced ones.

In the River Pechora, the anadromous omul, *C. autumnalis*, spawns 1,100 km upstream, close to a sympatric population of sparsely-rakered whitefish. Spontaneous hybrids or "omulevyg sig" are common, constituting some 30 % of the omul total and 6 % of the sparsely-rakered whitefish (Burkov and Solovkina 1976). The specific status of the omul, however, cannot be doubted.

Svärdson (1965) found the premating as well as the postmating isolating mechanisms of sympatric whitefish populations to be poorly developed. As is proved by numerous cases, cited in earlier sections, introgression is found wherever a thorough study is performed. The volume of gene flow, however, varies greatly and depends on several factors.

The lake habitat is one factor. Generally, larger lakes, with some rather deep areas and also islands or bays with feeding streams, give the sympatric populations their best chances of durable integrity.

Population size also influences the outcome. A supposedly small number of avant-garde blue whitefish colonists were swamped by the southern densely-rakered whitefish in Lake Stora Övsjön (Ljungan river) and Övre Särvsjön (Ljusnan river), being recognizable only by their growth tendencies. Likewise, the last specimens of large sparsely-rakered whitefish seem to be swamped by the lesser sparsely-rakered whitefish in several lakes, where again only growth histories could be used to identify them.

There is some evidence that hybrids display heterosis or hybrid vigour, as proved by the experiments on the Locknesjön fish. Since growth in early life is very important for future survival, hybrids should be selected for if their fertility is not low. The fertility of the Arjeplog hybrids has not been compared with that of the parent stocks. However, the F_2 and later generations had a wider variation span than the F_1 generation, as measured on gill rakers, suggesting genetic recombinations. They have been able to build up a self-reproducing population in Lake Norra Stensjön.

The Sällsjön whitefish did not respond to new environments when they were transplanted from Vänern to Sällsjön, Kallsjön and some other bodies of water, where they then lived allopatrically for up to a century. When, however, they slipped down into Lake Landösjön, which had two other indigenous species, introgression to the planktonsik took place and a local deme is evolving. Likewise, Järvi (1940, 1953) found that introgression modified the introduced densely-rakered whitefish of Lake Pyhäjärvi when a second population, of river whitefish, was also introduced into the lake. Shaposhnikova (1971) analysed the hybrid whitefish of Lake Sevan, into which stocks from Lakes Ladoga and Chudskoye had been introduced. The Sevan fish were more or less intermediate in all characters studied, including the morphology of the skull bones. The study on the Sevan fish in fact serves to stress the importance of quantitative rather than qualitative traits for *Coregonus* taxonomy.

The amount of introgression between sympatric populations suggests that they are semispecies or subspecies. Moore (1977) discussed the significance of narrow hybrid zones in vertebrates but did not consider cases like those of *Coregonus*, where the hybrids interbreed with their parent species, have no habitat of their own, are fertile and have hybrid vigour but nevertheless often fail to destroy the identity of the parent populations.

In the upper lakes of the parallel rivers Ljusnan, Ljungan and Indalsälven, four different whitefish are still discernible after eight or nine thousand years of introgression. A fifth species runs the lower part of the rivers. Exactly the same pattern is found in the Rhine. Lake Constance is (or was) inhabited by four sympatric whitefish populations, very much the same as those of the Scandinavian rivers (Wagler 1937). Formerly, the fifth species, the river whitefish, also ran the lower parts of the Rhine.

There is a considerable amount of evidence that six basic populations are responsible for the present abundance of whitefish demes in Scandinavia. They must have evolved, in geographical isolation, from Arctic or Siberian progenitors. They have spread widely in the postglacial period, met again and produced numerous new introgressed demes, but these are still recognizable as main types. They cannot therefore be termed subspecies since mostly all live sympatrically. Their evolutionary status is that of semispecies.

We thus end up with a situation where one group of semispecies (whitefishes) behave towards another group of semispecies (ciscoes) like semispecies, albeit rather close to the fully-fledged species category. For practical purposes all should be judged as species. Only if they are recognized as species can the lower categories, or clusters of demes, be treated as subspecies. Demes, however, should not normally be given scientific names, except in the case of well-studied populations, which may retain a subspecific name.

It remains to be discussed why the *Coregonus* and *Prosopium* (White 1974), as also the lake-living *Salvelinus* and, to some lesser extent, *Salmo* and *Oncorhynchus*, can experience the genetic imbalance of introgression and still remain fertile. It is conceivable that their polyploid descent is responsible. If vital chromosome segments are quadrupled, the risk of missing vital genes in hybrid recombinations is low. Foreign allels or blocks of genes, from a sympatric species, may also easily be incorporated into the genome.

Ecological factors such as diet preferences, hence also growth and size, and spawning periods act as isolating mechanisms. It follows that in a swamping process the ecological characters of two populations are the last to disappear, since they are selected for persistence. The evolution results in a morphologically more or less homogeneous population, while there remain dissimilarities in size and spawning habits (SVÄRDSON 1959 b). The advanced stage of enduring sympatric coexistence mimics a theoretical first stage of "sympatric speciation" where the first step is thought to be a kind of ecologic splitting. This is why many writers of the past have argued in favour of sympatric speciation and Soviet writers think that the *Coregonus* species utilize the lacustrine environment more fully by being "polymorphic".

Geographical isolation of freshwater fish tends to take place during periods of glaciation but also occurs in the interglacials. The short periods of transition between glacials and interglacials are the main opportunities of population reshuffling, spread and secondary contacts.

The classical European geological concept of four main glaciations has been swept away by recent studies of oxygen isotope records from the oceans, of deep pollen records from peat bogs and from loess records in central Europe (KUKLA 1977). During the last 700,000 years there have been eight glacials and interglacials and over 1.7 million years the number rises to 17. If there are two periods of freshwater fish isolation in each glacial cycle, there could, conceivably, be ample time and opportunities for geographical isolation to become a powerful factor in *Coregonus* speciation.

If and when more penetrating methods of gene analysis become available, the speciation pattern of *Coregonus* may very well be, not an embarrassment to the systematists as in the past, but a most convincing example of the significance of isolation, introgression and competitive sympatry. FRANZIN and CLAYTON (1977) have demonstrated the possibility of mapping the spread of *C. clupeaformis* out from different glacial refugia in Canada.

The Coregonus peled species group

Since the speciation among the coregonine fish is associated with the isolation and dispersal periods during glacial cycles, the centre for parental species is the non-glaciated area of eastern Siberia (map in FLINT 1971, p. 662). From this centre the speciation process has spread by successive steps not only to western Siberia, and northern and western Europe but also to the east, *viz.* to North America all the way to the Great Lakes region. The most evolved taxons should be found in western Europe and the Atlantic drainage of North America.

NIKOLSKY and RESHETNIKOV (1970) describe *Coregonus peled* as endemic to the U.S.S.R., being distributed from the Mezen river to the Kolyma. The species is characterized by many gill rakers, 46—68, and a terminal or upper mouth with the lower jaw being the longer. It is normally very high-bodied, a character which seems to be correlated to a rapid growth rate.

SMITT (1886) had material of *peled* from Archangel and Yenisey and he found some morphological differences between them. According to SMITT the name *peled* was first used by LEPECHIN in 1783 for the western form, while PALLAS named the eastern form *cyprinoides*, because of the high body.

NIKOLSKY and RESHETNIKOV in fact indicate that the differences between the eastern and western *peled* forms are of specific rank. The western form is called river *peled* and is said not to occur in Lena, Yana and Indigirka. More important, they find two different *peled* populations in some lakes. One is 40—50 cm long and weighs 1,500—2,000 g, the other is a dwarf of 30 cm weighing only 300—400 g. The dwarf is low-bodied and has a marked spotted pattern. In Soviet tradition this situation is not regarded as evidence of two species. With the biological species concept adopted by the present writer there would, however, be two *peled* species within the Soviet area.

Northern densely-rakered whitefish

The Archangel *peled* specimens, studied by SMITT, are still in the collections of the Museum of Natural History, Stockholm. When they were compared with the aspsik of Lake Storvindeln there were found obvious similarities in the numbers of gill rakers (more than 60) and lateral scales (76—87) and, above all, in the mouth, the lower jaw being the longer in most specimens. The Storvindeln fish looked like starved specimens

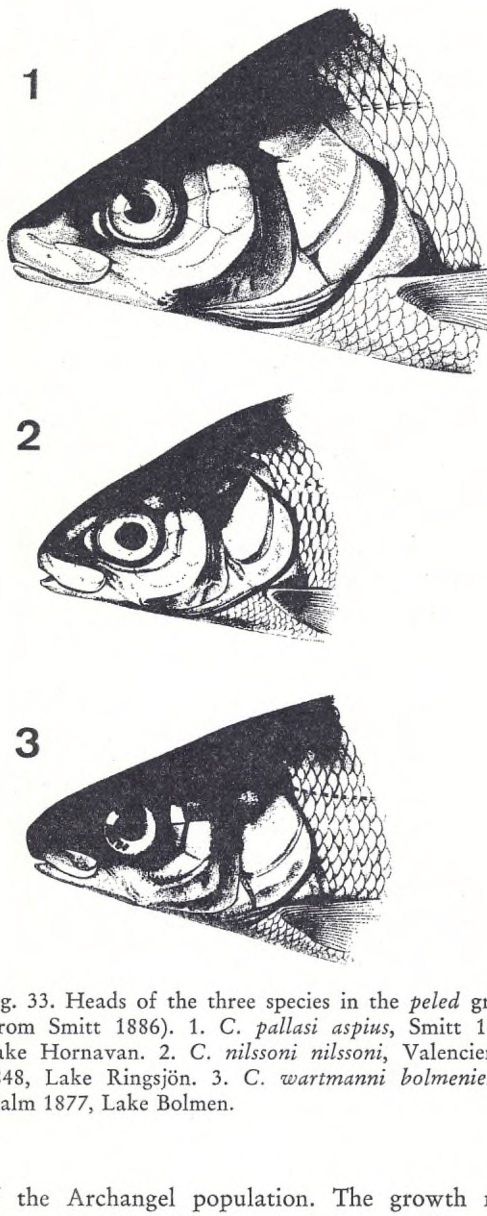


Fig. 33. Heads of the three species in the *peled* group (from Smitt 1886). 1. *C. pallasi aspius*, Smitt 1882, Lake Hornavan. 2. *C. nilssoni nilssoni*, Valenciennes 1848, Lake Ringsjön. 3. *C. wartmanni bolmeniensis*, Malm 1877, Lake Bolmen.

of the Archangel population. The growth rate was strikingly different; the Archangel fish were 33—37 cm in total length and 3—5 years old, while the Storvindeln specimens were 25 cm in ten seasons of growth. The big heads, big eyes and elongated bodies of the Storvindeln fish looked like those of emaciated fish, while the high-bodied *peled* from Archangel recalled the best-growing whitefish of the Kälarne experimental tarns (Fig. 7, p. 19).

The Storvindeln aspsik are one of four sympatric whitefish populations. It appears that they were the poorest competitors of the four. In that case, influx of genes from other, better adapted species, could conceivably be selected for. As detailed in the section on the aspsik (p. 17—26) and the Arjeplog lakes (p. 41—42), the Swedish populations grade into a series with an increasing amount of introgression. The stocks of Lakes Vojmsjön and Storuman were the most changed; their gill rakers numbered only 45—46, the association with rivers ("river *peled*") was lost and the dwarfing of spawning size had advanced. As dwarfing and living in cold deeper waters seem to be adaptations to a low ration of food (*cf.* p. 73—74), this further evolution seems natural for a less competitive species.

The aspsik is also found in central Finland and Soviet Karelia (Himberg 1970, 1972). It lives in many lakes from the Saima to the western shore of the White Sea. The known geographical distribution is consistent with a postglacial spread of a "river *peled*" into watersheds drained to the White Sea and, by headwater transfer, into the Gulf of Bothnia and the Ladoga-Onega system. The form is still associated with rivers, *e.g.* in Vuoksen, Neva and Narva from Lakes Saima, Ladoga and Chud (Peipus). Some of the local demes are rather different from "river *peled*" as far as the mouth is concerned. The gill rakers grade from 50 or more down to about 40. Everywhere the species seem to be a poor competitor but it is tolerant of warm eutrophic waters. No case is known where the aspsik lives sympatrically with the "river *peled*" of northern U.S.S.R.

Since the evolution of the aspsik seems to be postglacial, a specific rank of the aspsik probably is too high. However, to make the aspsik a subspecies of *C. peled* seem to be too hasty, until the relation between the two *peled* forms within the Soviet Union has been more closely studied and the statement by Smitt that *peled* should be the western "river *peled*" has been confirmed or rejected.

The Swedish stocks of aspsik were described as *C. aspius* by Smitt (1882) Fig. 33. The Karelian populations, including those of Ladoga-Onega, have generally been identified with *C. pallasi*, Valenciennes 1848.

For the time being, then, the aspsik should be called *C. pallasi* and the Swedish stocks may be named *C. pallasi aspius*. It should be recalled that the specific status of *C. pallasi* against the river *peled* is not proved but that a considerable evolution has occurred by introgression to Scandinavian and Finnish-Karelian whitefish populations belonging to other species. The least introgressed form so far known seems to be that of Lake Storvindeln.

Southern densely-rakered whitefish

What has happenend to the"river *peled*" during the postglacial era might conceivably have occurred earlier, in a period of dispersal before the last glacial peak 15,000 years ago. Then this earlier wave of densely-rakered whitefish should have evolved in a similar way to the postglacial one, being introgressed to other forms, having its competitive strength increased, its gill rakers being reduced in numbers, and its mouth being modified to an inferior position or terminal. The capacity to tolerate warm eutrophic lakes should not, however, have changed since it was already of survival value. The tendency towards dwarfing in cold, oligotrophic lakes should have increased.

All these characters fit into the planktonsik, which seems to be a western species that has survived the last glaciation in refugia of the present North Sea area (VALENTIN 1958, FLINT 1971, map at p. 594). The strongest piece of evidence for this interpretation is the existence of the planktonsik in small eutrophic lakes of the Jutland peninsula near Silkeborg, Denmark. The lakes are headwaters of rather small streams, which once were rivers draining the melting glacier in the earliest part of the deglaciation process. These whitefish have many gill rakers (OTTERSTRØM 1922). A recent sample from Lake Tjele Langsø of 18 specimens had 40—49 rakers, average 45 (courtesy Dr JØRGEN DAHL). Since this whitefish cannot tolerate salt water (in the Baltic the aspsik is only sporadic below Neva and Narva rivers), they must have colonized these small headwaters very early, from freshwaters downstream the valleys, *e.g.* from the present North Sea floor. There are also fossil finds of *Coregonus* in sediments of an ice-dammed lake, south-west of Aarhus, from the Older Dryas period. The evidence is convincing (LARSEN 1977) that freshwater fish colonized western Jutland from the west.

From the "Dogger Lake" refugium, the planktonsik spread postglacially, not only to the Danish lakes but also up the Rhine to the Alpine region, into the Lough Hibernia (MAITLAND 1970, WHEELER 1977), and the British Isles, to the northeast in flowing freshwaters from melting glaciers to the Swedish western coast and later into the Baltic basin up to the Torne river valley in the north.

In Lake Constance the planktonsik was described as *C. macrophthalmus* by NÜSSLIN (1882). It was probably an early colonist and it survives in many lakes: Constance 40.4 gill rakers, Thuner See 41.8, Vierwaldstättersee 39.4, Abersee 39.0, Faaker See 39.3, Wörthsee 40.2, Staffelsee 41.5 and Hallstätter See 42.2 according to WAGLER's material rearranged by SVÄRDSON (1957, p. 354).

In the British Isles it seems to live in Lakes Bala, Haweswater and Ullswater, judging by the gill-raker counts, around 38. The Bala population was described as *C. pennanti* by VALENCIENNES in 1848. However, FERGUSON *et al* (1978) found the Irish pollan to be conspecific to the arctic *C. autumnalis*. The severe climate and the known arctic fauna during the Loch Lomond stadial (Sissons 1979) suggest that pollan became landlocked from the *autumnalis*, associated to the cold polar sea water then penetrating to Ireland. There is a possibility that pollan may have inhabited more lakes and was swamped by planktonsik and other later whitefish colonists, arriving by fresh water routes. Some of the pollan genes may thus still recombine in the British populations (*cf.* Gasowska 1965).

REDEKE (1933) studied the "Rheinschnäpel" of Hollandsch Diep and Gelderschen Ijssel. He found that this fish lived sympatrically with a (very rare) cisco, had become much more sparse in recent times, possessed some 40 gill rakers, was a small fish and fed on plankton. All this suggests a planktonsik, which, however, should not have the long (blue) snout of the houting that lives anadromously in the lower parts of French, Belgian, Dutch, German and Danish rivers and is nowadays very rare. In other localities this "Schnäpel" is known to have fewer rakers, *e.g.* in the Elbe 31.5 rakers (THIENEMANN 1922), in Danish streams 31—32 (OTTERSTRØM, 1922, and recent material investigated by the present writer), in the River Schlei in schleswig-Holstein 31 rakers (THIENEMANN 1922) and in Norway about 30 rakers (THIENEMANN *op.cit.*).

The localities studied by REDEKE are very similar to the Danish small lakes, where cisco and planktonsik live and grade, downstream, into the anadromous long-snouted *oxyrhynchus* with about 31—32 rakers. It seems that REDEKE found a blue snout also on fish with 40 gill rakers, suggesting introgression from a vanishing houting into a surviving planktonsik. All characters except the snout evidently suggest that his fish belongs to the species southern densely-rakered whitefish.

SVÄRDSON (1957) followed REDEKE (1933) in maintaining that the Linnaean name *oxyrhynchus* should therefore be applied to the planktonsik. Now, however, this interpretation cannot be upheld. REDEKE may be correct when he suggests that ARTEDI in his paper of 1738, published by LINNAEUS, had the "Rheinschnäpel" in mind when he added "Locus in Flandria and Batavia". However, in the 1758 edition of the *Systema Naturae* the distribution is given as "Habitat in Oceano Atlantica". This wider locality includes also the stocks of the Elbe, the Danish streams, etc. and refers to the anadromous species. Moreover, since the time of ARTEDI, when the houting was abundant, the swamping process may have proceeded very far, and thus the recent "Rheinschnäpel" of REDEKE may be almost a different fish from the true "Schnäpel" of ARTEDI's time in Holland.

It follows that the name *C. oxyrhynchus* should not longer be used for the species southern densely-rakered whitefish, as suggested by SVÄRDSON (1957). What then should the planktonsik be called?

In the Vintapper-Ågård period of deglaciation, 13,750—12,400 yr BP, the province of Skåne (Scania) and the outer fringe of the Swedish west coast became free of ice (MÖRNER *et al.* 1977). The planktonsik could colonize Lake Ringsjön, where it was named *C. nilssoni* by VALENCIENNES 1848 as explained in detail in an earlier section. The species could later climb the Lagan valley to Lakes Kösen (41.6 rakers), Bolmen (41.7), Vidöstern (39.7) and Rusken (39.0).

When the blocking lobe of glacier disappeared in the warm Allerød period, the planktonsik could also penetrate into the Baltic basin and the River Mörrumsån and spread to the Polish area where it was later known as *C. generosus*, PETERS 1874. This *generosus* form has about 40 gill rakers in several populations (THIENEMANN 1928).

The main route of dispersal into the Baltic seems to have been through the Göta river valley, where it survives in Lakes Vänern (41.0 rakers), Fryken (43.0), and Femunden (45.0). The Yoldia stage of marine conditions was probably a period of no further spread, but when freshwater again prevailed, in the Ancylus stage, the planktonsik could continue northwards to the rivers Ljungan (42 rakers in Locknesjön, 41 in Stora Övsjön), Indalsälven (40 rakers in Lakes Hotagen and Vallsjön), to the Ångermanälven river (42 rakers in Tåsjön) and all the way up to the Torne river (38—40 rakers at Vieksalahti).

The Arjeplog lakes prove the planktonsik to be living sympatrically both with the aspsik and with the blåsik.

Apart from the gill rakers, some characters still suggest the *peled* origin. First, the mouth is often terminal, especially in small-sized populations. Second, the species is tolerant of warm lakes, as is the case of the stock of Lake Hjälmaren (40 rakers). Here one is reminded of the recent Soviet management program of stocking the *peled* in small, warm lakes.

Four names might be considered for the planktonsik. VALENCIENNES proposed two names, the *nilssoni* and *pennanti*, both from 1848. PETER's *generosus* dates from 1874 and NÜSSLIN's *macrophthalmus* from 1882. Page priority (497 versus 507) for *nilssoni* makes it the oldest name and the type locality is then Lake Ringsjön. There is some doubt whether the Bala *pennanti* population belongs to the planktonsik and moreover the *generosus* stock might be argued to be a marginal southern fringe of the *pallasi* population around the Gulf of Finland.

The planktonsik, derived from *peled* before the last glaciation, should therefore have the name *Coregonus nilssoni*, VALENCIENNES 1848 (Fig. 33).

The blue whitefish

One glacial cycle still earlier, another wave of *peled* could very well have spread to western Europe. It should later have evolved according to the same principles which have ruled the two later waves. The derived species should at present have a still better competitive edge and survival capacity in the environment of western Europe, a lower number of gill rakers because of introgression, a terminal mouth or slightly protruding nose, a diet of predominantly plankton but with some benthos being taken in periods of short food supply, and flexible spawning habits with associations to running or standing waters. It follows that the relations to the parent *peled* species should be more difficult to reveal. Finally, if the species had lived for a considerable time in western Europe it should also have had the opportunity to spread secondarily to the north-east. The species should be found in western Europe as well as along the Arctic coast and, as these populations were separated during the last glacial period, they might be different.

This is, of course, almost a description of the blue whitefish or blåsik. Among the 37 alpine coregonine populations tabulated by STEINMANN (1951, p. 105), some 26 can be judged to belong to the blue whitefish species or be strongly influenced by that species.

BLOCH (1783) described the "Blaufelchen" as *Salmo wartmanni.* This is the oldest name given to the blue whitefish anywhere. The "Blaufelchen" is the dominant species in Lake Constance; it has some 36 gill rakers and strange pelagic spawning habits, the eggs being shed over deep water.

LA CEPÈDE (1803) described the whitefish of Loch Lomond as *Coregonus clupeoides.* According to SLACK *et al.* (1957) and MAITLAND (1969) the powan of that lake has 33—34 gill rakers, feeds on plankton in summer and benthos in winter, dominates the lake and grows to 25—40 cm, all suggesting a blue whitefish stock.

There are no blue whitefish populations in northern Germany or Denmark, but the species seems to occur in southern Norway. Lake Gruda in the Jaeren peninsula, close to Stavanger, has a whitefish from which only one specimen has been studied by THIENEMANN (1922). The specimen had 31 rakers (the count should probably be one or two points higher), which indicates that it is not conspecific with the whitefish of Orrevann, also in Jaeren. The Gruda stock is said to consist of small fish, 30 cm in total length. Blue whitefish is also found in Lake Krøderen (60 km north-west of Oslo) as a small fish of 20—25 cm with 30—32 gill rakers (THIENEMANN, *op. cit.*).

ENGE (1959) studied Lake Randsfjorden, some 70 km north-north-west of Oslo in Norway. The lake is inhabited by three sympatric whitefish stocks, one of which, the "strømsik" with 34—35 gill rakers and spawning in Rivers Etna-Dokka in October, seems to be a blue whitefish.

SVÄRDSON (1957) presented material from some small lakes on the west coast of Sweden, on the Norwegian border, where the allopatric whitefish had 33—34 rakers. The stock of one lake, Bullaren, was named *C. lavaretus bullarenensis* by MALM (1877). Other stocks, in Bolmen and Vänern, were described as *C. lavaretus bolmeniensis* by MALM (1877) (Fig. 33) and *C. humilis* by GÜNTHER (1866).

In the Ancylus period the blue whitefish spread over the whole Baltic basin. In Ladoga it is known as the "black whitefish" and was named "mediospinatus" by PRAWDIN. Several populations live in Lake Onega, where PRAWDIN (1954) identified them as *C. lavaretus lavaretoides.* In Lakes Vänern, Ladoga and Onega the blue whitefish is fairly large and has a subterminal mouth.

The small-sized blue whitefish of northern Sweden might have come, by headwater transfer, from the Arctic drainage, just like the aspsik. KROGIUS (1926) described it as *C. lavaretus chibinae* from Lake Imandra and JÄRVI (1928) as *C. lavaretus borealis* from Lake Inarijärvi. Both lakes drain to the Arctic Ocean. In Sweden WIDEGREN (1862) described it as a new species, *C. megalops* from Lake Storsjön, Indalsälven river system.

In Lake Segozero of the Karelian Republic of the U.S.S.R. PRAWDIN (1954) described a form, probably the blue whitefish, as infraspecies *arnoldi.* This lake seems to have many sympatric whitefish stocks and would be an attractive object for modern whitefish research.

SHAPOSHNIKOVA (1974) states that sparsely-rakered whitefish in Siberian waters "frequently" live sympatrically with forms of the "mediospinatus" type. Obviously there are in Siberia small-sized whitefish which may be conspecific with the blue whitefish or constitute another species. They are all called subspecies of *lavaretus* by SHAPOSHNIKOVA (1974) and KALASHNIKOV (1968), *viz. C. lavaretus oronensis* KAHLASHNIKOV, etc. They have 33—36 gill rakers. It is not possible at present to judge their true status, except that they are probably not subspecies of *C. lavaretus.*

Summarizing the evidence at present available it can be said that the blue whitefish should have the name *C. wartmanni* (BLOCH). Subspecies in Europe may be *clupeoides*, *humilis* and *megalops.* It must be left to future studies to decide whether the complexities in the Gimån river, where *C. wartmanni* and *C. nilssoni* display a pattern of alternative size differences in the Ljungån and Gimån rivers are correlated to a secondary contact between a southern *humilis* and a northern *megalops* subspecies of *C. wartmanni.* It seems that the *wartmanni* species is mostly smaller than *nilssoni* in all rivers north of the Gimån, while the opposite is true in more southern rivers.

Peled in North America?

KOELZ (1929) gives the gill rakers of his *Leucichthys nipigon* as 54—66, average 58. His picture shows a high-bodied whitefish with a *peled* mouth. The *nipigon* population grows to be a large fish, maximum size about 45 cm. SCOTT and CROSSMAN (1973) range this population into the *C. artedii* complex, though they admit two populations in Lake Nipigon: one *artedii* proper with 41—57 gill rakers, and a second with 54—64. Two sympatric Lake Nipigon populations of *artedii*, with clear genetic differences, seem to be at variance with the species concept. Since the *artedii* proper of Lake Nipigon has the same number of gill rakers as the *artedii* populations of Lakes Superior, Michigan, Huron, Erie and Ontario (KOELZ, *op. cit*), it must be the *Leuchichthys nipigon* population that is outstanding in gill-raker numbers.

It seems a reasonable hypothesis that *C. peled* has spread from Siberia, during a glacial cycle in the long past, to the Hudson Bay area — like other coregonine fish — and colonized lakes, from which it was later ousted, except in the case of Lake Nipigon (*cf.* Lake Storvindeln in Sweden). In a process of intensive introgression to *artedii* and *clupeaformis* it has in fact become one of the parental species for the cluster of "chubs" originating in the Great Lakes area during subsequent glacial cycles. That would suggest a speciation process, involving the *peled*, both in western Europe and eastern North America, where introgression is a main factor.

The Coregonus pidschian species group

SHAPOSHNIKOVA (1974, 1977) discussed the "pyzhyan" whitefish within the U.S.S.R. In the non-glaciated area of Siberia *Coregonus pidschian* has 19—20 gill rakers and grows to be an old and large fish. Its diet is benthic. This is the parental species for a number of western European species but also for some species in North America.

SVÄRDSON (1957) thought that there were two large-sized sparsely-rakered whitefish species in the Baltic basin. Since there are also two such species along the Arctic coast, *viz. C. pidschian* and *C. nasus*, the simplest hypothesis was to make the two Arctic species conspecific with the Baltic two species. This interpretation, however, is no longer upheld (SVÄRDSON 1970). Instead, only one of the species, *C. pidschian*, is now thought to be involved in the speciation of western Europe, where in fact it has produced three derived species. The speciation has probably occurred — similarly to that of the *peled* group — by multiple waves of westward penetration, isolation in glacial cycles, secondary contacts and, when specific rank has been achieved, dispersal eastwards to produce sympatric Arctic coexistence.

SHAPOSHNIKOVA (1974) presents her Siberian *pidschian* — which she thinks belongs to the *lavaretus* species — grading westwards along the Arctic coast into populations with more rakers — 26 on average — and changed relative length of lower jaw. According to this view, there should be only one sparsely-rakered species in north-western U.S.S.R. This , however, cannot fit into the biological species concept.

RESHETNIKOW (1963) presents material investigated by KROGIUS from Lake Imandra. In this lake there are: first, one anadromous population with 26 rakers, secondly, the smaller *pelagicus/knipowitschi* fish with 17—28, average 22, and finally, the *chibinae* form with 32 rakers. The last one is the blue whitefish *C. wartmanni*, leaving two sparsely-rakered sympatric populations to be accounted for.

JÄRVI (1928) and TOIVONEN (1960) found in Lake Inarijärvi, Finland, a small-sized blue whitefish (33—35 rakers) but also two sparsely-rakered populations, one of which is larger in size, just as in Lake Imandra on the Kola peninsula.

The same pattern is repeated in Lake Iijärvi, Finland, which also drains to the Arctic. From Table 2 of TUUNAINEN's (1975) paper it can be seen that there is a small-sized *wartmanni* (32—34 rakers) but also two different populations of sparsely-rakered whitefish, one medium-sized with 19—20 rakers and the other, a larger one with 21—23.

PRAWDIN (1954) described the whitefish stocks of Lake Segozero, draining by the Wyg river to the White Sea. Apart from *C. pallasi* with 47 rakers, the *C. wartmanni* with 34 (called forma *arnoldi* by PRAWDIN) and the small stream-spawning form *kilone* (number of rakers unknown) there are two further sympatric stocks: *palloni*, which is large, silvery, high-bodied and small-headed with 27 rakers and the *melga/neschka* fish which are smaller, dark, and big-eyed, with elongated bodies and 25 rakers. Again at least two sparsely-rakered species live sympatrically in the lake, and there might be three.

Within the Baltic basin there are often two sparsely-rakered species in upper lakes of various river systems and a third living anadromously in the lower part of the river. When introduced by man the anadromous one, *C. lavaretus*, proved its independent specific status by living sympatrically with the other two species in Lakes Locknesjön and Ockesjön. The three species seldom occur spontanously in one lake, but this is the case in Lake Vänern and it might be true for Lake Ladoga also (SHAPOSHNIKOVA 1973).

Within the Alpine region there are again two sparsely-rakered species in some lakes while the third, the long-snouted *oxyrhynchus*, formerly lived in the Rhine. The lake forms are *C. fera*, (JURINE 1825) and the smaller, more deep-living species, *C. acronius*, RAPP 1854.

From the geographical distribution of the three species it is not possible to evaluate their age order, *i.e.* which of them is the last or the first to have become derived from *C. pidschian*.

Applying the principles that appear to have ruled the evolution of the *peled* group, the least competitive species and/or the one with fewest rakers should be the most recently evolved, while the species with most gill rakers and/or the most competitive one should have lived the longest in western Europe.

Large sparsely-rakered whitefish

The *C. fera* of the Alpine region and the large sparsely-rakered whitefish of Locknesjön and other Swedish lakes are thought to be conspecific and some Swedish stocks have as few as 19 rakers, *i.e.* just the same as the Siberian *pidschian*. At present the situation seems too uncertain, however, to make them only a subspecies of *pidschian*, though they might actually be sufficiently close to be so classified. The *fera* is most probably preglacial while the 19-rakered stock of Locknesjön might be a postglacial colonist from the White Sea area, by means of headwater transfer. In the Baltic Ice Lake period another stock with 21 rakers, probably also of this species, colonized some southern Swedish lakes together with the spring-spawning cisco *C. trybomi*.

Within Scandinavia the large sparsely-rakered whitefish has been described and named only in Lake Vänern, where GÜNTHER (1866) called it *C. maxillaris* (Fig. 34). If *C. fera* is preglacial, the *maxillaris* (though much introgressed in Vänern) should be the proper name for the postglacial form. The two forms then are *C. fera fera* in central Europe and *C. fera maxillaris* in Scandinavia.

Lesser sparsely-rakered whitefish

It has been discussed at some length (p. 50—51) that *C. widegreni*, MALMGREN 1863 is the correct name for this species within the Baltic basin. Again the fish might be a postglacial colonist from the east. In the Alpine region the species was described

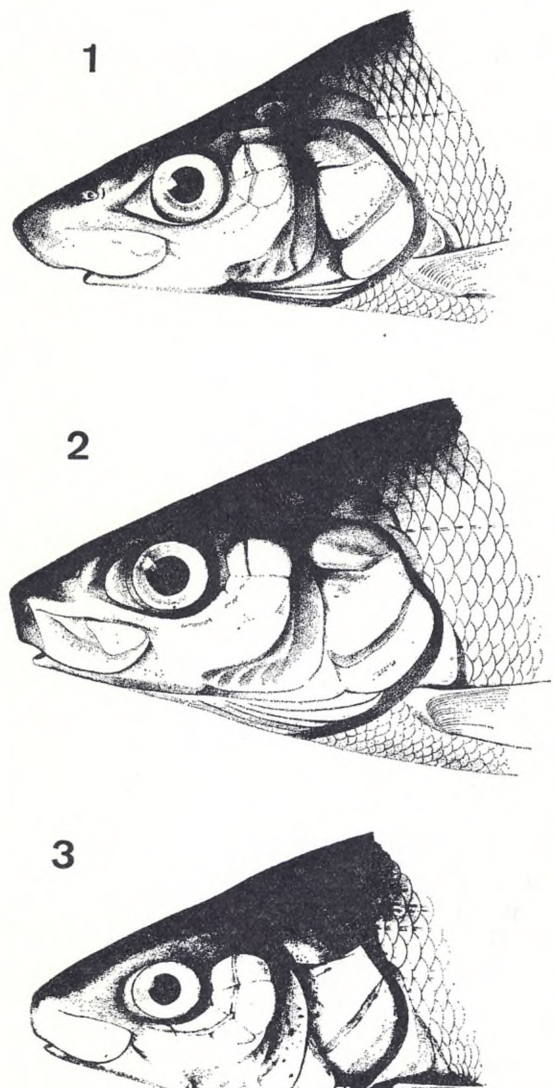


Fig. 34. Heads of the three species in the *pidschian* group (from Smitt 1886). 1. *C. lavaretus oxyrhynchus*, (Linnaeus 1758) Lake Vänern. 2. *C. fera maxillaris*, Günther 1866, Lake Vänern. 3. *C. acronius widegreni*, Malmgren 1863, Lake Vättern.

as *C. acronius* by Rapp 1854, which is then the oldest name. Subspecies should be named even in this case, since they are pre- and postglacial. Correct name for the Baltic stocks then is *C. acronius widegreni* (Fig. 34).

River whitefish

The *C. lavaretus* has the highest number of gill rakers of the three benthos-feeding sibling species. It is also the most evolved anadromous form.

However, there appear to be more land-locked populations of the species along the Arctic coast, and, if dispersal has taken place via the Alta river over to the Torne river drainage (*cf.* p. 55), it could explain the aberrant älvsik distribution inland within this system. The joint occurrence of *lavaretus* and *acronius* in the Arctic river systems of north-western U.S.S.R. could also explain why the *C. fera* is now rare or non-existent there, since *fera* is subdominant to both species, as is proved by Swedish lakes.

Long-snouted specimens of the *lavaretus* can be found now and then along the Swedish east coast, *viz.* off Stockholm. On the other hand the *oxyrhynchus*-populations of Lakes Vänern and Vättern are most probably relicts, presumably from the Littorina period (Fig. 34). If the *oxyrhynchus* subspecies evolved to the Atlantic houting during the Eem interglacial, in a warm and marine habitat, it should have had its most optimal postglacial period in the warm early Littorina period but later been swamped or ousted by the more temperate *lavaretus* subspecies of postglacial eastern origin.

It seems that no sparsely-rakered whitefish has colonized or survived in the British Isles. The *acronius* species probably survived in the "Dogger Lake" and could postglacially, not only climb the Rhine, but also ascend some rivers of Atlantic drainage in north-western Germany, where it still survives. It was called *C. lavaretus* forma *holsatus* by Thienemann (1916). From the North Sea floor it might also have reached the Stavanger area of Norway, though Svärdson (1976) and (Huitfeldt-Kaas 1923) suggested an alternative dispersal route, associated to the flushing of the Baltic Ice Lake.

Summarizing the interpretations put forward in this section, all three species *fera*, *acronius* and *lavaretus* are split into two subspecies, of which the Alpine or Atlantic population is preglacial and the other postglacial in western Europe. The real speciation process might be several glacial cycles older, since sympatric existence enabled the species to spread back to the Arctic coast area.

It remains for future studies to find out where along the Arctic coast they grade into the parental species *pidschian* or where their sympatric coexistence fades.

Pidschian species North America

As in Europe, the *pidschian* has produced progeny species of whitefish in North America. The *C. clupeaformis* complex involves much the same pattern as the European, with sympatric pairs, one of which is more or less dwarfed. There appears to be at least one western and one eastern American twin species pair, suggesting speciation from a common progenitor during glacial isolation in two independent refugia, giving a total of at least three species (Lindsey *et al.* 1970, Scott and Crossman 1973 and Franzin and Clayton 1977).

The Coregonus sardinella species group

Nikolsky and Reshetnikov (1970) presented the Siberian cisco, *C. sardinella* — which they thought to be a subspecies of *C. albula* — as one of the most valuable fishes of the rivers. The "rjapushka" is generally larger than the European cisco, having an average length of 30 cm and weighing up to 300 g, sometimes 500 g. It grows to be older and matures later than the cisco of western Europe. It feeds on plankton, benthic organisms and terrestrial insects. It runs the lower parts of the river for spawning and feeds in the estuaries.

Morphologically, *sardinella* is characterized by its mouth, where the lower jaw is clearly the longer. There are no certain morphological differences from *C. albula*, since Kanep (1976) found the predorsal distance — earlier thought to be diagnostic — to be an allometric character.

However, as in other cases, *C. sardinella* is more than one species. Ustyugov (1972, 1976) described in detail the existence of two distinct species in the Yenisey. They differ ecologically and morphologically but run the same river. Ustyugov suggested that the origin of their sympatry was connected with two waves of colonizing ciscoes invading the Kara Sea basin from the east. In Soviet tradition they are not given specific names but are regarded as "ecological forms".

Further west the *sardinella* is graded into *albula*. Solovkina (1974) found *sardinella* and *albula* characters mixed within the Pechora basin, while Pokrovsky (1967) thought the cisco of Lake Vodlozero, belonging to the Onega basin, draining to the Baltic, to be *C. sardinella*.

Sardinella and *albula* seem to live sympatrically as two species in Lakes Onega and Ladoga. Pokrovsky (1956) summarized the two forms in Ladoga like this:

Albula form	"Ripus" form
Back green or black, pectoral fins long, more than half the distance between pectoral and ventral fins, gill rakers 35—47, average 41, northern Ladoga, spawns on the west coast, 5—20 m depth, feeds on zooplankton and chironomids maturity at I+, 8—10 cm and 6—8 g, maximum size 20 cm, 90 g, oldest specimen VII+, sclerits in first growth zone 8—22.	Back dark blue or violet, pectoral fins shorter than half the distance between pectoral and ventral fins, gill rakers 38—52, average 45, southern Ladoga, spawns in Volchow bay at 5 m depth, feeds on zooplankton and relict crustaceans, sometimes fish fry, maturity at II+, 18 cm and 50—60 g, maximum size 40 cm, 1,000 g, oldest specimen IX+, sclerits in first growth zone 17—33.

The large-sized "ripus" lives in both Onega and Ladoga and was first described by Michailowsky (1903) as *C. albula kiletz*.

It appears that "ripus" is in fact conspecific with *sardinella* and thus obviously with the western species, which was not named by Ustyugov. *C. kiletz* thus seems to be the name of the western species of cisco along the Arctic coast, derived from *C. sardinella*. The introduction of "ripus" in the Saratov reservoir within the Volga system supports this interpretation. The "ripus" seems to live there sympatrically with the indigenous cisco and to have a better growth rate (Koskova 1977). The indigenous form is referred to as *C. sardinella vessicus* but should be ranged into the *albula* species instead.

It is interesting that "ripus" dominates southern

Ladoga, although it may also occur as the "mantsinsari" form of the northern part of the lake (DYATLOV 1978). The cisco of the innermost Gulf of Finland is large-sized (JÄRVI 1950, LIND *et al.* 1976), a fact which has up to now been associated with eutrophication from Leningrad, combined with a sparse population.

C. albula is the Baltic species described by LINNAEUS in 1758. The sibling species *C. trybomi*, has been described in a special section (p. 71). Both species seem to have colonized the Baltic basin from the east during the late phase of the glacial period.

The vendace or *C. vandesius* was described by RICHARDSON 1836. It has been regarded as a British form, conspecific with *C. albula* (FERGUSON *et al.* 1978). From the cisco distribution in western Jutland, in the small lakes around Silkeborg, it can be concluded that ciscoes survived the last glacial period in the "Dogger Lake". Later they spread through Lough Hibernia (MAITLAND 1970, WHEELER 1977) to its present lakes in the British Isles. REDEKE (1933) reported very rare finds in the Rhine delta, where the cisco could not climb the Rhine to the Alps as did the other coregonines. The same poor capacity for upstream spread was noted for cisco in Scandinavia. It could have spread from the Dogger Lake to the extreme locality Orrevann in the Jaeren peninsula, in south-western Norway, though there is also another route of possible dispersal (SVÄRDSON 1976).

Populations of ciscoes live in lakes of northwestern Germany, draining to the North Sea. The *vandesius* preglacial stock would be the one colonizing those lakes.

Somewhere further east in northern Germany *vandesius* should have met the postglacial *albula*. It is a striking fact that three small lakes in Mecklenburg, just within the probable area of secondary contact, have two sympatric ciscoes (THIENEMANN 1933). One is the typical, presumably *albula* form, while the second is small, deep-living and big-eyed and is known as "Quietschbükers" by the local people. Morphological differences between the two forms were small, except for consequences of growth and eye size. Both were autumn spawners, the deepwater form spawning somewhat later than the other. THIENEMANN thought the deepwater cisco of Lakes Breiter Lucin, Schmaler Lucin and Zansen was a primitive eastern form with benthic habitats. Certainly its diet of *Mysis* and chironomid larvae is abberrant.

It seems more likely at present that THIENEMANN's *C. albula lucinensis* actually proves *C. vandesius* to be an independent species, which would be quite conceivable if it has lived in western Europe for more than one glacial cycle.

In the speciation process within the cisco group — as interpreted by the present writer — the original *sardinella* has produced the western twin species *kiletz*, which in turn has produced *albula* and *trybomi*. The most westerly species is *vandesius*, which may have been the earliest one to become isolated in a colonization wave long ago. All the species have proved their specific status by sympatric coexistence in some lakes or rivers. The morphological differences between these biological species are slight and unreliable and in some cases no doubt made more pronounced by the sympatry and competition.

Sardinella in North America

C. sardinella is distributed to Alaska and northwestern Canada (SCOTT and CROSSMAN 1973). It has produced the species *C. laurettae*, with fewer gill rakers, in the Bering area and probably the *C. canadensis* in the east (Nova Scotia), with still fewer rakers. The derived species *C. artedii* is abundant over vast areas and this species hybridizes to *C. clupeaformis* ("mules"). Together with a presumed old *peled* population (*C. nipigon*), *artedii* and *clupeaformis* have produced a number of hybrid stocks, which in several glacial periods of isolation speciated to the cluster of "chubs" which seem to have been exterminated before they were studied in sufficient detail.

Why do some Coregonus species multiply?

In the same Siberian river the "tschir" *C. nasus* and the "rjapushka" *C. sardinella* both move up the river for spawning and down-stream into the estuary for feeding. In spite of their superficially similar ecology they differ strikingly in one respect. The "tschir" needs running waters for the gonad ripening (Nikolsky and Reshetnikov 1970), which makes the species difficult for fish-culture operations, while the "rjapushka" seems to become easily isolated in lake-spawning populations.

This ecological difference turns out to be most important for their speciation and dispersal. In glacial periods, when arctic rivers are blocked and turned to proglacial lakes with drainage through the glacier or by lateral flows, the "tschir" may not survive whereas the "rjapushka" can do so. After a series of glacial cycles the "tschir" still has a rather restricted distribution and is a fairly homogeneous species whereas the "rjapushka" has split into some ten different species, distributed from the British Isles to Kamchatka and from Alaska to Nova Scotia.

There has been much speculation in the past why *Coregonus* has some sort of extremely rapid evolution. Obviously this applies only to some of the species. It can now be stated that splitting up into species groups is found in species where landlocked or, to be more exact, lake-spawning populations are common(*C. sardinella*, *C. peled*, *C. pidschian*), while genuine anadromous or river forms are much more stable (*C. nasus*, *C. muksun*, *C. tugun*, *C. autumnalis*), and in consequence, are less widely distributed.

A second factor taking part in the speciation is the tolerance of the genome, because of its tetraploid origin, to interbreeding by formerly isolated stocks, producing excessive gene flow and new and more adaptive populations.

It was formerly argued by some students of *Coregonus* evolution that sympatric speciation could occur, because the fish tended to home to their spawning areas and hybridization between sympatric populations was insignificant or non-existent. It now appears that geographical isolation is the key factor in their evolution and that introgression is frequent and enters into the speciation process.

VI. SUMMARY

1. This paper is a revision, in the light of new evidence, of an earlier one (Svärdson 1957) on the same subject.
2. The biological species concept is adopted. Lake Locknesjön, headwater of the Gimån river, is inhabited by three indigenous species. The large sparsely-rakered whitefish has 19 gill rakers, the lesser sparsely-rakered whitefish 22 and the southern densely-rakered whitefish 42 rakers. Their ecology is different. Experiments show that the morphological as well as the ecological traits are mostly genetically based.
3. The river whitefish with about 30 gill rakers is a fourth Scandinavian species. Normally it runs the lower parts of the rivers. It was introduced in Lake Locknesjön in the 1940s and from Lake Vänern to upper lakes of the Indalsälven river system in 1870. If it lived allopatrically it was not changed, but if it lived sympatrically with native species introgression have occurred. In Lake Vänern it lives, spontaneously, sympatrically with both large and lesser sparsely-rakered whitefish. The alleged evolution of a new species in postglacial times (Svärdson 1970) was based on introduced fish whose origin was mistaken.
4. The northern densely-rakered whitefish is a fifth species. In Lake Storvindeln it has more than 60 gill rakers and is close to the "river *peled*" of north-western U.S.S.R. It grades by introgression to some 45 rakers in other lakes but proves its specific rank by living sympatrically with all the other forms.
5. The blue whitefish, with 30—35 gill rakers, is the sixth and most competitive species. It has a tendency to oust the southern densely-rakered species as well as the lesser sparsely-rakered one. Its specific status is proved by sympatric coexistence with all the other forms in several lakes.
6. There are five sympatric whitefish species in Lake Vänern as well as in the Arjeplog lakes of the Skellefte river. Two species live in the Baltic Sea.
7. The order of postglacial arrival from the Ancylus Lake could be studied in lakes of the upper Ljusnan river and a complex introgression pattern in the Gimån river system is discussed.
8. The spring-spawning cisco *Coregonus trybomi*,

sp. nov., is described and its place of origin and postglacial dispersal across the Baltic Ice Lake in Younger Dryas is discussed.

9. Isolating mechanisms in *Coregonus* are poor. Species groups behave towards one another (like ciscoes *versus* whitefish) as semispecies only, which could be interbred by man and produce viable, self-reproducing populations.
10. The Siberian *C. peled* is thought to have split by multiple invasions into a western Soviet species ("river *peled*"), *C. pallasi* (northern densely-rakered whitefish), *C. nilssoni* (southern densely-rakered whitefish) and *C. wartmanni* (blue whitefish). The last-mentioned species has a northern subspecies, *C. w. megalops*, in northern Fenno-Scandinavia and along the Arctic coast area.
11. The Siberian *C. pidschian* has in the same way produced three species, *C. fera*, *C. acronius* and *C. lavaretus* in western Europe. Each of them has a preglacial and a postglacial subspecies. Vernacular specific names are large sparsely-rakered, lesser sparsely-rakered and river whitefish.
12. The Siberian cisco, *C. sardinella*, is split into many species. A western Soviet Union species is *C. kiletz*, Scandinavian are *C. albula* and *C. trybomi* while the British and western European *C. vandesius* is found to be possibly a biological species of its own.
13. The stability of *Coregonus nasus* and some other species (*C. muksun*, *C. tugun* and *C. autumnalis*) is found to correlate to riverine life, while the multiplying species (*C. peled*, *C. pidschian* and *C. sardinella*) more easily develop lake-spawning populations. They are consequently more widely spread, from western Europe to the Atlantic drainage of North America.
14. Geographical isolation is a paramount prerequisite for speciation in *Coregonus*. Tolerance against genetic imbalance exists because of polyploid ancestry. Introgression is thus an important speciation factor.

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