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Reprinted from

BIOLOGY OF COREGONID FISHES

Edited by C. C. Lindsey and C. S. Woods

University of Manitoba Press, Winnipeg, Canada

1970

A SYSTEMATIC AND ZOOGEOGRAPHIC STUDY
OF SOME NORTH EUROPEAN COREGONIDS

by

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ABSTRACT

Geographic variation in the number of gillrakers and the geographic distribution of lavaretus whitefish from North Europe have been studied. The study is based on gillraker counts of spawning populations of C. nasus (Pallas) sensu Svärdson (1957) in the Archipelago of Åland and the Gulf of Bothnia. The study was completed with data of gillraker counts, mostly from North European whitefish collected from published and unpublished investigations. Maps showing geographic variation of means of gillraker counts are presented. Geographic clines in the gillraker counts have been found to exist in whitefish spawning in the Baltic Sea and in the rivers studied. The same phenomenon was seen in different regions of the distribution area of the lavaretus group. These clines are suggested to be genoclines, but in some cases may be caused by environmental factors. In general, clines of high counts ($X > 35$) decrease and low counts ($X < 25$) increase with increasing temperature. Gillraker frequencies of whitefish from different lakes inhabited by three or more forms, two forms, or only one form were compared. The results indicate that the lavaretus group in North Europe consists of three "cryptic species", one with high, another with low and a third with intermediate gillraker counts, probably a hybrid. The systematic position of the lavaretus group is discussed. The author's opinion is that C. nasus (Pallas) sensu Svärdson (1957) and C. pidschian (Gmelin) belong to the same species.

INTRODUCTION

The taxonomy of coregonids from western Europe is especially confusing. The lavaretus whitefish have been classified as species, subspecies, sibling species, races, ecotypes and local forms by different authors. There exist all kinds of morphological intergrades between sympatric populations of the lavaretus group, which differ in their ecology and in having different spawning times and places. There are apparent difficulties in treating the taxonomy of the Coregonus complex by a morphological "type concept". The taxonomic difficulties of whitefish have been stated to be due to their exceptional ecological plasticity and to their great variation in morphological and physiological characters. This variation, however, is mostly environmental and only partly genetic (Svärdson, 1958). It is also known that sympatric whitefish populations hybridize frequently in nature. The lack of a complete reproductive barrier between sympatric species of the lavaretus group also made it

difficult to treat them by the biological species concept. Gąsowska (1960) regards the populations of the lavaretus group as intrageneric units. Svärdson (1965) sees them as biological fractions, ecological races and spawning groups, which illustrate the most important evolutionary step, e.g. from isolated populations to the level of species. However, nobody knows which populations are most or least introgressed of probable postglacial invaders, and how many species have invaded Europe from the East, during postglacial time. As a first step in attacking this problem the author has tried to map out the morphological variation of lavaretus whitefish and correlate it to temperature conditions in the areas studied.

MATERIAL AND METHODS

This study is based partly on my own small collection of material from the Archipelago of Åland and from some localities on the Finnish coast of the Gulf of Bothnia and partly on material collected from the literature: Thienemann, 1915, 1922, 1926, 1928; Kulmatucký, 1926, 1927; Järvi, 1928, 1943, 1953, 1955; Koelz, 1929, 1931; Odenwall, 1929; Wagler, 1937; Segerstråle, 1938, and unpublished data; Weise, 1938; Wynne-Edwards, 1947; Berg, 1932, 1948; Steinmann, 1950, 1951; Pravdin, 1954; Walters, 1955; Svärdson, 1953, 1957, 1958; Dottrens, 1959; Gąsowska, 1960; Kulikova, 1960; Toivonen, 1960, and his unpublished material from the rivers Tornio and Muoniojoki 1961, and from the lake Pulmankijärve 1965; Lindsey, 1962, 1963; Peczalska, 1963; Reshetnikov, 1963; Mäkinen, 1963; Valtonen, 1964; McPhail, 1966; material collected by Kalataloussäätiö (Sormunen and Dahlström and Korhonen), 1960 - 1966, from the rivers Kemi and Iijoki, and from some lakes in the Kuusamo region.

My own material consists of eight samples of spawning populations of Coregonus nasus (Pallas) sensu Svärdson. The material was collected in the years 1962 - 1964 and includes altogether 252 whitefish. In this material the gillraker count was obtained from the anterior left gill arch, carefully dissected out under a dissecting microscope. Every bony rudiment was included. Counting was always done in the laboratory.

The average gillraker numbers have been plotted on maps and the means are presented without decimals, (16.0 - 16.9 = 16). To get a clear picture of the variability in gillraker counts for different regions the gillraker means were divided into highest and lowest recorded average number of gillrakers for different waters. Almost all samples used are representative and therefore even some smaller samples have been taken into account, but samples which are suggested to be mixed have been excluded. Frequencies of the means of gillraker numbers from different regions have been divided into classes: 16.0 - 17.9 ... 55.0 - 56.9. If, from smaller lakes, several samples of a certain whitefish species have been presented they have been combined to comprise one sample. In some cases modal values have been used as the gillraker frequencies of the sample clearly show bimodal or trimodal distribution. Transplanted populations have been excluded. It is evident that there are many sources of error as the material used in this study consists of several hundred populations examined by different investigators. The errors may be

caused by sampling, the size of the examined whitefish and the time when the samples have been collected.

DELIMITATION OF THE LAVARETUS WHITEFISH

The delimitation and subdivision of the genus Coregonus has been discussed in numerous papers. Round whitefish, whitefish and ciscoes have been alternately referred to the same genus Coregonus (Svårdson, 1957; Berg, 1948) or split off in three distinct genera (Koelz, 1929). According to present opinion whitefish and ciscoes are lumped in the same genus Coregonus, and round whitefish are recognized as a distinct genus Prosopium (Gąsowska, 1960; Norden, 1961).

Higher taxonomic categories than species are mostly based on morphological characters. As only a few morphological characters hitherto are known to be stable, there has been confusion in grouping the whitefish and ciscoes. Gąsowska (1960) has demonstrated that the genus Coregonus may be divided into four - the paralavaretus, lavaretus, leucichthys and albula groups - on the basis of the proportion and the shape of the maxillary and supramaxillary. Undoubtedly these, and the position of the upper jaw relative to the front margin of the eye, are the best morphological features to distinguish lavaretus whitefish from ciscoes. By using only secondary characters, such as the number of gillrakers, pyloric caeca, and the vertebrae, different species of the genus Coregonus may be separated rather well. Data of these three characters have been combined for the species C. albula L., C. peled (Gmelin), C. autumnalis (Pallas), for the lavaretus complex, and the artedi complex. The result is presented in a three-dimensional figure (Fig. 1). The total range of variation (R) and the range of the means (\bar{X}) are indicated for the characters. Though the material for the pyloric caeca and the vertebrae consists of only a few allopatric populations and the range of the characters of the different species overlap, we can see that the species of the leucichthys group are intermediate in position between the albula and the lavaretus groups for these characters. Gąsowska (1960) has also earlier demonstrated their intermediate position with respect to the maxillary. From all this we may conclude that C. peled (Gmelin) stays distinct from C. muksun (Pallas), and that they should be ranked as two different species (Gąsowska, 1960). C. peled (Gmelin) sensu Svårdson is apparently synonymous with C. muksun (Pallas). In Europe C. muksun (Pallas) has introgressed with other whitefish species.

From the literature (Smitt, 1886; Berg, 1948; Gąsowska, 1960; Lindsey, 1962, 1963; McPhail, 1966) it has also become evident that none of these species (C. autumnalis (Pallas), C. migratorius (Georgi), C. ussuriensis (Berg), C. tugun (Pallas), C. laurettae (Bean) and C. nasus (Pallas) are synonymous with any of Svårdson's (1957) sibling species of the lavaretus group.

The species of the lavaretus group stand relatively distinct from other species of the genus Coregonus. Exceptions are, however, Coregonus ussuriensis (Berg), which exhibits lavaretus as well as leucichthys characters (Gąsowska, 1960; Shaposhnikova, 1968) and C. nasus (Pallas) which morphologically have many lavaretus features.

THE SYSTEMATIC DIVISION OF EUROPEAN LAVARETUS WHITEFISH

The division of the lavaretus whitefish into species of north and middle Europe has been actively discussed. The most important taxonomic works are compared in Table 1. The only diagnostically valuable morphological character is the number of gillrakers combined with ecological features. These characters have been used by most investigators; their opinions are, however, contradictory. Smitt (1886), Collet (1903), Odenwall (1929), Gąsowska (1960) and Reshetnikov (1963) include all whitefish populations of northern Europe in the species Coregonus lavaretus L. Steinmann (1950, 1951) shares the same opinion regarding the Alpine whitefish in middle Europe, although he distinguishes five ecotypes. Their gillraker counts are indicated in Table 1. Berg (1932) divides C. lavaretus into two subspecies: C. lavaretus sensu str. L. and C. lavaretus pidschian (Gmelin), and distinguishes further another species C. muksun aspius (Pallas) in eastern Fennoscandia. Berg (1948) and Pravdin (1954) made, however, the systematics of Karelian whitefish complicated by naming numerous local forms. Järvi (1943)

Table 1. The average gillraker number of west European lavaretus whitefish species according to the most important systematic works. X = Range of means of the numbers of gillrakers. R = Total range of the numbers of gillrakers.

THIENEMANN 1921	JÄRVI 1943	STEINMANN 1950, 1951	SVÄRDSON 1957	DOTTRENS 1959
Fera-holsatus X 19 - 25 R 15 - 28	C. pidschian X 19 - 25 R 14 - 29	profundis X 19 - 20	C. pidschian X 19 - 20	C. arconicus X 20 - 22
		litoralis X 22 - 29	C. nasus X 23 - 24	C. fera X 24 - 25
Lavaretus X 29 - 32 R 25 - 36	C. lavaretus X 29 - 32 R 22 - 39	primigenius X 24 - 34	C. lavaretus X 33 - 34	C. lavaretus X 29 - 30
Generosus- Wartmanni X 35 - 54 R 35 - 56	C. lavaretus F. järvi X 33 - 38	pelagicus X 31 - 36	C. oxy- rhynchus X 38 - 41	C. wartmanni X 35 - 36
		nanus X 28 - 40		C. macroph- almus X 40
	C. muksun X 42 - 56		C. peled X 45 - 50	

has much the same opinion as Berg. He separates three whitefish species in Finland, namely: Coregonus pidschian (Gmelin), C. lavaretus L. and C. muksun (Pallas) all with a relatively restricted geographic distribution. Svårdson (1957), again, has concluded that the whole Palearctic region is inhabited by a group of five sympatric sibling species of the lavaretus group, namely: Coregonus pidschian (Gmelin), C. nasus (Pallas), C. lavaretus L., C. oxyrhynchus L. and C. peled (Pallas). He based his opinion on the geographic distribution of the number of gillrakers, and on a comparison of the ecology, the size differences, and spawning conditions of sympatric populations in Sweden.

The differences between the opinions of coregonid investigators are mostly due to the fact that each has examined whitefish populations from different regions, in which the populations do not differ more than allopatric populations of a certain species may be expected to do. The existence of ecologically well distinguished sympatric whitefish populations of the lavaretus group, however,

Table 2. Typical differences between lavaretus whitefish with low and high gillraker counts, in North Europe.

Character	Low counts	High counts
- Position of mouth in general	inferior	slightly terminal
- Finrays in dorsal and anal fin - on average	usually fewer	usually more
- Most important food	bottom organisms	plankton
- Span of life	long	short
- Growth capacity in northern regions	mostly good	often poor
- Biotype	rivers, lakes	lakes
- Ecological niches in lakes	benthic region	pelagic region
- Geographic distribution	abundant in northern regions	abundant in southern regions
- Their relationship to temperature	occurs mostly in cold waters	tolerates warm waters better
- Spawning places	mostly running water	often in pelagic region of lakes
- Spawning time	varies	varies

motivates a subdivision. Whitefish with high and low gillraker counts are different in many respects, especially in their ecological characters. Table 2 combines features in which north European whitefish with high and low gillraker counts differ, in general.

The variation in ecological and physiological as well as morphological properties are, however, great. They are most stable for whitefish with low gillraker counts. The genetic background for the ecological characters has not been studied, but Svärdson (1965) states that there is a genetically based tendency for diet preference. Environmental conditions should be taken into consideration as they modify most characters to a high degree.

TEMPERATURE AND THE MORPHOLOGICAL CHARACTERS OF LAVARETUS WHITEFISH

If one has to systematically classify sympatric or allopatric populations of lavaretus whitefish, the constancy of morphological characters has to be taken into account. According to experimental data (Tåning, 1944, 1950 and others) and zoogeographic studies (Jordan 1892 and others), countable characters change with environmental conditions. Svärdson (1950) has already shown that morphometric characters of whitefish are heavily influenced by environmental factors. When studying whitefish data from Koelz (1929), Berg (1948) and Lindsey (1962), one can see that the number of the dorsal fin rays increases with decreasing temperature. Another character often used in whitefish systematics is the depth of the caudal peduncle. Gąsowska (1960) distinguishes C. pidschian (Gmelin) from C. lavaretus L. by this morphological feature. From the distribution pattern of C. lavaretus L. *sensu str.* and C. lavaretus pidschian (Gmelin), according to data given by Berg (1948), it was concluded that the height of the caudal peduncle is correlated with temperature conditions. The limit between C. lavaretus and C. pidschian might roughly be drawn along the 0°C annual isotherm (Figs. 2 and 3). The increase of the peduncle ratio with decreasing temperature seems to be valid for other fish species. Data given by Lindsey (1956) for Lota lota L., were checked and plotted on a map. They correlated well with the temperature conditions. Svärdson (1965) has also stated that the depth of the body increased in whitefish transplanted into higher (colder) altitudes. The difference in predorsal length between C. albula L. and C. sardinella Val. is apparently also a morphological feature which depends on temperature. Svärdson (1957) has seen that there exist small whitefish populations with sardinella properties in Sweden. Freidenfelt's (1933) and Svärdson's (1950) material also shows that there exist whitefish populations with pidschian properties in Sweden. It does not seem reasonable to distinguish between Asiatic and European lavaretus whitefish by such features.

The main morphological feature of lavaretus whitefish is the number of gillrakers. This character has been shown to be one of the most stable morphological characters for fish in general (Frank, 1965). Svärdson (1957, 1965) has shown their polygenic character, that they are intermediate in hybrids, that they do not change with time, and that they are only slightly influenced by environmental conditions, but that they might change in response to selection. According to Järvi (1940) and others the full number of gillrakers is developed during the first year, but it has been shown that the number may increase with age and size (Pravdin, 1929; Peczalska, 1963; Svärdson, 1965). Airaksinen (1967) has found this to be valid

Fig. 2. Geographic distribution of the *lavaretus* whitefish species. Nomenclature according to Berg. (1948). 1. *Coregonus clupeaformis*. 2. *C. l. pidschian*. 3. *C. chadary*. 4. *C. ussuriensis*. 5. *C. l. baunti* (according to Anpilova, 1956). 6. *C. l. baicalensis*. 7. *C. muk-sun*. 8. *C. lavaretus sensu str.* →

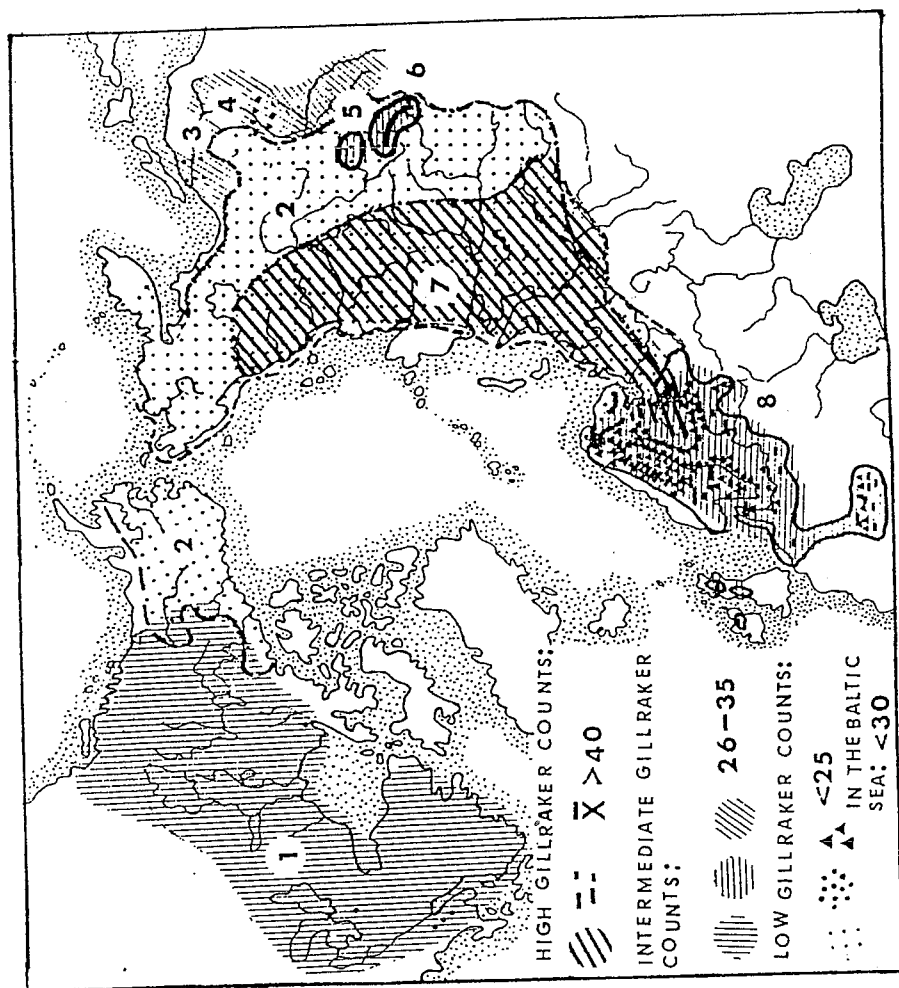
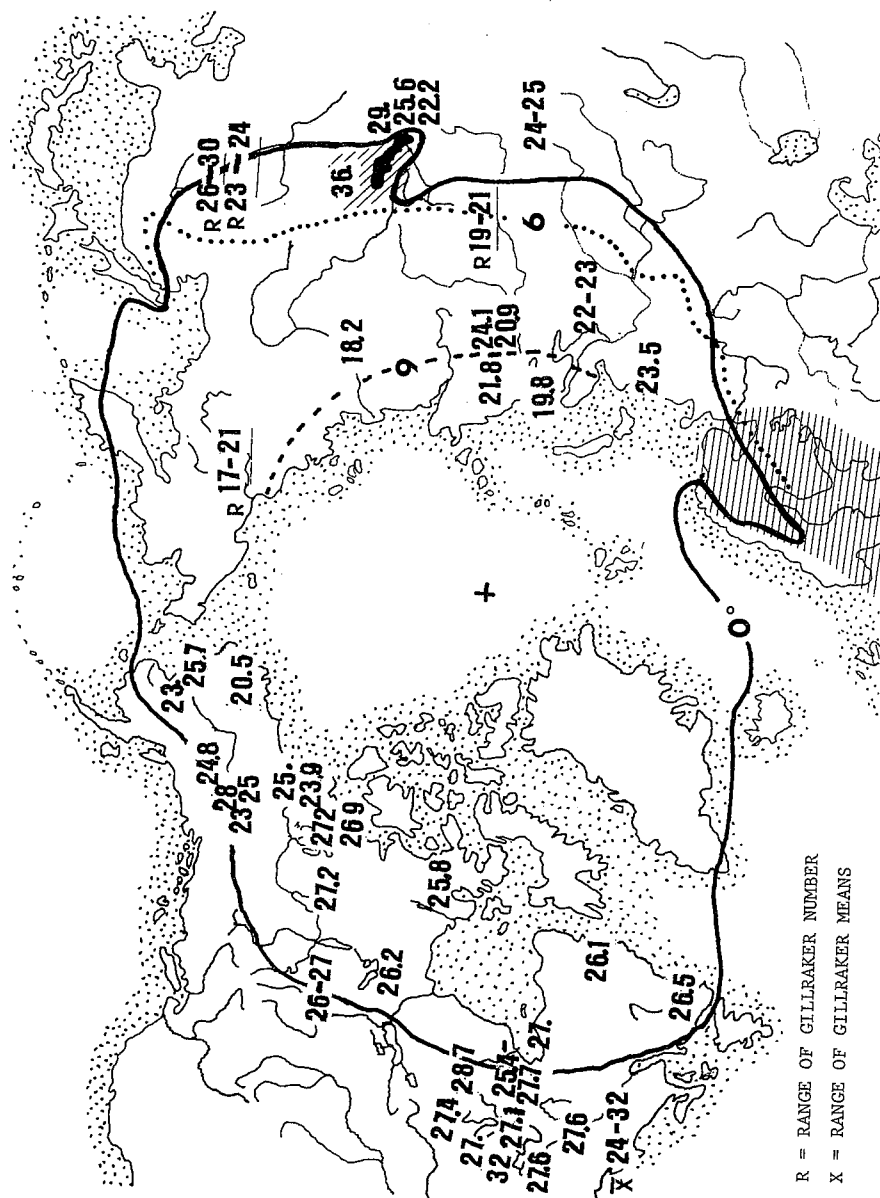


Fig. 3. Geographic variation map of the mean gillraker number of the species *C. lavaretus pidschian*, *C. ussuriensis*, *C. l. baicalensis* and *C. clupeaformis* according to data given by Koelz (1929), Berg (1948), Walters (1955) and Lindsey (1962, 1963). The 0°C annual isotherm of the Palearctic region, and the Asiatic region with six and nine month snow-blanket duration, are indicated. →



also for C. albula, and Seppovaara (1962) for Salmo salar L. When analysing Järvi's material presented by Airaksinen (1967), one can see that the average length is directly proportional to the average gillraker number. The smallest albula population differed from the biggest by 10 units in gillraker counts on the average (42 : 52). Differences in gillraker number may also be caused by Lee's phenomenon (Svårdson, 1965).

RESULTS

Fig. 2 shows the total distribution of lavaretus whitefish, and the limits of the various forms. According to Berg (1948) there are two distinct whitefish species of the lavaretus group in the western and northern part of Siberia, namely: Coregonus muksun (Pallas) and C. lavaretus pidschian (Gmelin). Coregonus muksun has 45 - 78 gillrakers; the means range between 50.8 - 64.4. The highest average gillraker number is recorded from Lake Melkoe, in the basin of Pyasina. From Fig. 4 it is found that high counts of the gillraker number decline towards the west, the north and the south from the Finnish and the Soviet-Karelian lake plateau. The highest gillraker count in the periphery in Europe is 40 - 42. Coregonus lavaretus pidschian has, according to Berg, 16 - 33 gillrakers; means range between 18.2 - 25(26). From Figs. 2 and 3 we see that average gillraker numbers increase from the cold center in Siberia towards the periphery of its distribution area. Berg (1948) does not describe any lavaretus whitefish with intermediate gillraker counts (26 - 34) in the northern part of Siberia; all populations of the lavaretus group with intermediate gillraker counts are found only south of the 0°C annual isotherm, except in North America, North Europe and the Baunt region (Fig. 3). In Europe gillraker means between 16.8 - 56.6 have been recorded. The lack of intergrades in Siberia indicates that the two sympatric lavaretus whitefish C. muksun and C. lavaretus pidschian co-exist there as two good species. As stated earlier the other Siberian Coregonus species do not belong to the lavaretus group. One might therefore suggest that Europe has been invaded by only two species during post-glacial time. The complicated taxonomic situation in Europe is apparently a result of hybridization between these two invaders. Evidence that this assumption might be correct is : 1) found in the existence of geographical clines in high and low gillraker counts 2) in comparing the means of the gillraker number from different regions of Europe, and 3) from gillraker frequencies of lakes and rivers inhabited by three or more forms, or by two forms, or by only one form.

1. The geographical distribution of gillraker numbers of North European lavaretus whitefish. Svårdson (1957) has declared that the number of gillrakers is determined by polygenes. However, how many genes are concerned is not yet known. One might suggest that there are a certain number of genes which determine on the one hand high gillraker numbers (35 - 78), and on the other hand low gillraker numbers (14 - 25). Based on this assumption we have tried to study the genetic variability of lavaretus whitefish. The material has

been divided into parts: the highest and the lowest count, according to the average gillraker number, from different regions. The results are presented in Figs. 4 and 5. For the high counts there exist obvious optimal regions in North and South Sweden, the Finnish lake district, the Soviet-Karelian lake system and in Denmark. Clear geographic clines are seen in Fig. 4. For the low counts, on the other hand, there exist clear minimal centers, (Fig. 5, but also Fig. 3). Whitefish with high and low counts have to some extent a different geographical distribution, but comparing Figs. 4 and 5 we see that extremely high and extremely low counts almost occur together. Where high counts decrease, low counts increase, in general, until they could not be separated. This suggests that populations with high and low gillraker numbers exchange genes. In regions of North Europe where there are whitefish with extremely high and low counts there are also populations with almost intermediate counts. There exist also geographic clines in gillraker counts in the Baltic Sea for the sea-spawning populations of *C. nasus* (Pallas) sensu Svärdson (Fig. 6). The average gillraker number decreases from the Archipelago of Åland, northwards along both sides of the Gulf of Bothnia and southwards along the Swedish coast of the Baltic Sea. Clines are also seen in the rivers Tornio, Muonio and Iijoke (Fig. 7). The average number of gillrakers shows a tendency to increase in populations spawning in estuaries of the basin of the Baltic Sea from the northern end of Bothnia Bay (Fig. 7).

The geographic clines may first be interpreted as genoclines. The decline for high, and increase for low, counts is a result of hybridization between whitefish populations with respectively high and low gillraker numbers. The degree of hybridization between these two forms seems to depend on the topography of the rivers and the lakes. In very deep lakes different whitefish populations do not interbreed to the same extent as in shallow lakes or in regions with easily passable rapids and in very large waters with stable temperature conditions. Lakes inhabited by sympatric whitefish populations with extremely high and low gillraker counts occur most frequently in the upper parts of the river systems in North Europe. Whitefish populations with extremely high or low gillraker counts are seldom found in the lower parts of the river systems, and they are only frequently in the upper parts of the river systems, and they are only rarely found sympatrically in shallow lakes, rivers, river estuaries or in large lakes such as Ladoga, Onega or Vänern. If there are sympatric whitefish populations in these localities, they have about 24 - 29 and 30 - 34 gillrakers on the average. In summary, from the upper lakes downstream to the estuaries of river systems in North Europe the highest and the lowest gillraker counts for sympatric populations gradually decrease and increase respectively.

Another interesting feature is that the clines for gillraker counts seem to correlate with the temperature conditions. We found that the highest and the lowest counts are recorded in almost the coldest regions in Sweden, Finland and Asia. In North America (Fig. 3) there is also a tendency for lower counts in the colder regions. Geographic clines in gillraker counts seem also to exist here. The high counts decrease with increasing temperature, in general. This phenomenon has been observed in Asia, Sweden, Finland and in the Alpine region of middle Europe. In Sweden (Fig. 4) high counts decline gradually southwards and the lowest recorded gillraker counts

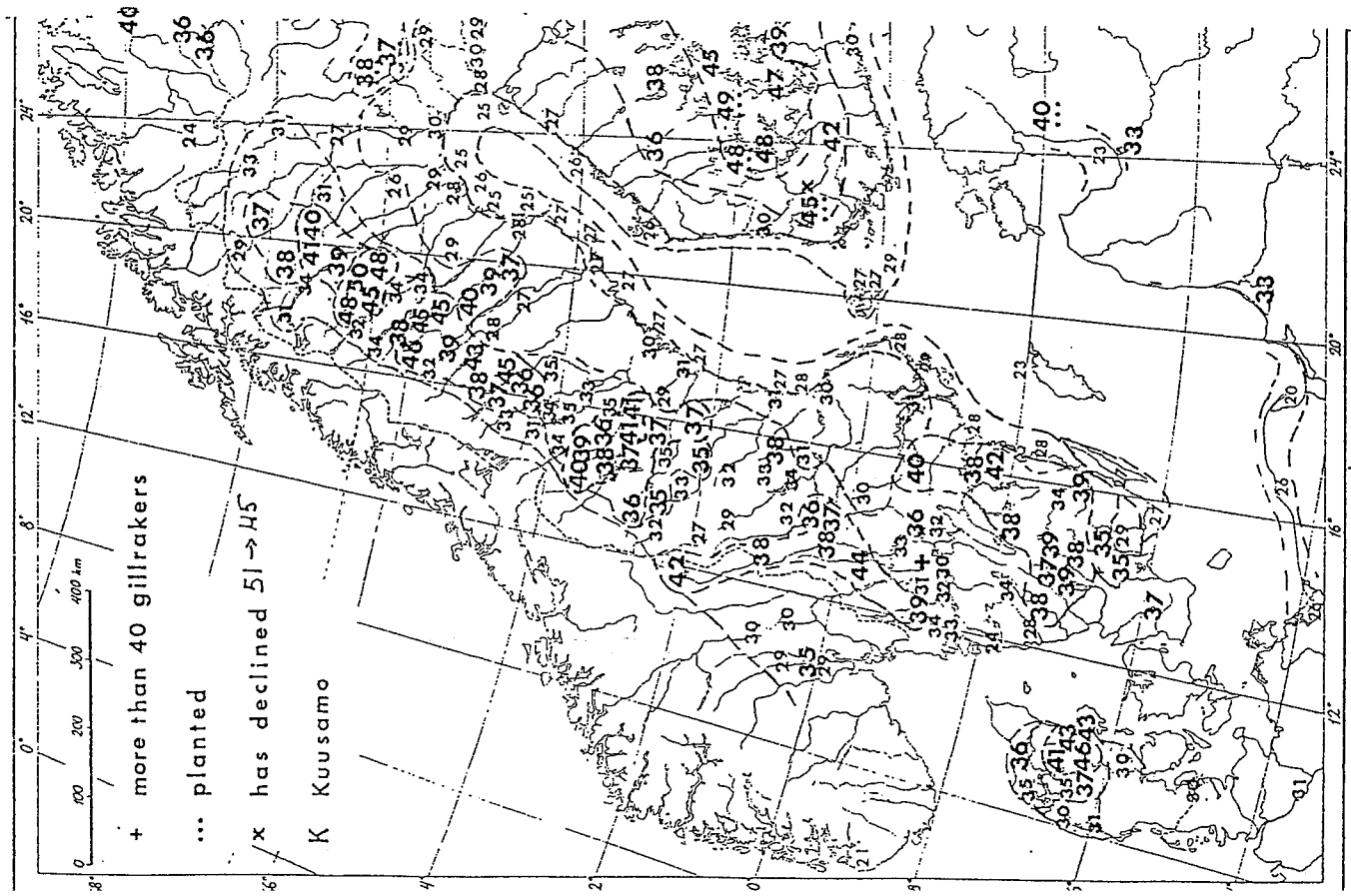
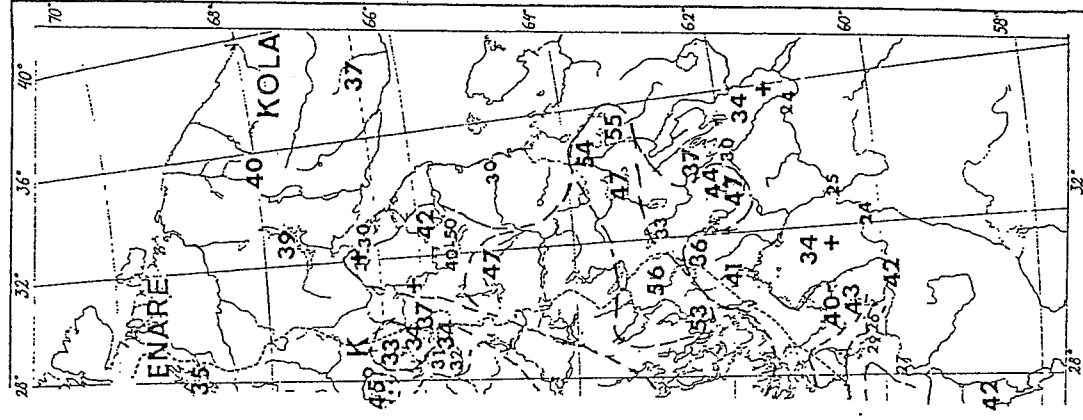


Fig. 4. Highest recorded gillraker means from different regions of North Europe. Data collected from the literature.



tend on the other hand to increase southwards in the parallel river systems. In the Alpine regions, the author found that whitefish populations with an average of over 40 gillrakers are most frequent in the top lakes of the river systems. These lakes of higher altitudes are, in general, colder. Even for other species of the genus *Coregonus* the number of gillrakers seems to correlate with temperature. There is a slight tendency towards decrease of gillraker number with higher latitude in *C. nasus* (Pallas) in Alaska (Lindsey, 1962). In the colder regions of Siberia *C. autumnalis* has more gillrakers on the average than have *C. autumnalis* populations in Alaska. The number of gillrakers also decreases in the species *Prosopium coulteri* = *Coregonus coulteri* Eigenmann and Eigenmann with decreasing latitude, according to data given by Eschmeyer and Bailey (1954). These indicate that temperature possibly has a slight direct effect on the development rate of the gillraker number. The differences in gillraker count between *C. pidschian* and *C. nasus* (Pallas) sensu Svardson are almost so small that they might be caused by different temperature conditions.

There is a third possibility to explain the geographic clines in gillraker numbers. This is that the temperature may have a selective effect on the genes which determine the number of gillrakers. From Figs. 3 and 5 we see that the low gillraker counts (if we don't distinguish the whitefish to species) increase outwards from the colder regions in Asia, North America and Europe. Whitefish populations with 29 - 32 - (36) gillrakers on average appear at first in regions with an annual temperature of approximately 0°C. The differences in gillraker number between these populations and the populations with very

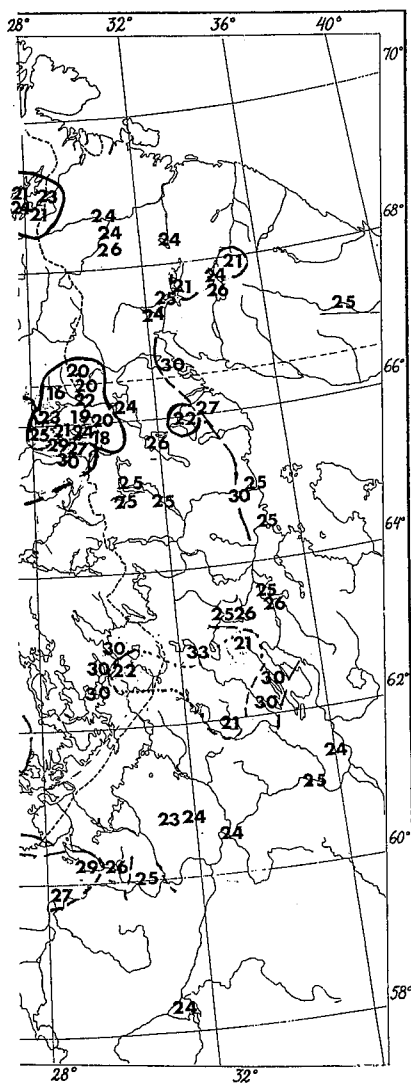
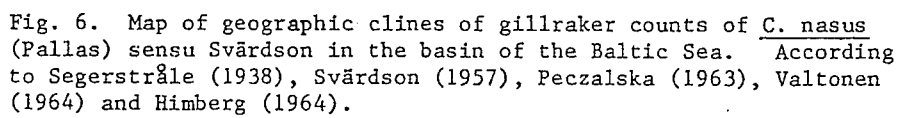


Fig. 5. Lowest recorded gillraker means from different regions of North Europe. Data collected from the literature.

low gillraker counts from colder regions are very great. Whether these differences have been influenced directly by the temperature or are a result of selection could not be judged without experimental research. Whether all whitefish populations belong to the lavaretus type is another question. It might be that all originate from the same C. pidschian type except for C. ussuriensis and C. nasus which are morphologically very distinct.

The geographic clines in the gillraker counts in the Baltic Sea cannot be judged as pure genoclines. The clines might also to some degree be caused by temperature and salinity gradients, which decrease gradually northwards in the Baltic Sea into the Gulf of Bothnia and the Gulf of Finland. To some extent, possibly, the clines in gillraker number in the Gulf of Bothnia depend on the northward decrease in size of whitefish. Experimental work is needed to be sure of the extent to which gradients in gillraker number are a product of environmental gradients (temperature, salinity).

2. The frequencies of the average gillraker count from different regions of North Europe. To estimate genetic differences between different whitefish forms inhabiting restricted areas of Europe, frequencies of mean gillraker number have been used to measure hypothetical gene-frequencies of "high" and "low" genes. The frequencies of gillraker means from different restricted areas varies, but one can recognize that the frequency distribution tends to be either tri-, bi- or unimodal. The total frequency distribution of gillraker means shows an apparent trimodal distribution for North Sweden, the Kusamo region, the Finnish lake district, and the Soviet Karelian lake district (Fig. 8). Even in



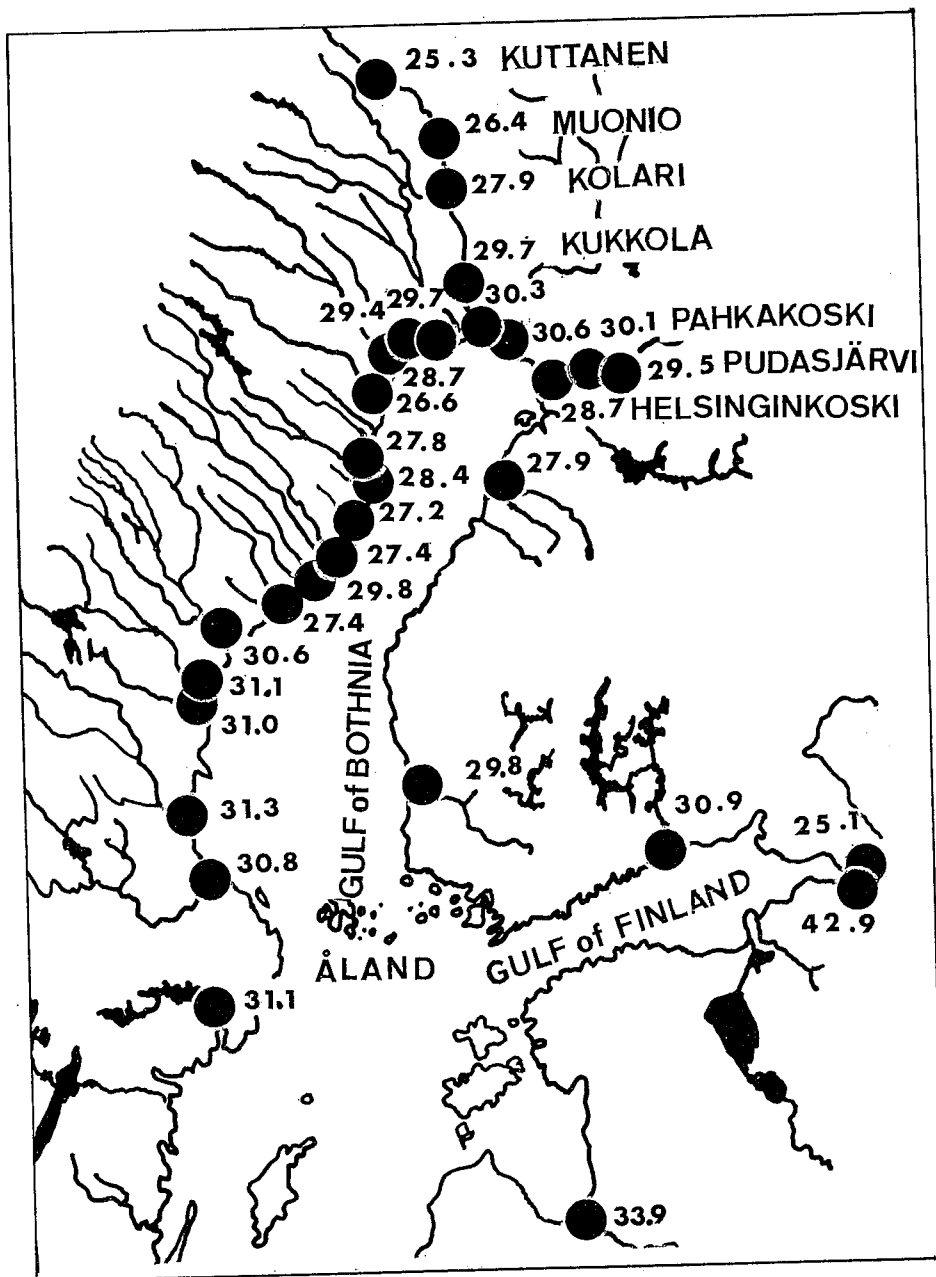


Fig. 7. Map of geographic clines of gillraker counts of *C. lavaretus* populations from estuaries of rivers descending into the basin of the Baltic Sea. According to Svärdson (1957) and for whitefish populations of rivers Tornio, Muonio and Iijoki according to Toivonen and Sormunen.

the Alpine region of middle Europe the gillraker frequency distribution shows a tendency towards trimodality. However, in the Alpine region high counts are more frequent than low counts. i.e. there are more genes for high counts than for low counts.

The situation is different in the Enare (Inari) region, the Kola Peninsula, and in the Kuusamo region (Fig. 9). The three frequency curves show the same tendency towards bimodal shape. The means of the low counts are roughly normally distributed. We suggest that all populations with low average gillraker counts

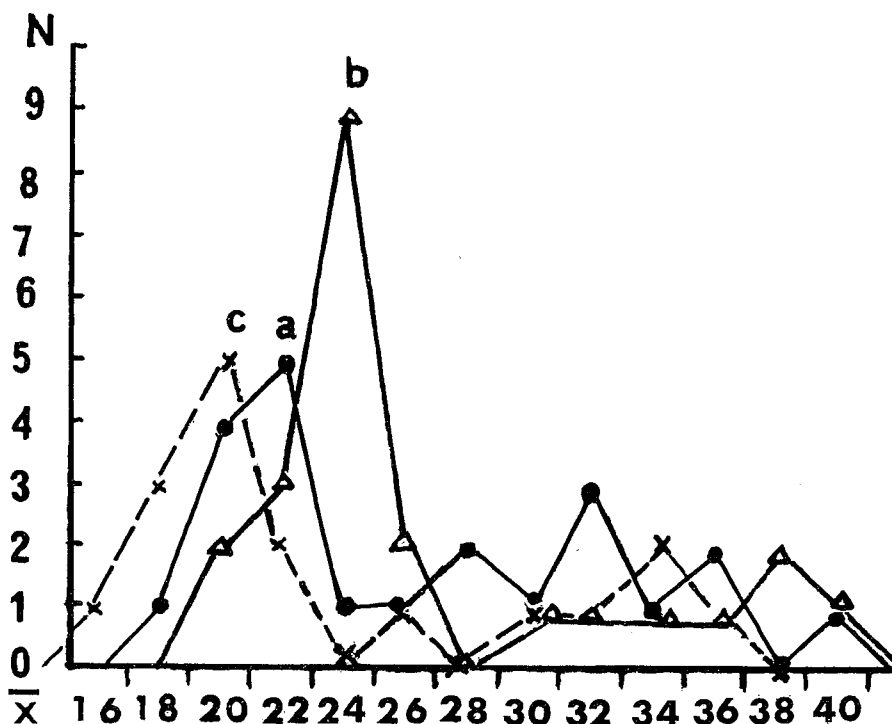


Fig. 9. Frequencies of average numbers of gillrakers from: a) Enare region (Järvi, 1928; Toivonen, 1960, 1965). b) Kola Peninsula (Reshetnikov, 1963). c) Kuusamo region (Järvi, 1943).

belong to the same species in North Europe.

The frequency distribution of mean gillraker numbers for all populations recorded in the Baltic Sea and for the estuary populations from the rivers descending into the Baltic Sea are unimodal (Fig. 10).

The trimodal frequency distribution of gillraker means for lavaretus whitefish in North Europe is remarkable. All other described species of the genus Coregonus seem to be unimodal, except

the C. artedii complex, which also exhibits a trimodal frequency distribution of gillraker means in the Great Lakes. This trimodality is suggested to be caused by genetic reasons rather than by selection. From this trimodal distribution pattern one might conclude that there exist two different types (species?) one with high gillraker count and another with low, which hybridize. Populations with intermediate gillraker counts are assumed to be heterozygotic regarding "high" and "low" gillraker genes. The differences in the numbers of gillrakers in different regions might be caused by: 1) Different degree of hybridization between different whitefish species. 2) Selection. 3) Random genetic drift. 4) Unsuitable environmental conditions for some of the different whitefish species. 5) Intra- and interspecific competition. 6) The time which has passed since the region has been invaded by whitefish. 7) Environmental changes in the region since it has been occupied by whitefish. 8) The topography of the water inhabited by whitefish as well as its latitudinal and altitudinal position. 9) Whitefish transplantation and fishing. 10) Mutation. The last point may be a rare explanation according to Kosswig (1963). Point 4) might explain the lack of low counts in the shallow lakes, in the Finnish lake plateau, Denmark and the Baltic in which temperatures increase rapidly in summer.

3. An analysis of gillraker frequencies of different Swedish lakes inhabited by three or more forms, two forms or only one whitefish form. The analysis, based on Svårdson's (1957) material, is presented in Figs. 10 and 11. In the estuaries of rivers descending into the basin of the Baltic Sea the frequency distribution of the means of gillraker numbers has a mode of 26 - 27 for populations of C. nasus (Pallas) sensu Svårdson, and 30 - 31 for C. lavaretus (Fig. 10 D, a and b). Both these species show very little variation in gillraker number. The frequency distribution of means of gillraker numbers from localities with only one recorded whitefish population is bimodal (Fig. 10 C). The modal values are 24 - 25 and 33 - 34. For localities with two populations recorded the distribution is also bimodal, with modal values of 18 - 21 and 38 - 39 (Fig. 10 B). When all counts for certain lakes inhabited by several whitefish populations have been combined together, the total gillraker frequency may exhibit an almost trimodal distribution. Therefore lakes with more than two populations have been treated as one group. The frequency distribution of average gillraker numbers for these lakes is based on few data, but the distribution is approximately trimodal. The modal values are 22 - 23, (30 - 35) and 40 - 41 (Fig. 10 A).

Comparing the range of the means in Fig. 10 we observe that it is broadest in the sample consisting of three or more populations and then gradually becomes narrower in the Figs. 10 B, C, D, a and b. This is interpreted to be caused by a different degree of hybridization. The samples in Fig. 10 A come from deep lakes, but the samples in Fig. 10 B and C are mostly from smaller lakes and rivers. In the smaller lakes all kinds of hybrid populations are common, probably due to the fewer ecological niches in smaller lakes (Svårdson, 1958), but in deeper lakes different whitefish species can

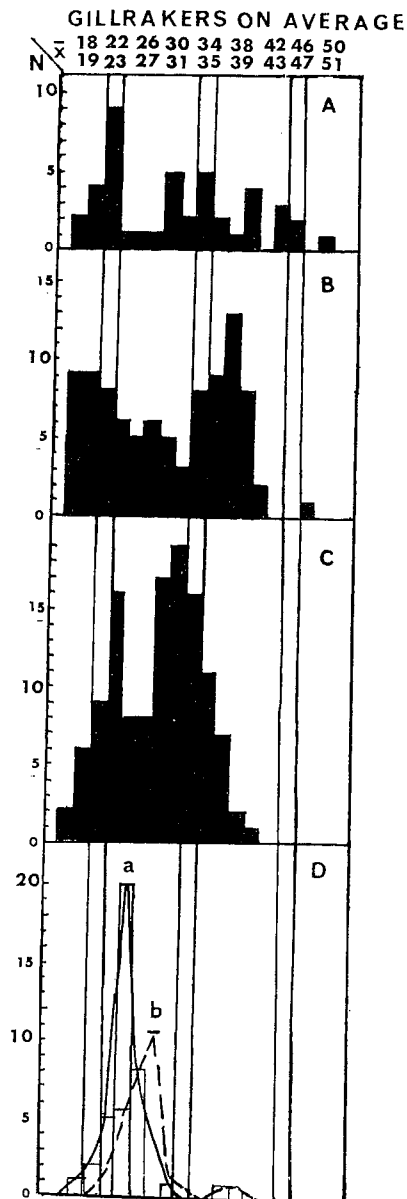


Fig. 10. Comparison of mean gillraker frequencies of whitefish populations from different Swedish water drainages according to Svärdson (1957), inhabited by: A) three or more whitefish populations, B) two, C) one recorded population, and D) - a) *C. nasus* sensu Svärdson from different localities of the Baltic basin, and b) *C. lavaretus* from different estuaries of rivers descending into the basin of the Baltic Sea.

co-exist rather well. A further analysis of lakes inhabited by three populations indicates, however, that hybrid populations might also exist here (Fig. 11). The different lakes are arranged in succession according to the population with the highest average gillraker number. In each lake the population between the two extreme populations is almost intermediate. We suggest that these populations have arisen by hybridization between whitefish with low and high counts. One might also come to the same conclusion in comparing lakes with two sympatric whitefish populations. When the gillraker count for the one population is extremely low (18 - 22) the average for the other populations is frequently more than 36. These populations are almost all found in upper lakes of river drainages, usually in deep lakes. Whitefish with average counts of 23 - 25 gillrakers occur most frequently together with populations with 33 - 35 gillrakers. These populations are mostly found in shallow lakes in the middle and lower parts of river drainages. Svärdson (1957) came to the conclusion that the whitefish populations with extremely low gillraker counts and those with 23 - 24 are two different species, *C. pidschian* (Gmelin) and *C. nasus* (Pallas). *C. pidschian* occurs together with *C. oxyrhynchus*, which is characterized by an average of 40 gillrakers. *C. nasus* occurs sympatrically with *C. lavaretus*, which is characterized by 33 - 34 gillrakers. Our opinion

is that these pairs of means represent different degrees of hybridization or are introgressed populations between whitefish with high and low gillraker counts. The effect of environmental factors should naturally be taken into account.

DISCUSSION

During the last decades modern investigators have reduced the number of species of the genus Coregonus in all parts of its distribution area to comprise relatively few species. The close relationship between the European, Asiatic and North American lavaretus

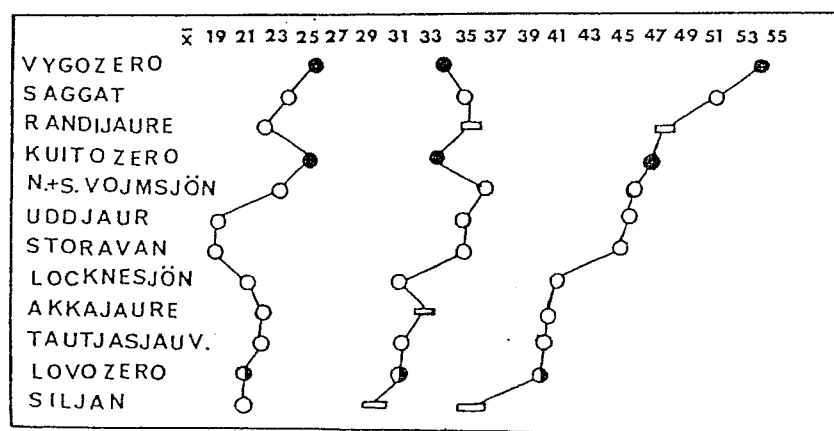


Fig. 11. Comparison of the gillraker means of north European lakes inhabited by three sympatric types. Data collected from Pravdin, 1954; Svårdson, 1957; Reshetnikov, 1963.

whitefish has been pointed out by numerous writers. It has been suggested that the numerous whitefish forms in Europe arose by rapid evolution.

Steinmann (1950, 1951) considers that the Alpine region has been invaded by one form, "Urfelchen". This has occupied the Alpine lakes during postglacial time, and it has split off in each lake into different ecotypes. A parallel process has taken place in different lakes by sympatric speciation. Steinmann has been criticised because he suggests that evolution of the ecotypes has arisen sympatrically and in a very short time. The present distribution of lavaretus whitefish species and the small variability of whitefish within other regions with similar conditions contradict Steinmann's hypothesis of sympatric speciation.

Svårdson (1958, 1961) has concluded that Europe has been invaded by five sibling species, which came in two waves. In the first wave came Coregonus pidschian, C. oxyrhynchus and C. peled, already living in the Baltic Ice Lake. In the second wave came C. nasus and C. lavaretus, rather late, during the Littorina era. C. oxyrhynchus,

according to Svärdson (1961), probably developed in the Great Siberian Ice Lake during the Riss interglacial. At the same time in other refuges lavaretus and peled evolved. Svärdson (1958) concluded that C. oxyrhynchus has the widest distribution of all whitefish species. However, lavaretus whitefish populations with gillraker averages of 38 - 40 are found only in Europe. There exists one whitefish species with gillraker averages of 40 - 46 in North Siberia, but this species does not belong to the lavaretus group. It seems questionable whether there are really two different whitefish species with high gillraker counts in Europe. In regions with extremely high gillraker counts of 45 - 50 (a characteristic feature for C. peled sensu Svärdson) there occur very few populations with averages of 38 - 40 gillrakers. Further, the geographic clines in the high gillraker counts indicate that populations with 40 gillrakers in the periphery of the whitefish distribution area have arisen by introgression. Therefore we prefer to lump C. oxyrhynchus and C. peled sensu Svärdson together to comprise only one "species" and tentatively call it the C. muksun type. Nor are we inclined to distinguish two whitefish species with low gillraker counts. We consider that C. pidschian and C. nasus sensu Svärdson belong to one "species" for the following reasons: 1) The means of low gillrakers in different regions are normally distributed. This normal distribution comprises most probably populations of the same species. According to Mayr (1963) a species consists of populations, and it is known that all populations differ genetically from one another. 2) C. pidschian and C. nasus sensu Svärdson rarely occur together. Gillraker means 18 - 21 (22) seldom occur together with 23 - 25. If they do, they are found almost always in large lakes, where the environmental conditions vary in different parts of the lake. Differences in gillraker counts might, on the one hand, reflect genetic differences, or on the other hand, purely phenotypic modifications between different populations. Populations with 23 - 25 - (29) can here have arisen by hybridization or by introgression. 3) Geographic clines in low gillraker counts have been concluded to be a result of hybridization. The correlation with temperature conditions might also partly explain the clines and the geographic distribution of the extremely low gillraker counts. 4) They do not differ in their biology. Both forms are found in cold waters, they live on the same food (mostly bottom organisms) and they both frequently exhibit a very good growth rate in northern regions.

Populations with low gillraker counts we prefer tentatively to call the C. pidschian type. The sea spawning C. nasus sensu Svärdson in the Baltic Sea probably originated from the Siberian C. pidschian, which has spread along the coast. The rather high gillraker number of C. nasus sensu Svärdson in the Baltic Sea might have arisen by a combination of introgression, selection, and influences of temperature and salinity.

If our assumption is correct that C. pidschian and C. nasus sensu Svärdson represent one "species", and C. oxyrhynchus is an introgressed C. muksun, then Europe has probably not been invaded by five sibling species. One might also reject the hypothesis of only one invader. The genetic basis for the great variability within the

European whitefish can scarcely have evolved during the 10,000 - 15,000 years since Europe has been invaded by whitefish. The extreme forms in Europe, which are two morphologically and ecologically homogenous groups, do not represent phases of one species, but comprise two different evolutionary lines, evolved in geographical isolation. Hence, Europe has probably been invaded by two or three different types.

In North Europe is the most common whitefish of intermediate type, frequently with gillraker averages of 30 - 35. Are the intermediate forms in Europe really a species which originated from the East, or are they of hybrid origin? Svärdson (1957) has demonstrated that the gillraker number is intermediate in hybrids. The hybrids are also intermediate in their diet between that of the parents (Svärdson, 1965). From Fig. 11 it was seen that in lakes with three sympatric whitefish forms there is one type whose gillraker count is almost intermediate between the extreme forms. This intermediate type has been suggested to be a hybrid. The apparent lack of such a type in Siberia strengthens the hypothesis that European whitefish with intermediate gillraker counts might either be hybrids or introgressed forms. Thus the European whitefish with intermediate gillraker numbers do not comprise a taxonomic entity. In Siberia, *C. tugun* must be excluded as a distinct species. *C. lavaretus baunti* might be an introgressed *C. muksun* population, and *C. lavaretus baicalensis* a *C. pidschian* form.

It is very unlikely that a whitefish refugium existed in Europe during the last glacial epoch. More probably the whole European whitefish stock originated from the East. The similarities between the European and the Siberian *lavaretus* fish are conspicuous, regarding both the morphology and biology. The European whitefish with low gillraker numbers and the Siberian *C. pidschian* occur especially in running waters. They occupy the uppermost part of the rivers. They are both spread along the coastal waters. The European whitefish with high gillraker number and the Siberian *C. muksun* inhabit great lakes and broad rivers; they both seem also to be better adapted to warm water temperatures than the preceding pair. The only morphological character by which European *lavaretus* whitefish and the Siberian have been distinguished is the peduncle ratio. This has been concluded to lack diagnostic value. Its correlation with temperature conditions might explain the discontinuous distribution of the *C. lavaretus* forms described by Gasowska (1960). The genoclines in the high and low gillraker counts, which gradually change westwards from the cold center in Siberia, indicate that the European *lavaretus* whitefish are a continuation of the Siberian. Because the intermediate whitefish forms in Europe are apparently hybrids or introgressed forms, it is most logical that Europe has been invaded by only two whitefish types during the postglacial time. The one type has been a *C. pidschian* and the other a *C. muksun*, which both behave as good species.

Kosswig (1963), who regards Svärdson's sibling species as ecotypes, has a similar belief in only two ancestral forms, the one a bottom feeder with a small number of brachiospines and the other a plankton feeder with numerous and long brachiospines. Kosswig

suggests that the two "species" have hybridized in a large ice lake long before it separated into different lakes of modern time. A large gene pool would have evolved. Many later formed lakes received part of this ancestral gene pool. Occupants of each lake have then evolved into as many as four ecotypes, as a result of recombination and selection in empty niches.

We find it questionable, however, whether a vigorous fusion of the two ancestral types has taken place in an ice lake. It is true that whitefish "species" of the lavaretus group frequently hybridize, and that the hybrids are fertile in later generations. Nevertheless, different whitefish forms are kept genetically isolated by size segregation (Svårdson, 1965) and by a well developed homing instinct. It is therefore more likely that the two ancestral forms have remained genetically isolated by size segregation, and have hybridized only to a small extent. Being ecologically different, they may have occupied empty niches in an ice lake, and used different spawning places, so they could later have spread widely in new water drainages, without heavy hybridization. Under suitable conditions, especially in deep lakes, they may have preserved their identity to the present time. Hybridization, where it has occurred, has possibly taken place during a long period influenced by environmental conditions.

The poorly developed isolating mechanisms indicate that the European whitefish originated from rather young species. However, the differences in morphology and biology between the Siberian C. pidschian and C. muksun are rather remarkable. C. muksun differs not only from C. pidschian, in Siberia, in having higher numbers of gillrakers, but also in having a higher number of pyloric caeca. C. muksun has 163 - 326 pyloric caeca, and C. pidschian has 90 - 267 (Behnke, personal communication). To some extent this character is a valuable diagnostic feature. The number might change with physiological conditions, but the much higher number of pyloric caeca in C. muksun than in any other species of the genus Coregonus is apparently due to genetic differences. These differences have most probably evolved in geographic isolation according to the modern theory of speciation. The geographic distribution of high and low gillraker counts indicates that they also may have developed in different regions. Lavaretus whitefish with high gillraker counts have possibly evolved in the ice free part of West Siberia, in the basin of the Ob, during the last glacial epoch. Lavaretus whitefish with low gillraker counts probably had an East Siberian origin, perhaps in the basin of the Lena. The numerous whitefish forms in Europe would hardly have evolved by sympatric speciation. This being the case, one would also expect to find numerous lavaretus forms in North America, where the same favourable environmental conditions exist.

The present distribution pattern of C. pidschian and C. muksun may be explained by their different biological properties. The wider distribution of C. pidschian is possibly due to its greater ability to disperse in running water. C. pidschian occurs especially in the uppermost parts of the rivers, and thus more easily crosses over watersheds. It seems also to be more euryhaline, and is there-

fore more easily dispersed along coastal waters. C. muksun, which occurs predominantly in broad rivers and great lakes, and is restricted to river deltas, seems to have a lower capacity for dispersal.

Zandt (1938) has concluded, based on the distribution of whitefish parasites, that Europe has been invaded by whitefish in two different waves. The scarcity of low gillraker counts in western Europe might be because C. muksun arrived earlier than C. pidschian. The distribution of C. muksun eastwards has apparently taken place more recently. According to Walters (1955) the Novosiberian ice sheet was a barrier to dispersal of some "fringe elements" of Siberian freshwater fishes. The Novosiberian ice sheet began to recede 4,000 - 6,000 years ago. Long before this time, 8,000 - 15,000 years ago, Europe was probably invaded by whitefish.

The complicated taxonomic situation in European whitefish has most probably arisen by hybridization between two ancestral forms. This might also explain the great variability and the rapidity of evolution of the lavaretus whitefish in Europe. Hybridization in freshwater fishes has been stated to be a common phenomenon in deglaciated areas (Hubbs, 1955).

The role of hybridization in whitefish speciation has been stressed by Svårdson (1957), Dottrens (1959), Kosswig (1963) and Karbe (1964). Undoubtedly there are created new types when two still fertile but genetically different whitefish stocks interbreed. By recombination and selection of genetic material from fertile hybrid populations rather stable ecotypes might be established.

The occurrence of hybrid and introgressed forms of lavaretus whitefish in North Europe makes their systematic division troublesome. No sharp limit between whitefish with low and intermediate gillraker counts, nor between whitefish with intermediate and high counts, could be drawn. Nevertheless, when all localities with three whitefish populations were combined in North Europe there could be distinguished three groups based on the frequency distribution of gillraker means, with 18 - 25, 30 - 35 and 40 - 56 gillrakers on the average. (Fig. 10 A represents only North Sweden.) They also represent three rather well defined ecological units. Under certain environmental conditions these three categories seem to behave as biological species.

If one must divide North European whitefish into systematic units, Järvi's (1943) division is, in our opinion, the best one, which corresponds to the evolutionary situation. One might call them ecotypes; however, here we tentatively call them "cryptic species". Whitefish with low gillrakers seem to be a rather homogenous group, but whitefish with high gillraker counts seem to be the most introgressed group. Based on the gillraker numbers of whitefish in North Europe, they might be divided into three types: C. pidschian type, 18 - 25 gillrakers on average; C. lavaretus type, 30 - 35 gillrakers on average; C. muksun type, 40 - 56 gillrakers on average. In the Baltic Sea we refer the sea spawning whitefish with 26 - 29 gillrakers to C. pidschian. The sea spawning whitefish and the migratory river spawner C. lavaretus behave as subspecies, as there exist intergrades between their neighbouring populations. Populations with 26 - 29 gillrakers might

be regarded as introgressed C. pidschian, and populations with 36 - 39 as introgressed C. muksun, but they might also be regarded as hybrid populations. These categories based only on the number of gillrakers are diagnostic units for comparing allopatric populations.

An adequate systematic division of the North European lavaretus whitefish, accepted by all investigators, needs further research. We suggest that comparative experimental, physiological, ecological, cytogenetical and biochemical studies, of allopatric populations might bring order to the chaotic taxonomy of whitefish.

ACKNOWLEDGEMENTS

The author is indebted to Svenska Kulturfonden, Åbo Akademi and Ålands Landskapsstyrelse, Finland, which have supported this investigation. But the author is further chiefly indebted to Prof. Bo-J. Wikgren for many suggestions and criticisms, and for very valuable support. The author wishes also to express particular appreciation to Prof. C.C. Lindsey, Dr. R. Behnke and Dr. G. Svärdson for their criticisms, and for material and data given by Messrs: J. Toivonen, T. Sormunen, H. Dahlström, M. Korhonen, B. Mollis, H. Heusala and A. Ahrner.

REFERENCES

- Airaksinen, K.J. 1967. Varmavirran muikku. Summary: The vendace (Coregonus albula L.) of Varmavirta in the northern part of lake Saimaa. Suomen kalastus (Finlands Fiskerier) 30: 1-31.
- Anpilova, V.I. 1956. (On the taxonomic position of Coregonus sardinella baunti Muchomedijarov, 1948.) Dokl. Akad. Nauk SSSR. 111: 898-900. (In Russian).
- Berg, L.S. 1932. Übersicht der Verbreitung der Süßwasserfische Europas. Zoogeografica, 1(2): 121-131.
- 1948. Ryby presnykh vod SSSR i sopredehykh stran. 4 Vol.1. Opreditelipo Faune SSSR. No. 27. Akad. Nauk SSSR. 466 pp.
- Collet, R. 1903. Meddel. om Norges Fiske 1884-1901. Vid. selsk. Forh. 9.
- Dottrens, E. 1959. Systematique des coregones de l'Europe occidentale, basée sur une étude biométrique. Rev. Suisse Zool. 66: 1-66.
- Eschmeyer, P.H. and R.M. Bailey. 1955. The pygmy whitefish Coregonus coulteri, in Lake Superior. Trans. Amer. Fish. Soc. 84: 161-199.
- Frank, S. 1965. A contribution to the knowledge of the pharyngeal filter of some species of fishes of the suborder Characinoidei and Cyprinoidei. Věstník Českosl. Acta Soc. Zool. Bohemsl. XXIX (2): 146-155.
- Freidenfelt, T. 1934. Untersuchungen über die Coregonen des Wenersees. Int. Rev. Hydrobiol. Leipzig. 30: 49-163.
- Gasowska, M. 1960. Genus Coregonus L. discussed in connection with a new systematic feature that of shape of os maxillare and os supramaxillare. Ann. Zool. Polon. 18(26): 471-513.
- Hubbs, C.L. 1955. Hybridization between fish species in nature. Syst. Zool. 4(1): 1-20.
- Jordan, D.S. 1892. Relations of temperature to vertebrae among fishes.

- Proc. U.S. Nat. Mus. Vol. XIV: 107-120, 1891.
- Järvi, T.H. 1928. Über die Arten und Formen der Coregonen s. str. in Finnland. Acta Zool. Fennica. 5:1-259 (Finland Fiskerier 10).
- 1940. Pyhäjärven siikakanta. Maataloushallituksen tiedonantoja No. 269. Suomen kalatalous, nide 14: 1-93.
 - 1943. Zur Kenntnis der Coregonenformen Nord-Finnlands insbesondere des Kuusamo-Gebietes. Acta Zool. Fennica. 40: 1-91.
 - 1953. Über die Coregonen s. str. im Päijänne und in einigen anderen Gewässern Mittelfinnlands. Acta Zool. Fennica. 74: 1-33.
 - 1955. Über eingeführte Maränenbestände in einigen Kleingewässern der Gegend von Rovaniemi in Nordfinland. Acta Zool. Fennica. 89: 1-74.
- Karbe, L. 1964. Die Chromosomenverhältnisse bei den Coregonen des Bodensees und einiger weiterer voralpiner Seen, ein Beitrag zum Problem der Speciation in der Gattung Coregonus. Z. Zool. Syst. Evol. 2: 18-40.
- Koelz, W. 1929. Coregonid fishes of the Great Lakes. Bull. U.S. Bur. Fish. 43(2): 297-643. (Document No. 1048).
- 1931. The coregonid fishes of Northeastern America. Pap. Mich. Acad. Sci. 13: 303-432. 1930.
- Koli, L. 1969. Eräistä kalastomme taksonomisista kysymyksistä. Luonnon tutkija 73(3): 93-105.
- Kosswig, C. 1963. Ways of Speciation in Fishes. Copeia 1963(2): 238-244.
- 1964. Problems on polymorphism in fishes. Copeia 10: 65-75.
- Kulikova, K.E. 1960. Sigi Yamala. Trudy Inst. Okeanologii Akad. Nauk. SSSR. 31: 111-144.
- Kulmatycki, W.J. 1926-1927. Studien an Coregonen Polens. Arch. Hydrobiol. Ichtyol. Suwalki. 1(4): 275-356. 2(1/2): 1-40.
- Lindroth, A. 1957. A study of the Whitefish (Coregonus) of the Sundsvall Bay District. Rep. Inst. Freshw. Res. Drottningholm, 38: 70-108.
- Lindsey, C.C. 1956. Distribution and taxonomy of fishes in the Mackenzie drainage of British Columbia. J. Fish. Res. Bd Can. 13(6): 756-789.
- 1962. Distinction between the Broad Whitefish Coregonus nasus and other North American Whitefishes. J. Fish. Res. Bd Can. 19(4): 687-714.
 - 1963. Sympatric occurrence of two species of humpback whitefish in Squanga Lake, Yukon Territory. J. Fish. Res. Bd Can. 20(3): 749-767.
- Lindström, Th. 1962. Life history of whitefish young (Coregonus) in two lakes reservoirs. Rep. Inst. Freshw. Res. Drottningholm, 44: 113-144.
- Mansfield, W. 1930. Studien an Coregonen des Ostbaltikums. Arch. Hydrobiol. 21: 65-94.
- Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Mass. 630 p.
- McPhail, J.D. 1966. The Coregonus autumnalis-complex in Alaska and northeastern Canada. J. Fish. Res. Bd Can. 23(1): 141-148.
- Mäkinen, K. 1963. Eräiden Pohjois-Karjalan järvien siikamuodoista. (Mimeo.) The Univ. of Helsinki, Helsinki, 63 p.

- Nikanorov, Yu.I. 1964. Morphological peculiarities of local stocks of European cisco (Coregonus albula) depending on conditions of existence (Russian). Voprosy Ichtiol. Vol. 4: 3(32): 411-422.
- Norden, C.R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (Thymallus arcticus) and its phylogeny. J. Fish. Res. Bd Can. 18(5): 679-791.
- Odenwall, E. 1929. On the classification of the various forms of Coregoni s. str. of Northern Europe. Memoranda Soc. Fauna et Flora Fennica. 5: 116-125.
- Peczalska, A. 1963. Badabia nad sieja (C. lavaretus lavaretus L.) zatoki Pomorskiej I salewu Szczecinskiego w latach 1956-1958. Prace Morskiego Instytutu Rybackiego w Gdyni Nr 11/A: 287-320.
- Redeke, H.C. 1934. Über den Rheinschnäpel, Coregonus oxyrhynchus L. Verh. intern. Ver. Teoret. u. angew. Limnologi. VI(2): 352-357.
- Reshetnikov, Yu. S. 1963. Ob ismenchivosti sigov (Coregonus variability). Zoologicheskyy Zhurnal. Tom XLI. Vyp. 8: 1187-1199.
- Pravdin, I.F. 1929. Sunskii sigi, Coregonus lavaretus lavaretoides Poljakow natio sunensis nova. Sistematika. Izv. Otdela prikladnoi Ikhtiol. 10(1): 166-235.
- 1954. Sigi vodojemov Karelo-Finskoj SSR. Akad. Nauk. SSSR. Moskva 1954. 324 p.
- Segerstråle, C. 1938. Fiskeribiologiska undersökningar rörande sik (Coregonus lavaretus L.) och gös (Lucioperca sandra) i östligaste delen av Finska viken. (Unpublished manuscript, 1938) Kalataloudellinen tutkimustoimisto. Helsinki.
- Seppovaara, O. 1962. Zur Systematik und Ökologie des Lachses und der Forellen in den Binnengewässern Finnlands. Ann. Zool. Soc. "Vanamo". 24: 1-86.
- Shaposhnikova, G.Kh. 1968. Sravnitelno-morfologicheskii analiz, sigov Sovetskogo-Souza. (Comparative morphology of the whitefish (Coregoninae) from the USSR.) Trudy Zool. Inst. Akad. Nauk. SSSR. 46: 207-256.
- Smith, S.H. 1957. Evolution and distribution of the coregonids. J. Fish. Res. Bd Can. 14(4): 599-604.
- Smitt, F.A. 1886. Kritisk förteckning öfver de i Riksmuseum befintliga Salmonider. Kongl. Svenska Ver. Akad. Handl. Bd. 21(8): 1-290.
- Sormunen, T.H. Kemijärven säästöelälyn kalataloudellinen ja limnologinen tutkimus. I. Kalataloussäätiön monistettuja julkaisuja. 8: 1-90. (Mimeo.).
- Alustava lausunto Kuusijoen Myllykoskeen rakennetun vesivoimalaitoksen vaikutuksesta Kuusijokeen ja sen vaikutuksesta kalatalouteen. Kalataloussäätiön monistettuja julkaisuja. 30.
- Sormunen, T.H., H. Dahlström, M. Korhonen and I. Iijokilausunto. Kalataloussäätiön monistettuja julkaisuja. 7: 1-37.
- Steinmann, P. 1950-1951. Monographie der schweizerischen Koregonen. Beitrag zum Problem der Entstehung neuer Arten. Schweiz. Zeitschr. Hydrol. 12: 109-189, 340-491.
- 1951. Monographie der schweizerischen Koregonen. Schweiz. Zeitschr. Hydrol. 13: 54-155.
- Svärdson, G. 1945. Chromosome studies on Salmonidae. Rept. Inst. Freshw. Res. Drottningholm, 23: 1-151.
- 1949. The Coregonid problem. I. Some general aspects of the

- problem. Rept. Inst. Freshw. Res. Drottningholm, 29: 89-101.
- Svårdson, G. 1950. The Coregonid problem. II. Morphology of two Coregonid species in different environments. Rept. Inst. Freshw. Res. Drottningholm, 31: 151-162.
- 1951. The Coregonid problem. III. Whitefish from the Baltic, successfully introduced into freshwater in the North of Sweden. Rept. Inst. Freshw. Res. Drottningholm, 32: 79-125.
 - 1952. The Coregonid problem. IV. The significance of scales and gillrakers. Rept. Inst. Freshw. Res. Drottningholm, 33: 204-232.
 - 1953. The Coregonid problem. V. Sympatric whitefish species of Lakes Idsjön, Storsjön and Hornavan. Rept. Inst. Freshw. Res. Drottningholm, 34: 141-166.
 - 1957. The Coregonid problem. VI. The Palearctic species and their intergrades. Rept. Inst. Freshw. Res. Drottningholm, 38: 267-356.
 - 1958. Interspecific hybrid populations in Coregonus. Uppsala Universitets Årsskrift 6: 231-239.
 - 1959. Sikarna i Locknesjön. Svensk Fiskeritidskrift. 68: 137-139.
 - 1961. Young sibling fish species in northwestern Europe. In: W.F. Blair, ed. Vertebrate speciation. Univ. Texas Press. 498-513.
 - 1965. The Coregonid problem. VII. The isolating mechanisms in sympatric species. Rept. Inst. Freshw. Res. Drottningholm, 46: 95-123.
- Thienemann, A. 1915. Untersuchungen an Coregonen. Arch. Hydrobiol. 13: 415-471.
- 1922. Weitere Untersuchungen an Coregonen. Zeitschr. Fischerei. N.F. Bd. 1: 168-196.
 - 1926. Coregonen aus dem Ladogasee. Vanamon Julkaisuja. 6(7): 1-8.
 - 1928. Über die Edelmaräne (Coregonus lavaretus forma generosus Peters) und die von ihr bewohnten Seen. Arch. Hydrobiol. 19: 1-36.
- Toivonen, J. 1960. Inarin ja sen lähijärvien kääpiösiiloista. Maataloushallituksen kalataloudellinen tutkimustoimisto. Monistettu ja julkaisuja No. 12. 45 p. (Mimeo.)
- Täning, A.V. 1944. Experiments on meristic and other characters in fishes. Meddelelser fra Komm. fra Danmarks Fiskeriog Havundersogelser. 11: 1-57.
- 1950. Influence of the environment on number of vertebrae in teleostean fishes. Nature, 165: 28.
- Valtonen, T. 1964. Perämeren merikutuisesta siikakannasta. Suomen kalastuslehti. 5: 147-149.
- Wagler, E. 1937. Die Coregonen in den Seen des Voralpengebietes. IX. Die Systematik der Voralpencoregonen. Int. Rev. Hydrobiol. 35: 345-446.
- Walters, V. 1955. Fishes of western Arctic America and Eastern Arctic Siberia. Bull. Amer. Mus. Nat. Hist., 106(5): 261-368.
- Wynne-Edwards, V.C. 1952. Freshwater Vertebrates of the Arctic and Subarctic. Bull. Fish. Res. Bd Can., 94: 10-16.
- Zandt, F. 1938. Die Einwanderung der Coregonen in ihre heutigen Wohnbezirke. Arch. Hydrobiol. 33(4): 688-699.

Appendix 1 (= Tables 3 - 9).

Table 3. Frequencies of gillraker counts in whitefish samples from the Pulmankijärvi (1965) (Utsjoki region) according to data given by Toivonen (unpublished).

<u>Lake</u>	<u>Date</u>	20	21	22	23	24	25	26	27	28	N	mean			
Pulmankijärvi	Sept. '65	1	1	4	4	5	4	2			21	23.5			
		35	36	37	38	39	40	41	42	43	44	45	46	N	mean
"	"	1	1	1	2	1	2	3	3	1	-	-	1	16	40.6

Table 4. Frequencies of gillraker counts in whitefish samples from the rivers Tornio- and Muoniojoki (1961) according to data given by Toivonen (unpublished).

Locality	Date	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	N	mean
Enontekiö																		
Kuttanen	?		1	-	1	-	-	1									3	25.3
Muonio																		
Muonionalusta	Oct.'61	1	-	4	5	4	8	3	2	4	5						36	26.4
Kolari	Oct.'61				2	5	2	-	5	1	1	1					17	27.9
Kukkola	Oct-Nov.'61				1	-	3	8	8	9	1	2	2	3	1		38	29.7

Table 5. Frequencies of gillraker counts in whitefish samples from the river Ijoki according to Sormunen *et al.* (unpublished).

Lake, locality	Date	24	25	26	27	28	29	30	31	32	33	34	35	36	N	mean
Helsginkoski	Oct-Nov.'62	2	2	1	5	13	5	8	3	1	2				42	28.6
Pahkakoski	Oct-Nov.'62		1	4	5	11	18	8	14	12	4	4	2	1	84	30.1
Pudasjärvi	Oct.'60			1	4	6	5	9	4	2	2				33	29.5
Iijärvi	Oct.'66			30	-	34	(range)								10	32.4
Poussunjärvi	Sept.'66			30	-	34	(range)								4	31.8
Soivio	Sept.'66			24	-	33	(range)								26	29.1
Livojärvi	Oct.'66			19	-	39	(range)								37	25.2

Table 6. Frequencies of gillraker counts in whitefish samples from the Kuusamo region according to data given by Sormunen (1966, unpublished).

Lake, locality	Date	N	mean
Varisjoki	Oct.'66	29 - 38 (range)	26 33.9
Suinkki	"	16 - 38 (")	48 28.8
Kiitama	"	16 - 25 (")	5 19.8
Kuusamojärvi	"	16 - 32 (")	53 22.7
Kirpisto	"	17 - 36 (")	32 22.8
Virrassalmi	"	23 - 33 (")	43 27.5
Muojärvi	"	19 - 28 (")	40 24.4

Table 7. Frequencies of gillraker counts in whitefish samples from the Gulf of Finland. Data according to Segerstråle (unpublished).

Locality	Date	22	23	24	25	26	27	28	29	30	31	32	N	mean
Kyrosenniemi	Oct-Nov.'36				1	1	4	3	6	6	6	1	28	29.1
Kuokkala	Nov.'36	1	-	2	2	3	3	6	1	1	1		20	26.9

Table 8. Frequencies of gillraker counts in sea spawning whitefish samples from the Archipelago of Åland, Himberg (1964).

Locality	Date	21	22	23	24	25	26	27	28	29	30	31	32	33	34	N	mean
Langgards-	17.10.'64			1	1	4	5	4	3	4	1					23	27.4
odavik	1.11.'64			3	1	4	4	5	8	2	1	1				30	27.9
Bertbyvik	11.11.'64			1	1	3	2	1	5	4	2					19	27.2
Foglo	2.11.'64			1	3	5	5	5	5	4	-	1	-	1		30	27.8
Kokar	15.11.'62	1	-	1	3	3	5	11	6	3	8	4	3	2		50	29.0

Appendix 1 (contd.)

Table 9. Frequencies of gillraker counts in sea spawning whitefish samples from some localities along the Gulf of Bothnia, Himberg (1964).

Locality	Date	21	22	23	24	25	26	27	28	29	30	31	N	mean
Maakalla	16.10.'64	1	1	2	8	11	9	5	10	3	2		52	26.0
Maxmo	26.20.'64					2	5	1	1				9	26.1
Malax	26.10.64		1	-	5	4	5	7	6	-	-	1	29	26.2