FISHERY BOARD OF SWEDEN

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DROTTNINGHOLM

Report No 55

LUND 1976
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Contents

Age at Maturity, Testicular Development and Seasonal Changes in the Testes of the Ide *Idus idus* (L.) (Pisces, Cyprinidae) in the River Kävlingeån, South Sweden

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I. INTRODUCTION

There are few studies of the spermatogenesis of fish and most information available has been summarized, for instance, by HENDERSON (1962) and DIXIT and AGRAWALA (1974). No work on the sexual development of the male ide, *Idus idus* (L.), has been carried out, as far as I am aware.

The main purpose of the present research was to establish at what age the male ides in a population inhabiting the River Kävlingeån, South Sweden, reach maturity and to describe the development of their spermatogenic cycle in relation to the environment.

II. MATERIAL AND METHODS

The fish material was collected in the lower part of the River Kävlingeån from April 1966 to March 1967. For a description of the area, see CALA (1970 a). The age of the fishes was determined by examination of the scales, and their total length (tip of the snout to tip of the tail, lobes compressed) was measured to the nearest millimetre.

The males were either kept alive (<36 hours) until used or dissected immediately. The gonads from immature individuals were removed and fixed *in toto* in Bouin's fixative (25 parts sat. aqueous picric acid, 5 parts 40 % formaldehyde and 1 part glacial acetic acid). But only part of the gonad of mature fish, or of fish about to spawn in the next spawning season was fixed. Young-of-the-year ide were fixed *in toto* in Bouin's fixative, larger specimens were opened ventrally to allow the fluid to penetrate efficiently.

Subsequently the material was washed several times in 70 % ethanol. Transversal sections of about 5 mm in length, each of which produced 10 slides with approximately 10 sections per slide, were taken from anterior, central, and posterior portions of the testis of each fish, except fry shorter than 44 mm on which sections were made through whole body. The sections were dehydrated in tetrahydrofuran and embedded in paraffin. Sections were cut at 8 μm and stained with Heidenhain's haematoxylin, and with Ehrlich's haematoxylin and eosin. The later technique, however, was inadequate for the differentiation of the spermatogenic stages. In all, about 1150 slides were prepared from 37 fishes (Table 1).

III. GENERAL STRUCTURE OF THE TESTES

The testes are paired elongate organs, extending back from a blunt anterior tip to join at a point

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Table 1. *Testicular histology and spermatogenic development in the ide from the River Kävlingeån (1966—67) in relation to body length and age.*

Stage of spermatogenic development	Length of the ide in mm			Age group
	No.	Mean	Range	
1	2	44	43—45	0 (July)
1	3	58	57—59	0 (Sept.)
2	2	64	61—66	0+
3	1	147	—	II
3	9	209	180—261	III
3 and 4	2	287	275—300	IV
3, 4 and 5	2	435	395—475	VI
3, 4 and 5	5	439	425—453	VII
3, 4, 5, 6 and 7	5	463	455—473	VIII
3, 4 and 5	2	478	475—482	IX
3, 4 and 5	4	482	440—505	X

just prior to the common sperm duct, covering almost the full length of the coelom.

In this study the spermatogenic process of the ide has been divided into three stages in the immature fish and four in the mature specimens, on the basis of the morpho-histological changes in the testes.

Immature ide

STAGE 1. Gonad invisible. This stage prevails in fry up to about 50 mm in length, corresponding the size obtained during their first growth season (Fig. 1).

STAGE 2. Sexually undifferentiated gonad. Consisting of a pair of strings located in the body cavity ventral to the kidneys and lateral to the gas bladder, and being firmly attached to the body wall. The gonad consists of different types of cells, including the reproductive ones which at this stage are still sex undifferentiated (fig. 2). At this stage the internal structure of the gonad is diffuse.

STAGE 3. Formation of spermatogonia. Early at this stage, the internal structure of the testes is still ill-defined since the lobules are small and lumina are not formed until germ cell proliferation is well under way. The interlobular spaces are filled with dense stroma consisting of loose connective tissue, blood vessels and lymph spaces (Figs. 3 and 4).

The wall of the lobule is composed of a layer of fibrous connective tissue which has been termed the "lobule boundary cells" by MARSHALL and LOFTS (1956). The periphery of the lobule is occupied by primordial germ cells (PGC) which are easily recognized since they occur in clusters and are the largest cells found in the testis (Fig. 4). These cells undergo division. Some of the division products form the primary spermatogonial, the remainder constitute a reserve of primordial cells which persist throughout all stages of the spermatogenic cycle.

Later on during this process, the lobules are filled with aggregates or cysts of spermatogonia. Each cyst arises from a number of consecutive divisions of a single primary spermatogonium and is surrounded by a thin membranous capsule that appears to be continuous with the boundary cell layer. A rapid thickening of the walls of the lobules occurs thereafter (Fig. 5).

Mature ide

STAGE 4. Beginning of maturing or formation of the first spermatocytes. Through this stage (mid July to about mid November) the spermatogonia become clearly organized in clusters well separated from each other, the lumina are highly distinct, and the walls of the lobules or boundary cell layer increase in thickness (Fig. 6). The testes have reached intermediate size. Thus, male

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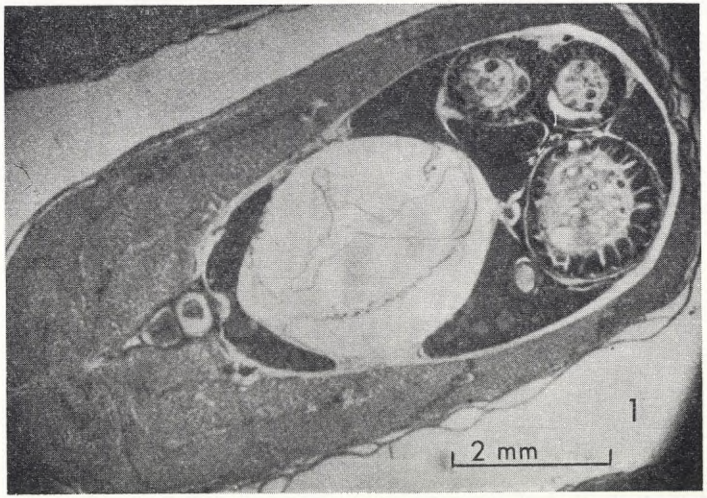
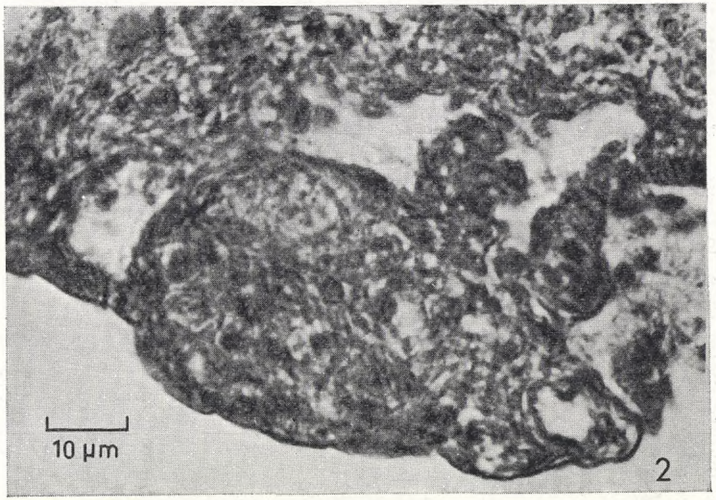
All photomicrographs are of transverse sections cut at 8 µm and stained with HEIDENHAIN's haematoxylin.

1. Mid section of a 32 mm-long ide fry, caught on 20 July 1966, showing the site for the future pair of gonads ventral to the kidneys and lateral to the air bladder.
2. Posterior section of a gonad of 61 mm total length (age group 0+) ide, showing sexually undifferentiated gonad (CALA 1970 b, Fig. 2).
3. Anterior portion of testis of 147 mm total length (age group II) immature ide, collected on 6 May 1966, showing early stage 3.
4. Anterior region of testis of 215 mm total length (age group III) immature ide, collected on 27 April 1966, showing the "lobule boundary cells" (arrow), primordial germ cells (PGC) and lumen (L). Early stage 3.


1
2 mm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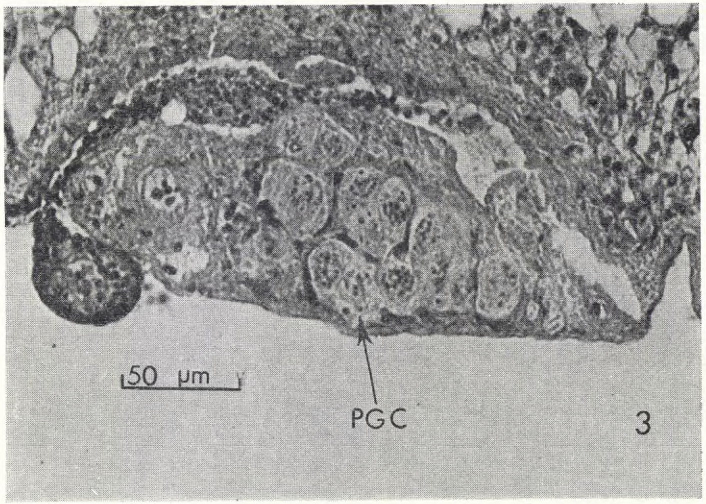
50 µm
PGC
3


30 µm
PGC
L
4

ide in stage 4 (with spermatocytes) may be considered mature, *i. e.* they will spawn in the next spawning season. At the end of this stage, the boundary cell layer of the lobules starts to become thinner, the cysts of spermatogonia become more clearly separated and the size of the lobules continues to increase owing to the formation of more cysts and repeated spermatogonial divisions within each cyst (Fig. 7).

STAGE 5. Formation of spermatids and spermatozoa. During this stage (mid November to late March), the external appearence of the testes changes from reddish to whitish, indicating the presence of spermatozoa (CALA 1971). This macroscopical observation was confirmed by the present histological study of the ide testes. Now, the cysts of spermatogonia are much more clearly separated, the interlobular connective tissue starts to reduce and breaks down at places, thus allowing passage of spermatozoa (Figs. 7 and 8).

Germ cell maturation begins in a small number of lobules which lie adjacent to the sperm duct. Observations of the number of spermatocytes per cyst suggest that each of the cellular units arises from several divisions of a single primary spermatogonium (Fig. 7). The membrane surrounding a cyst breaks down when the enclosed cells reach a late spermatid stage and the spermatids complete metamorphosis or maturation while lying free in the lumina (Figs. 7 and 8).

A cyst matures as an independent entity. Almost all its cells are in the same spermatogonic stage at any one time. and there is no serial development of the cysts along the main axis of the lobule (Fig. 7). The lobules near the sperm duct contain a larger proportion of spermatocytes, spermatids, and mature sperm than do those farther from the sperm duct.

At the end of this stage (February—March), the picture has changed, chiefly by the appearance of a larger amount of mature sperm in the lobules. Thus, only about one month before the spawning, the lumina become filled with spermatozoa which lie free within the cavities (Fig. 9). Even now, all stages of spermatogenesis are recognizable. Finally, mature sperms are discharged from the lobules and begin to fill the efferent sperm ducts.

STAGE 6. Completely mature viable spermatozoa. In this stage, late March to mid April (CALA 1970 a), the males are physiologically ready to spawn. Spermatozoa are shed when the fish is stripped. The lumina are packed with spermatozoa, and clusters of primordial germ cells occur at the margins of the lobules, but spermatogonial, spermatocyte and spermatid stages are absent. The primary and secondary sperm ducts are filled with mature spermatozoa (Fig. 10).

STAGE 7. Period of involution. After spawning (April to May) the connective tissue collapses, the walls of the lobules grow thicker again, and the diameter of the lobules becomes smaller. A large proportion of the mature spermatozoa are not shed during the spawning time, but are retained within the seminiferous lobules as well as the efferent duct system (Figs. 11 and 12). Residual sperm in the lobules was observed as late as in November, *i.e.* about seven months after the spawning period. In optimal weather conditions most of the ide spawn during two to three days (CALA 1970 a). TURNER (1919), MATHEWS (1938) and JAMES (1946) observed residual sperm in the lobules of fishes captured one to two months after

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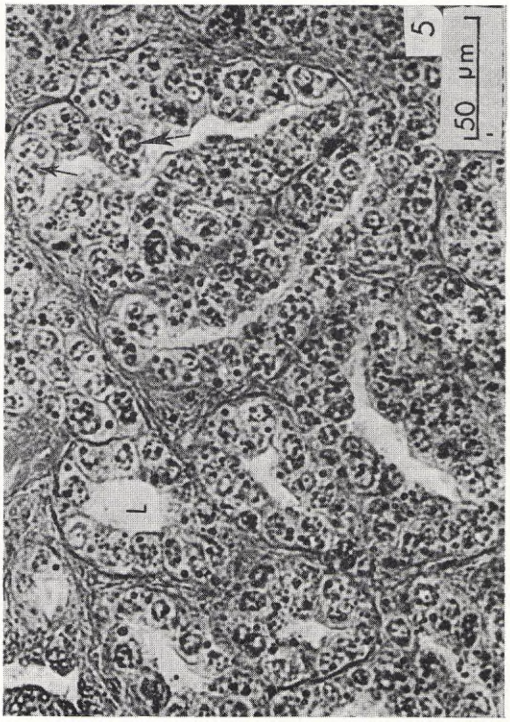
All photomicrographs are of transverse sections cut at 8 µm and stained with HEIDENHAIN's haematoxylin.

5. Anterior part of testis of 395 mm total length (age group VI) immature ide, caught on 5 December 1966, showing cysts of primary spermatogonia (arrows), thick boundary cell layer, and large lumina (L.). Advanced stage 3.
6. Anterior section of testis of 485 mm total length (age group X) mature ide, netted on 11 September 1966, showing thicker walls of the lobules, highly distinct lumen (L), secondary spermatogonia (SPG) clearly organized in clusters and formation of first spermatocytes (arrow). Stage 4.
7. Anterior portion of testis of 482 mm total length (age group IX) mature ide, caught on 21 November 1966, showing much more clearly separated cysts of spermatogonia in advanced stage of development and formation of first spermatids (arrow). Early stage 5.
8. Anterior part of testis of 500 mm-long (age group X) mature ide, caught on 27 February 1967, showing spermatogonia (SPG), spermatocytes (SPC), spermatids (SPT) and spermatozoa (SP). The membrane surrounding the cysts is in the process of breaking down. Advanced stage 5.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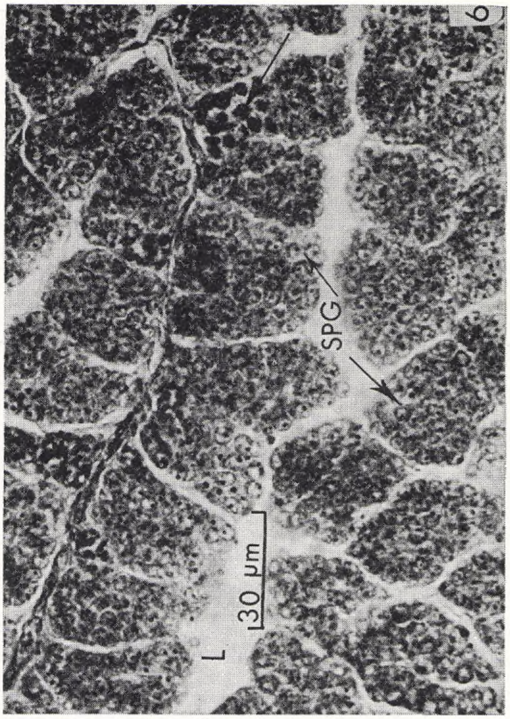
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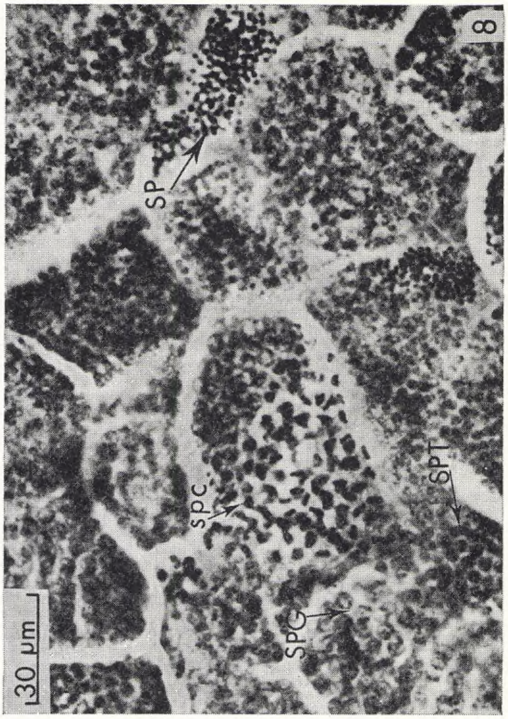
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the spawning season. HENDERSON (1962) found that the removal of residual sperm frequently takes as long as six months in laboratory stocks of brook trout.

During this period, the primordial germ cells again begin a phase of intense spermatogenic activity, forming the early generations of spermatogonia which will give rise to mature gametes at the end of the following reproductive cycle. Meanwhile, phagocytes invade the lobules and sperm ducts and engulf the residual sperm.

IV. DISCUSSION

Age at maturity

The first sign of a sexually undifferentiated gonad appeared (in ide from River Kävlingeån) after the first growth season, *i.e.* in fish about six months old or class 0+ (CALA 1970 b). The first spermatogonia appear during the second growth season. Spermatocytes (stage 4), as a rule appear in testes of fish belonging to age group IV. Thus, in nine months the ide develop into stage 6, when the fish is mature and the spermatogonia start to mature. That means, the male ide may become mature at an age of four years and spawn for the first time at five years of age. This agrees with the age at maturation of oogonia (CALA 1970 b) and with other observations of spawning ide in the field (CALA 1970 a). One specimen did not spawn until it was six years old.

The sexes of the ide can not be distinguished with certainty by examination of the gonads until during and after the second summer or growth season, although the gonads are already formed during the first summer (*cf.* CALA 1970 b). No significant difference was found in the spermatogenic process in the anterior, central and posterior portions of the testes, even if spermatogenesis seems to begin in the anterior part of the testis.

The annual cycle of the germ cells

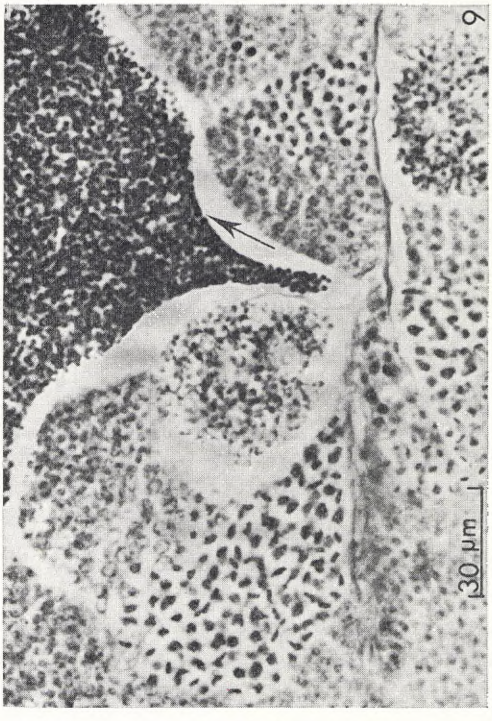
The microscopical structure of the testes and the maturation cycle of the germ cells in the ide agree in general with the description given for other marine and freshwater teleosts from temperate areas.

According to previous work, teleosts that spawn during the spring, undergo a period of gonadal inactivity during the winter months. This quiescent period may occur either before, or following, the completion of the spermatogenic cycle. Thus, in *Phoxinus laevis* (BULLOUGH 1939) and *Notropis bifrenatus* (HARRINGTON 1957), only spermatogonial formation occurs before winter and spermatogenesis does not begin until late winter. In *Perca flavescens* (TURNER 1919), *Umbra limi* (FOLEY 1926), *Gasterosteus aculeatus* (CRAIG—BENNETT 1931), *Enneacanthus obesus* (HARRINGTON 1956) and *Esox lucius* (LOFTS and MARSHALL 1957), spermatogonial proliferation and spermatogenesis are completed during the autumn. No further gonadal activity takes place until spring, when the spermatozoa are shed and spawning occurs.

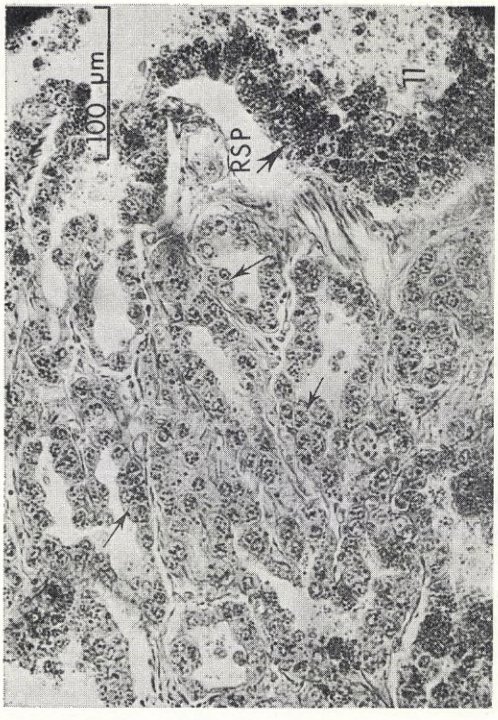
However, HENDERSON (1962) stated there is no period of quiescence in *Salvelinus fontinalis* which spawns during autumn. This means that spermatogonial proliferation begins as soon as the period of 'functional maturity' is terminated and continues at a slow rate throughout the winter and spring months. A period of intense activity begins in summer which involves a rapid proliferation and maturation of spermatogonia and culminates in the attainment of functional or gonadal maturity in early autumn.

All photomicrographs are of transverse sections cut at 8 µm and stained with HEIDENHAIN's haematoxylin.

9. Anterior section from the same testis as in Fig. 8, showing packed lumen with spermatozoa (arrow).
10. Anterior section of partially spent testis of 465 mm-long (age group VIII) mature ide, caught on 29 March 1967, The lumina contain a few mature sperm (MSP) and primordial germ cells (PGC). Stage 6.
11. Anterior section of spent testis of 473 mm-long (age group VIII) mature ide, caught on 12 May 1966, showing residual sperm (RSP) and early generations of spermatogonia (arrows). Stage 7.
12. Section of spent testis of 455 mm-long (age group VIII) mature ide, caught on 24 May 1966, showing collapsed connective tissue and the walls of the lobules that are growing thicker again (arrow). Note cysts of spermatogonia (SPG) and primordial germ cells (PGC). Stage 7.


9
30 µm


10
50 µm
PGC
MSP


11
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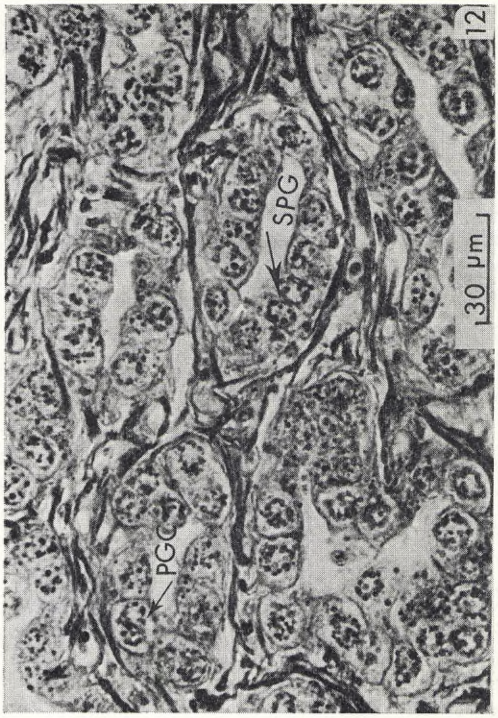
RSP


12
30 µm
SPG
PGC

This description fits in with the observations of the testes of ide, but this fish nevertheless spawns in early spring. Spermatogonial proliferation begins as soon as the period of mature spermatozoa (stage 6) is terminated, or the fish has spawned. In other words, a new cycle of spermatogenesis has commenced. However, a certain period of quiescence is presumably interjected between the second and the fourth years of the male ide's life, since spermatogonia are formed in the testes of immature ide during the second period of growth or class I+, while the male fish does not spawn until the end of its fourth year. Furthermore, the spermatogenesis in mature fish takes only one year. Hence, the first spermatogonia need about three years to mature, whereas in mature ide a period of one year is sufficient.

The annual development of germ cells

Two general theories have been advanced with respect to the origin of the annual production of germ cells.

1. The lobules contain a permanent stock of undifferentiated germ cells. HANN (1927) wrote that "dormant germ cells" are present in *Cottus bairdii* at all times of the year. These cells lie quiescent along the sides of the lobules during the months of spermatogenesis and spawning, and divide during the post-spawning period to yield the next generation of spermatogonia. A similar description was given by BENNINGTON (1936) for *Betta splendens*, BULLOUGH (1939) for *Phoxinus laevis*, WEISEL (1943) for *Oncorhynchus nerka*, STENGER (1959) for *Mugil cephalus*, and HENDERSON (1962) for *Salvelinus fontinalis*.

2. Each season the germ cells are formed anew from migratory cells which originate from some point outside of the testis. TURNER (1919), basing his observations on a single specimen of *Perca flavescens*, reported that spermatogonia arose from cells which migrated into the lobules from a "cord of germ cells" lying outside the testis. Migration of primordial germ cells into the lobule during the postspawning period has been described by FOLEY (1926) in *Umbra limi* and by LOFTS and MARSHALL (1957) in *Esox lucius*. The latter authors were unable to determine the point of origin of the cells, but FOLEY suggested that the source might be extratesticular.

Recently, RAI (1965) for *Tor tor*, KHANNA and PANT (1966) for *Glyptosternum pectinopterum*, and DIXIT and AGRAWALA (1974) for *Puntius sophore*, stated that spermatogonia are present throughout the year though their number is greatly reduced during spawning season.

The origin of the germ cells in the male ide is in agreement with the first of the models outlined above. Thus, primordial germ cells are present along the sides of the lobules throughout all phases of the reproductive cycle, and as such, form a permanent source of mature germ cells. Intense division of these cells takes place during stage 7 or involution and during summer. However, it seems that the primordial germ cells lie quiescent during the stages 5 and 6. Consequently, some of the division products of these cells form spermatogonia and the remainder constitute the "reserve germ cells", as SUZUKI (1939) called them. WEISEL (*op.cit.*) also called them "resting germ cells".

The relation between testicular histology and spermatogenic process on the one hand, and the length and age of the ide on the other, may be summarized as follows (*cf.* Table 1):

Age group I. At the end of the first year of the life of the fry the gonads are composed of isolated groups of sexually undifferentiated reproductive cells. Stage 2.

Age group II. The testis is composed of spermatogonia. This stage begins during the second summer of the fish life. Early stage 3.

Age group III. In the third year the testis is composed of larger number of spermatogonia, forming clearly differentiated cysts in lobules with large lumina. Advanced stage 3.

Age group IV. At the end of the fourth year the testis usually is composed of spermatogonia ready to develop into spermatocytes during the next growth season. The morphohistology of the testis in this age group is similar to that of age group III, but the testis contains a larger number of spermatogonia. End of stage 3.

Age group V. Most of the males approach maturity during the sixth growth season, and the testis is then composed of spermatogonia, spermatocytes and spermatids. The first spermatozoa are formed at the end of the growth season (November), *i.e.* the testis begins maturing and most males will spawn at an age of five years (class V+).

The data available show that all male ide older than age group VI were mature and that some become mature during the fifth growth season.

V. SUMMARY

This study established at which age the male ide in a population inhabiting the River Kävlingeån, South Sweden, reaches maturity and describes the development of the spermatogenic cycle in relation to the environment. The spermatogenic process of the ide has been divided into three stages in the immature fish and four in the mature specimens, on the basis of the morpho-histological changes in the testes.

Stage 1. Gonad invisible. Stage 2. Sexually undifferentiated gonad. Stage 3. Formation of spermatogonia. Stage 4. Beginning of maturing or formation of the first spermatocytes. Stage 5. Formation of spermatids and spermatozoa. Stage 6. Completely mature viable spermatozoa. Stage 7. Period of involution.

The first sign of a sexually undifferentiated gonad appeared at about six months of age or class 0+ (Cala 1970 b). The first spermatogonia appear during the second growth season. Spermatocytes (stage 4), appear as a rule in testes of ide belonging to age group IV. Thus, in nine months the ide develop into stage 6, when the fish is mature and the spermatogonia start to mature. That is, the male ide becomes mature at an age of four years and spawns for the first time at five years of age. This agrees with the age at maturation of oogonia (Cala 1970 a).

VI. ACKNOWLEDGMENTS

The work was carried out at the Department of Animal Ecology, University of Lund, Sweden. To the Head of the Department, Professor Per Brinck, I wish to express my sincere gratitude for his help and interest during the investigation. Professor Erik Dahl, Director of the Zoological Institute at Lund, and Professor Staffan Ulfstrand, Acting Head of the Department of Animal Ecology, provided economic support that allowed a technician to assist me during the routine sectioning of the testes and preparing of the slides. I further thank Dr. Michael Moon for correcting my English. The photomicrographs were taken at the photographic laboratory of the Zoological Institute.

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The Ecological and Genetical Segregation of Two Sympatric Species of Dwarfed Char (*Salvelinus alpinus* (L.) Species Complex)

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I INTRODUCTION

According to Nyman (1972) at least three sibling species of char within the so called *Salvelinus alpinus* (L.) complex can be distinguished in Scandinavia. Two of these are generally dwarfs with usually a littoral or benthic way of life, whereas the "normal" char is more pelagic. They also differ in their food habits, growth, spawning time etc. (Nilsson and Filipsson 1971). In certain lakes, where the isolating mechanisms have not been complete, hybridization has occurred and the gene flow has resulted in various stages of introgression.

Parasitological data can often contribute to an understanding of various biological problems in fish, for example population structure, feeding habits and phylogenetic problems (Kabata 1963, Margolis 1965). Makhovenko (1972) used parasites as indicators of different forms of char from Kamchatka. In Sweden whitefish (Coregonus spp.), which constitute a complex of sibling species in various stages of introgression (Svärdson 1957), have been investigated for their cestodan parasites by Petersson (1971 a). Mayr (1970) states that parasites may aid in the discrimination of sibling species since "sibling species often differ in the number or the kind of parasites they carry".

In connection with a parasitological investigation in a lake in southern Swedish Lapland it became evident that the char population could not be homogeneous. The present study has been undertaken 1/ to determine if more than one species of char inhabits the lake system and if so 2/ to determine which species are involved, 3/ to examine if the parasite faunas of two sibling species of char may contribute to the discrimination between them and 4/ to test what set of parameters would prove most suitable to assign individual fish to species.

One problem in the study of sibling species is to classify the individual specimen as belonging to one species or the other. This property is usually not directly measurable but evaluated using empirical measurements which are a priori known to be related in some way. All too often a single discriminating character cannot be found, and only a combination of measurements can provide the necessary information. When the number of parameters is large (> 3) and the objects numerous, one can use methods of numerical taxonomy (Sneath and Sokal 1973) also called methods of pattern recognition (Kowalski and Bender 1972). In the present study the chars were classified by a method based on modelling each separate class by a separate principal components model (Wold 1974, 1975 b).

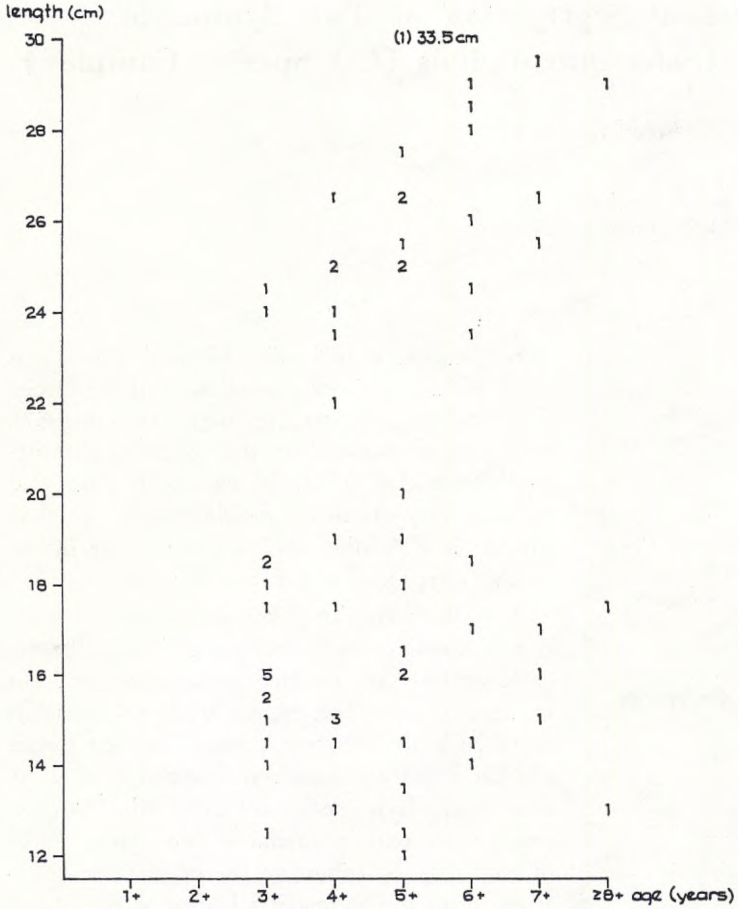

Fig. 1. Size and age distribution of char in the sample from the winter 1970—71 in Lake Fättjaure. Numbers indicate number of fishes.

II MATERIALS AND METHODS

Parasite investigation

A total of 239 char from Lake Fättjaure in southern Swedish Lapland were examined for their helminth and copepod parasites during the years 1970—73

Time	n	
Winter 1970—71	67	(November—January, Fig. 1)
Winter 1972—73	67	(November—March, Fig. 2)
Summer 1973	34	(June, Fig. 3)
Autumn 1973	71	(September—October, Fig. 4)

Fättjaure is situated in the Ångermanälven river system at about lat. 65°3′N. The lake area is 10 km^2 and the altitude 560 m above sea level. The only fish species in the lake are char and brown trout (*Salmo trutta* L.). The fish were caught by set gill nets.

In the samples from the years 1972—73 the flesh colour was estimated by the subjective method used by NILSSON and FILIPSSON (1971). The food habits of the fish were analysed by means of the "frequency" and "dominance by number" methods (NILSSON 1955). The degree of filling of the stomachs was also determined by classifying the stomachs as "empty" = 0, "nearly empty" = 1, "half filled" = 2 and "filled" = 3. The amount of each food item was determined using a subjective scale, 0 = nothing, 1 = remains, 2 = some specimens, 3 = many (>12).

Age was determined from the otoliths as described by FILIPSSON(1967), but instead of xylole, propylenglycole was used.

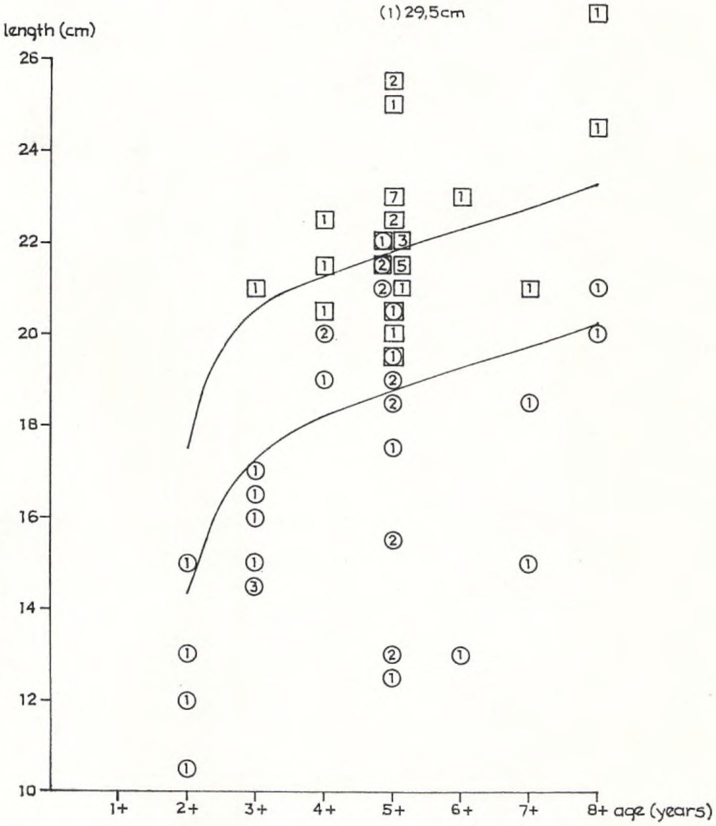

Fig. 2. Size and age distribution of char in the sample from the winter 1972—73 in Lake Fättjaure. Classification made by the program-system SIMCA. ○=belong to species "B", □=belong to species "A", ⊡=belong to both classes, ( )=do not belong to any class. Numbers indicate number of fish. The fish between the lines are treated as test set. For further explanations, see text.

Seven parasite species were found. Two were larval cestodes, *Diphyllobothrium dendriticum* (Nitzsch 1824) and *D. ditremum* (Creplin 1825). The *Diphyllobothrium* plerocercoids were recovered by the pepsin — HCL digestion technique described by Meyer and Vik (1963) and identification was based upon the investigations by Vik (1957, 1964), Wikgren (1964), Bylund (1969, 1973) and Halvorsen (1970).

Three cestodes using char as their final host were found, *Eubothrium salvelini* (Schrank 1790), *Cyathocephalus truncatus* (Pallas 1781) and *Proteocephalus* sp. Weinland 1858. The number of these three cestodes was estimated as 0=0, 1=1—3, 2=4—10 and 3=more than 10 worms. The fish caught in 1970—71 were not examined for these parasites. The genus *Proteocephalus* is difficult to treat taxonomically (Wardle and McLeod 1952, Borgström and Lien 1973) and no attempt was made to identify the species.

One intestinal trematode *Crepidostomum metoecus* (Braun 1900) and one gill parasite, the copepod *Salmincola edwardsii* (Olsson 1869) were also found. *S. edwardsii* was determined according to Kabata (1969).

Gene frequency analysis

Of the 239 char from lake Fättjaure, which were analysed for parasites, 163 were also sampled for blood serum esterase analysis by starch gel electrophoresis. In addition to the char from Lake Fättjaure samples of fish were also obtained (taken by gill nets in September 1973) from two other lakes, *viz.* Lower Fättjaure Lake (n=104) and Lake Borkajaure (n=171) which are located directly downstream of Lake Fättjaure. A total of 438 char were thus analysed by electrophoresis. Sampling was performed either by severing the heart of fresh fish in the field, or by direct samp-

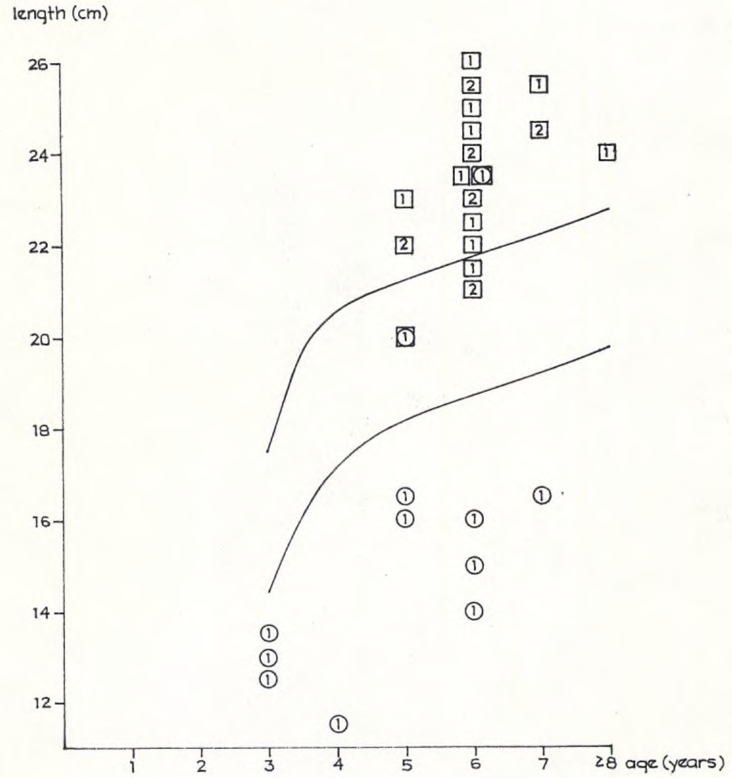

Fig. 3. Size and age distribution of char in the sample from the summer 1973 in Lake Fättjaure. Classification made by the program-system SIMCA. For explanation see Fig. 2.

ling from thawed fish which had been kept frozen for several months. For a detailed description of the blood sampling procedure the reader is referred to a previous publication (NYMAN 1972).

The electrophoretic procedure is based on an apparatus utilizing starch slabs, cooled by tap water and with detachable buffer vessels (NYMAN 1967).

Age determinations (by otolith reading) were performed on all fish except for a single specimen from Lake Borkajaure.

Multivariate data-analysis

The data of each fish were punched on three types of data cards, one for data on the fish, one for the parasite data and one for the stomach content. Most of the statistical treatment was done using a CDC 3300 computer at the Umeå University Data Center (UMDAC).

The fish caught during the winter 1970—71 were fairly well separated in two groups on the basis of length on age (Fig. 1). Those above the gap were treated as species "A" those below as species "B".

In order to classify the char caught during the years 1972—73 (when more parameters were measured), methods for pattern recognition were used. The program systems ARTHUR and SIMCA, which together constitute a collection of routines for multivariate data-analysis with pattern recognition methods, are available at UMDAC (WOLD 1975 a). SIMCA treats the pattern recognition problem by means of principal components models. Each of a number of classes is defined by a set of objects, the reference set of the class, and M variables are measured on each of these objects. The behaviour of the objects in a separate class is described by means of an empirical mathematical model (principal components model). The parameters in this class model are estimated from the data in the reference set. Unclassified objects are then fitted to all the parametrized class models

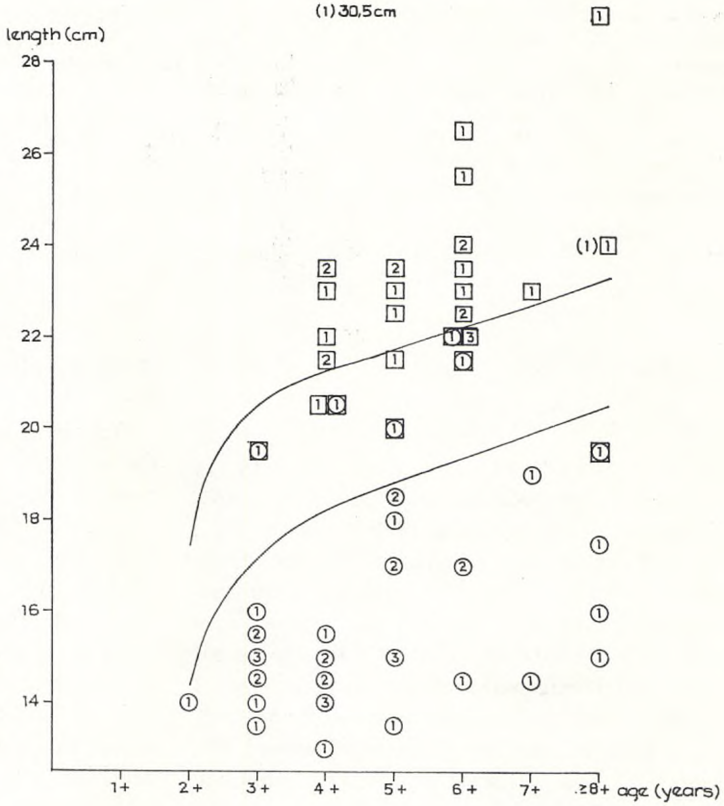

Fig. 4. Size and age distribution of char in the sample from the autumn 1973 in Lake Fättjaure. Classification made by the program-system SIMCA. For explanation see Fig. 2.

and classified according to which model they fit best.

The specimens in the arbitrarily chosen zone of overlap in the growth diagrams (Figs 2—4) were treated as unclassified and constituted the *test set.* The fish below this zone were classified as species "B" (class 1) and those above as species "A" (class 2). They constituted the *reference sets.* The variables tried in the analysis were fork length (L), weight (W), age (AGE), flesh colour (FLC), frequency of the gene F (FF), number of the parasites *D. dendriticum* (DEN), *D. ditremum* (DIT), *S. edwardsii* (SALM), *E. salvelini* (EUBO), *C. truncatus* (CYAT) and *Proteocephalus sp.* (PROT). Because the frequency distribution of DIT was overdispersed, approximately fitting the negative binomial distribution, this variable was transformed using log (DIT+1). To give the variables equal weight they were autoscaled. Autoscaling gives every variable the mean 0 and the variance 1.0 (Kowalski and Bender 1972, Wold 1975 b).

To get a 2-dimensional picture (display) of the data structure an eigenvector plot was generated (Kowalski and Bender 1973) (Fig. 5).

The main analysis was made using the program system SIMCA (Wold 1975 b). A separate principal components model was fitted to each of the reference sets. All objects in the reference sets and the test set were then fitted by linear regressions to all class-models. The residuals for each object give information about "closest class" for that object, whether this closest class is close enough for the object to be classified as belonging to that class, and whether the closest class is significantly closer than the next closest class (F-test). It might well happen that an object is classified as belonging to several classes (in this case two) or as not belonging to any of the classes. The residuals also give information about "distances" between classes and the variable "relevance".

Table 1. *Measures of variable relevance for the char data. The first row indicates the importance of the variables within the classes. The closer to one, the larger the relevance and the closer to zero, the smaller the relevance. The second row is a measure of how much the variables participate in the discrimination between the classes. For explanation of the abbreviations see text.*

Variable	L	W	AGE	FLC	DEN	EUBO	CYAT	PROT	FF	DIT	SALM
Explanatory power	0.208	0.063	0.652	0.213	0.708	0.225	0.392	0.070	0.206	0.660	0.425
Discriminatory power	26.0	10.4	2.6	5.3	3.7	1.1	1.1	1.0	1.1	1.5	1.0

III. RESULTS

Classification of the char

(A) by multivariate data-analysis

The number of product terms were, by cross-validation, found to be 2 in both classes of char. The most explanatory variables within the classes were AGE, DEN and DIT and the most discriminatory variables between the classes were L, W, FLC and DEN (Table 1.) By fitting all objects in reference-set 1 to the calibrated model for class 2 and vice versa a measure of the "distance" between the classes were obtained. The species "A" and "B" were significantly separated ($F=2.3$ df=420, 420).

For the final classification of the objects in the reference sets the analysis was then repeated, using only the most relevant variables (L, W, AGE, FLC, DEN, DIT), which were weighed according to their discriminating power (Table 1.) The number of product terms again was found to be 2 for both classes ($F=18.5$, df=372, 297 for class 1 and $F=11.3$, df=348, 278 for class 2). The "distance" between the classes was increased ($F=6.8$, df=200, 200) showing that there was a better separation when only the six most relevant variables were used (Table 2). Fig. 5 shows an eigenvector plot of the data.

For the final classification of the objects in the test set, for which the length was not so discriminating because they were of about the same length, L, AGE, FLC, DEN and DIT were used with equal weights.

The result of the classification is shown in Figs 2—4. The reference set of species "B" consisted of 70 fish. Sixtynine of them were classified as belonging to that species ($F < 2.7$, $p > 0.05$, df=3,140). Fiftyseven had a very close fit falling within 1.0 times the reference set residual standard deviation. One fish was classified as belonging to both species. The reference set of species "A" consisted of 65 fish. Sixty of them were classified to the species "A" class ($F < 2.7$, $p > 0.05$, df=3,140) and 50 fell within 1.0 times the reference set residual standard deviation. Three fell outside both species and two could belong to both species. There were 37 specimens in the test set, 9 of which were classified as species "B" and 18 as species "A". Ten could belong to both species.

Hence a total of thirteen fish were classified as belonging to both classes either because of lack of information or because, as a result of intro-

Table 2. *"Distances" between the two char classes expressed as the standard deviation of the objects in reference set r when these are fitted to the class model q. Only the weighed values of the six most relevant variables are used.*

	q=1	q=2	Mean, $\frac{\text{highest value}}{\text{lowest value}}$	Statistical test
r=1	0.221	0.771	2.61	$F=6.83$ $p < 0.005$
r=2	0.537	0.309		df=200, 200

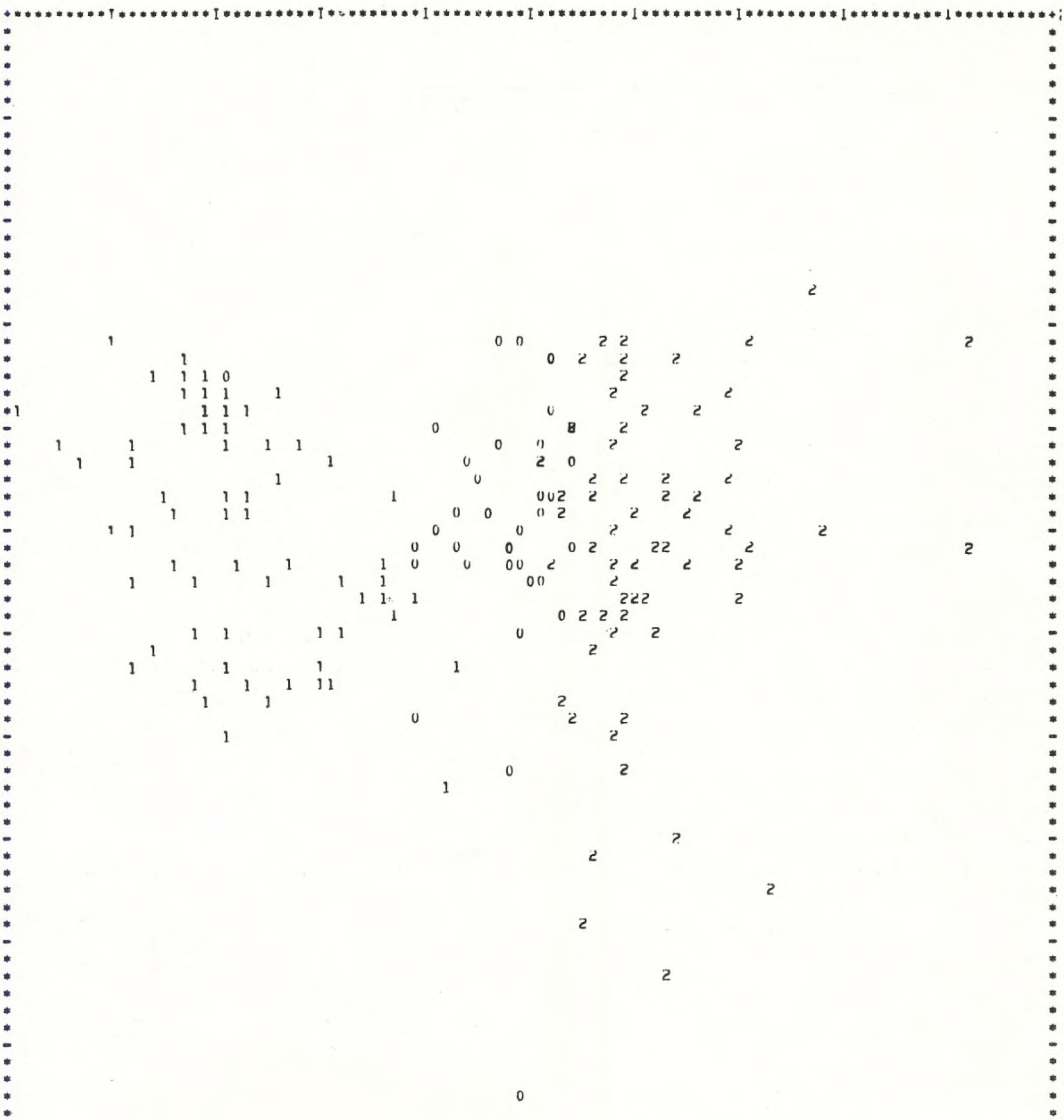

Fig. 5. Eigenvector plot of the data, giving a two-dimensional picture of the data structure. Variables used in the analysis are L, W, AGE, FLC, DEN and DIT. 1 and 2=reference sets (1=species "B", 2=species "A"). 0=test set (unclassified).

gression, they were "true" intermediates between the populations. The fish classified as belonging to both or none of the two classes were omitted from the following calculations.

(B) by gene frequency analysis

The blood serum esterases of Arctic char contain a polymorphism founded on two codominant alleles at a locus. The hereditary mechanism of

Table 3. *Distribution of phenotypes and agreement with CHW equilibrium in the four samples of Arctic char (expected values given below the observed).*

Locality	Esterase phenotype F/F	F/S	S/S	Total	f(F)
Lake Fättjaure (1973)	29 27.6	49 50.9	24 23.5	102	.52
Lake Fättjaure (1972)	18 18.5	31 30.2	12 12.4	61	.55
Lower Fättj. Lake (1973)	25 29.2	60 51.8	19 23.0	104	.53
Lake Borkajaure (1973)	39 39.4	85 85.4	47 46.2	171	.48

this polymorphism has been validated in a variety of ways (NYMAN 1972) and gene frequency data from a great number of sympatric and allopatric populations made possible the establishment of gene frequency criteria for species classification within the Arctic char complex of Scandinavia. The theoretical basis for this discrimination is the presence of (at least) three different gene frequency clines, adapted to the same number of independent homeostatic systems (*cf* NYMAN and SHAW 1971). By applying this information to an increasing number of populations sampled, and also by adding growth data and ecological parameters, it has become possible not only to identify sympatric populations of char with similar growth rate and external morphology, but also to establish if and how far introgression has proceeded (NYMAN and FILIPSSON 1972). The phenotype distribution of the various samples is compared with the expected ratio assuming CHW (CASTLE—HARDY—WEINBERG) equilibrium (Table 3). One of the samples (Lower Fättjaure Lake) deviates significantly from the expected values, but pooling the four samples from this lake system completely eliminates the deviation (chisquare 0.34, df=1, probability of worse fit 0.50—0.75). The difference in gene frequency between the samples from the three lakes is insignificant which may be taken as an indication that the same species of char inhabit all the lakes. This conclusion is far from astonishing, all data available (NYMAN, unpublished) indicate that the same species pair is usually present within a whole river system. This in turn reflects the possible colonization theory (SVÄRDSON 1961) involving the presence of at least three distinct species of anadromous char which in the postglacial period invaded the different river systems.

When plotting the resulting graphs of the length-age relationship from the lakes (Fig. 6) three different types of diagram emerge. In Lake Fättjaure two growth curves are evident, whereas the other two lakes display more uniform patterns. Since the same species of char should occur in the three lakes (no impassable falls) and it is evident that two species occur in Lake Fättjaure, this overlap of growth patterns is an indication of introgression. To get a firm basis to start from, the gene frequency data from the two separate groups in Lake Fättjaure are presented (Table 4). The two groups are in perfect accordance with CHW ratios, which is good evidence of their belonging to different gene pools. The 95 % confidence intervals overlap slightly.

By subjectively dividing the population samples from the other two lakes in "fast" and "slow" growing individuals, the two groups segregate in a similar manner. These two groups correspond to species "A" and "B" mentioned earlier. The allele frequencies thus obtained in the three lakes give the following pattern:

	species "A"	species "B"
Lake Fättjaure	0.46	0.61
Lower Fättjaure Lake	0.50	0.56
Lake Borkjaure	0.42	0.58

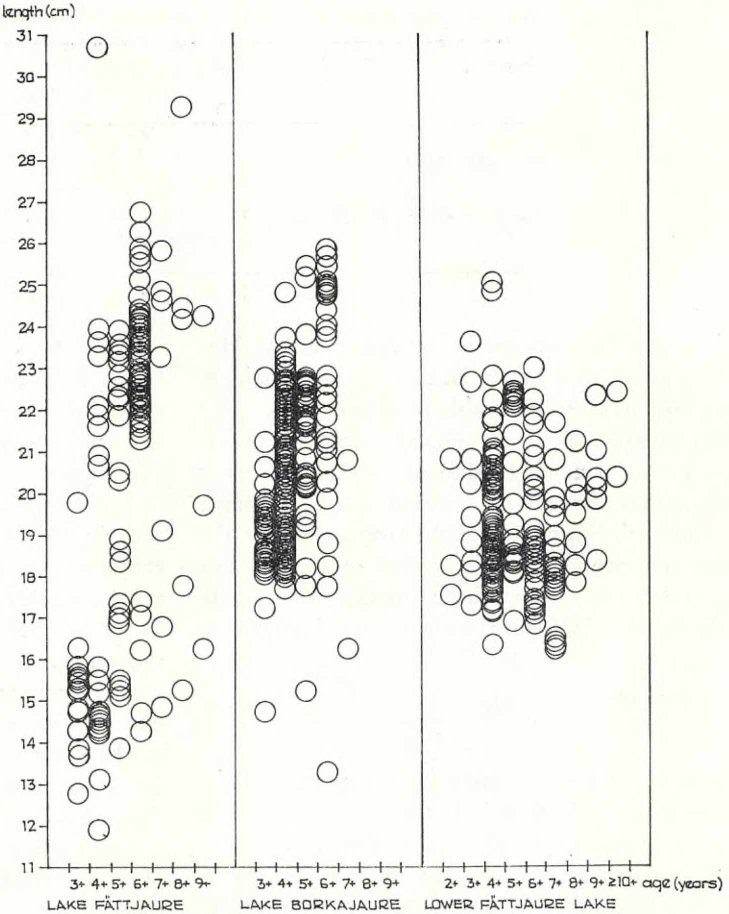

Fig. 6. Approximate growth diagrams of char sampled for blood serum esterase analysis in the three lakes.

Obviously, the gene flow between the two species has progressed very far in Lower Fättjaure Lake, which is evident from the growth diagram also. On the other hand, in Lake Fättjaure and Lake Borkajaure, there is still considerable difference between the two. To establish the most probable allele frequencies in the least altered populations, the data from Lake Fättjaure and Lake Borkajaure in 1973 were pooled (Table 5). These frequencies are well separated at the 95 % level of significance (the intervals being 0.378—0.482 for species "A" and 0.534—0.666 for species "B").

Two important taxonomical questions remain.

Table 4. *Gene frequency data from the separate growth curves in Lake Fättjaure (1973).*

	Esterase phenotype					
	F/F	F/S	S/S	Total	f(F)	95 % c.i.
char with rapid growth rate	12	28	17	57	.46	.553—.367
	12.1	28.3	16.6			
char with slow growth rate	17	21	7	45	.61	.713—.507
	16.7	21.4	6.8			

Table 5. *Pooled data from Lakes Fättjaure and Borkajaure*

	Esterase phenotype					
	F/F	F/S	S/S	Total	f(F)	95 % c.i.
char with rapid growth rate	31	83	53	167	.43	.482—.378
	30.9	81.9	54.3			
char with slow growth rate	37	51	17	105	.60	.666—.534
	37.8	50.4	16.8			

Which are the two species of char present? Has introgression also taken place in Lakes Fättjaure and Borkajaure? To be able to answer these questions we must look at the species situation in adjacent river systems. Preliminary screening of char populations throughout Swedish Lapland makes possible calculations of allele frequencies for the three commonly occurring species of char in this region (NYMAN, unpublished data). These data indicate the following approximate frequencies:

normal char	(N)	0,40
dwarfed char	(T_F)	0,98
dwarfed char	(T_S)	0,12

T_F denotes a species with a high frequency of the F allele, and T_S thus indicates a species with a high frequency of the alternative allele (S).

It can immediately be seen that neither species in the three lakes fit any of the three "normal" frequencies. Thus the frequencies observed must be the result of introgression between two species, an introgression which has altered both considerably.

If we consider the pooled frequencies of Table 5 as representative of the present level of introgression between the species, the following relationship may be used to get an approximate value of the relative strength of the two species:

$$\frac{\text{frequency of species "B"—frequency of total sample}}{\text{frequency of species "B"—frequency of species "A"}}$$

$=\frac{0.60—0.51}{0.60—0.43}=0.53$. This means that 53 % of the total sample consists of species "A".

Direct counting of individual fish belonging to the two separate growth classes found in the Lake Fättjaure sample enhances the validity of this figure, since it gives a 54 % proportion of species "A".

Since the species combination most commonly found includes a normal pelagic char (N) and either of the dwarfs, the combination involving the dwarf with a high frequency of the F allele (T_F) seems most likely. When applying the "normal" frequencies of the region for the normal char (0.40), the T_F dwarf (0.98) and the observed frequency of the pooled samples to the relationship mentioned above, the resulting figure is 81 % normal char (species "A"). This contrasts the observed 54 %. Also, the presence of this species combination would imply that the T_F dwarf had lowered its frequency from 0.98 to 0.60, but at the same time hardly at all affecting the frequency of the normal char (0.40 versus 0.43), even though introgression must have had similar impact on both species since they occur in roughly the same number. These criteria seem to exclude the combination of a normal char and a T_F dwarf. The other combination involving a normal char and a dwarf may also be refuted. In all known cases of sympatry where a normal char has occurred in combination with a dwarf, the normal char has had a superior growth rate. In the present case this would imply that the frequency of the normal allopatric char — 0.40 — should be compared with species "A" — 0.43 — and that the corresponding figures for the dwarfed char would be — 0.12 and 0.60! The only possible combination remaining (if the three original species are considered) would involve sympatry of the two dwarfs. If we apply the respective frequencies to the same relationship as above, the following figures result:

$\frac{0.98—0.51}{0.98—0.12}=0.55$. That is, if the two dwarfs were mixed in the same proportion as that found in the pooled sample from the three lakes, the dwarf

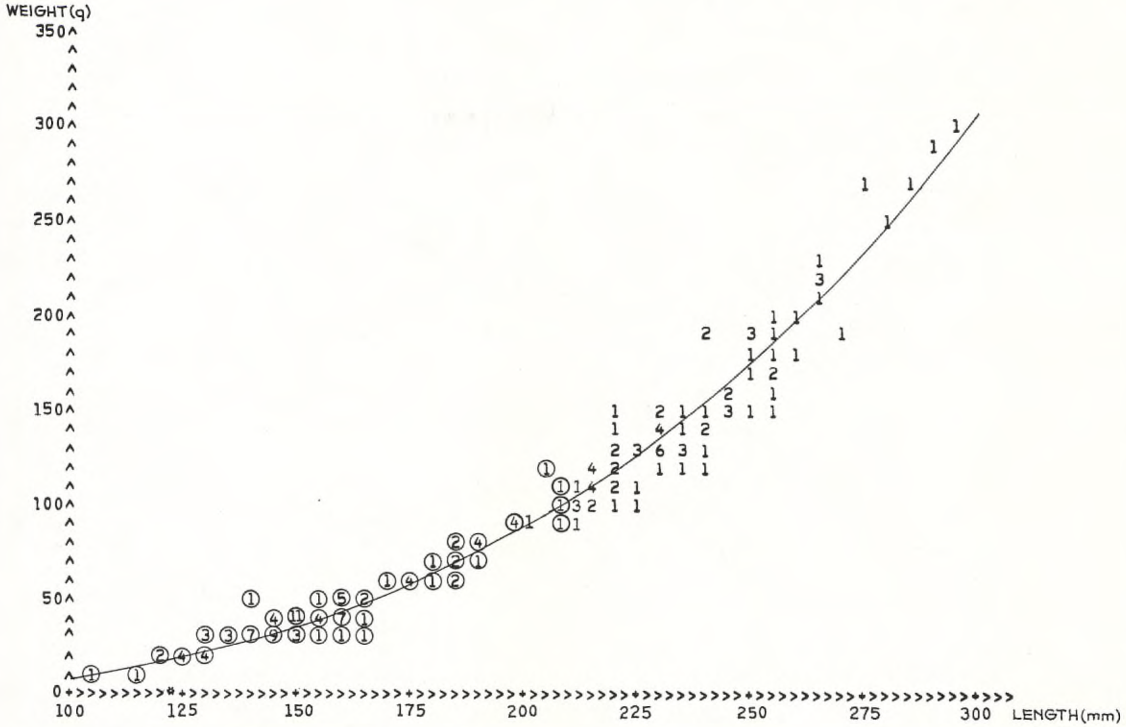

Fig. 7. Length-weigth relationship of species "B" (encircled) and species "A" from Lake Fättjaure and fitted curve: $W=0.955 \cdot 10^{-5}L^{3.03}$. The numbers indicate number of fish at each position.

with the lowest frequency should constitute roughly 55 % of the sample. This figure agrees well with the observed 54 %, and is good evidence of the validity of the hypothesis. Thus, species "A" may be substituted for dwarf T_S and species "B" substituted for dwarf T_F.

Growth and length-weight relationship

Figs 1—4 show the growth rate of the char analysed for parasites caught during different seasons. Age group 3+ consisted almost entirely of species "B" and is excluded from several of the following calculations. The two sympatric populations were not completely separated in their size at different ages, 18.5 % of the total number of fish occurred in the zone of overlap.

To examine the length-weight relationship of the two species, the functional regression of log weight on log length was calculated for each of them (Ricker 1973). Spawning fish were omitted from the calculations. There was no significant difference between them, both approximately fitting the functional regression line:
$\log W = -5.02 + 3.03 \log L$ (Fig. 7).

Food habits

Figs 8—10 and Table 6 illustrate the food habits of the two species of char from Lake Fättjaure. During the winter there was only a slight difference in their choice of food. The most frequent food items for both species were *Gammarus*, *Ephemeroptera* larvae and *Chironomidae* larvae. The most dominating food objects for species "B" were chironomid larvae and fly nymphs (*Ephemeroptera*, *Plecoptera* and *Trichoptera*), for species "A" *Gammarus* and to a certain extent *Ephemeroptera* larvae. The relatively low number of species "B" with *Gammarus* as a dominating food item compared with species "A" may depend on the many young fish (3+) of species "B" caught in March 1973 (10 out of 18 individuals). *Gammarus* was

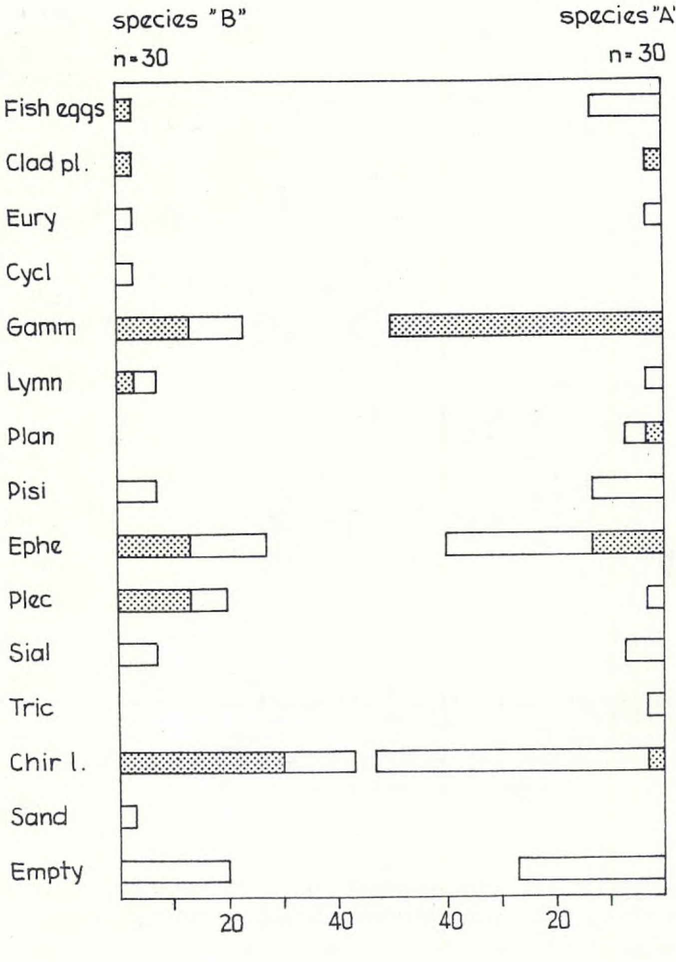

Fig. 8. The food of char caught during the winter 1972—73. □= frequency of food items (%), ⁙= dominating food items (%). Clad pl.=planktonic *Cladocera*, Eury=*Eurycercus*, Cycl=*Cyclops*, Gamm=*Gammarus*, Lymn=*Lymnea*, Plan=*Planorbidae*, Pisi=*Pisidium*, Ephe=*Ephemeroptera larvae*, Plec=*Plecoptera* larvae, Sial=*Sialis* larvae, Tric=*Trichoptera larvae*, Chir l. =*Chironomidae larvae.*

obviously less important as food for the young of species "B". The difference between the age-groups $\leq 4+$ (frequency of *Gammarus* 45 %) and $\geq 5+$ (frequency of *Gammarus* 88 %) during the autumn 1973 was significant (Fisher exact probability test, $p=0.02$). There were more "A" chars with half-filled and filled stomachs than "B" during the winter 1972—73 ("B"=7 % and "A"=50 %; $X^2=11.82$, $p < 0.001$).

In June there was a certain food segregation. *Chironomidae* larvae, *Ephemeroptera* larvae and *Plecoptera* larva were frequent food objects for both species, but *Gammarus* was more important for the "B" char and *Chironomidae* pupae and terrestrial insects for the "A" char. *Gammarus* was also more important for "B" and *Ephemeroptera* larvae for "A" as dominating food items.

In the autumn (Sept—Oct) the present material reflects a pronounced food segregation between

Table 6. *The food of species "B" caught during the winter 1970—71 in Lake Fättjaure. n=18.*

Food item	Frequency %	Dominating %
Gammarus	44	28
Lymnea	6	0
Pisidium	6	6
Trichoptera	6	0
Chironomidae l.	56	33
Empty	33	33

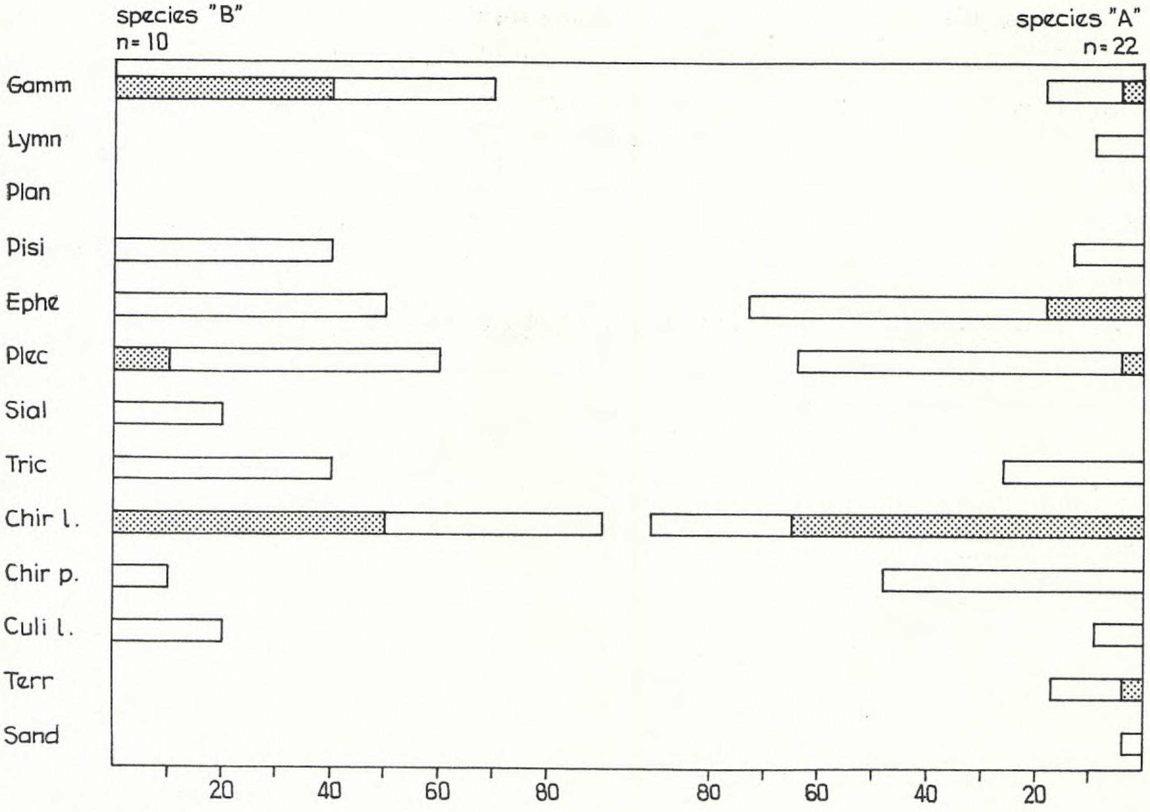

Fig. 9. The food of char caught in June 1973. □=frequency of food items (%), ░=dominating food items (%). Chir p.=*Chironomidae pupae*, Culi l.=*Culicidae larvae*, Terr=terrestrial insects. (See also Fig. 8.)

the two species. The most frequent food items for the "B" char were *Chironomidae* larvae, fly nymphs (*Ephemeroptera, Plecoptera, Trichoptera*) 46 %, *Gammarus* and the semi-benthic *Eurycercus*. "A" char, on the other hand, had eaten planktonic *Cladocera* very frequently (81 %). Terrestrial insects occurred in 35 % of the "A" chars but in none of the "B". Nineteen of the 26 stomachs from "A" char (73 %) were dominated by "pelagic food", whereas 33 of the 37 stomachs from "B" char (89 %) were dominated by "bottom food".

Flesh colour

There was a highly significant difference in flesh colour between the two species. Char "A" more frequently had "slightly pink" or "pink" flesh than char "B" (Fig. 11) ($X^2=82.3$, $p < 0.001$).

Parasites

There were no qualitative differences in the parasite faunas of the two species since they both carried all 7 parasite species found. Quantitatively, however, differences occurred.

The incidence and intensity of infection with *Diphyllobothrium dendriticum* is shown in Table 7. The intensity of infection was low but char "A" was more heavily infected in all samples. In the winter 1972—73 and the summer 1973 the difference was significant for age class 4+ and older. In the autumn 1973 there were also more "A" char (23 %) than "B" (4 %) which harboured more than one plerocercoid ($X^2=2.64$, $p < 0.2$).

There was an increase in the incidence of infection during the period of investigation. The incidence in char "B" was significantly higher in the autumn 1973 than in the winter 1970—71

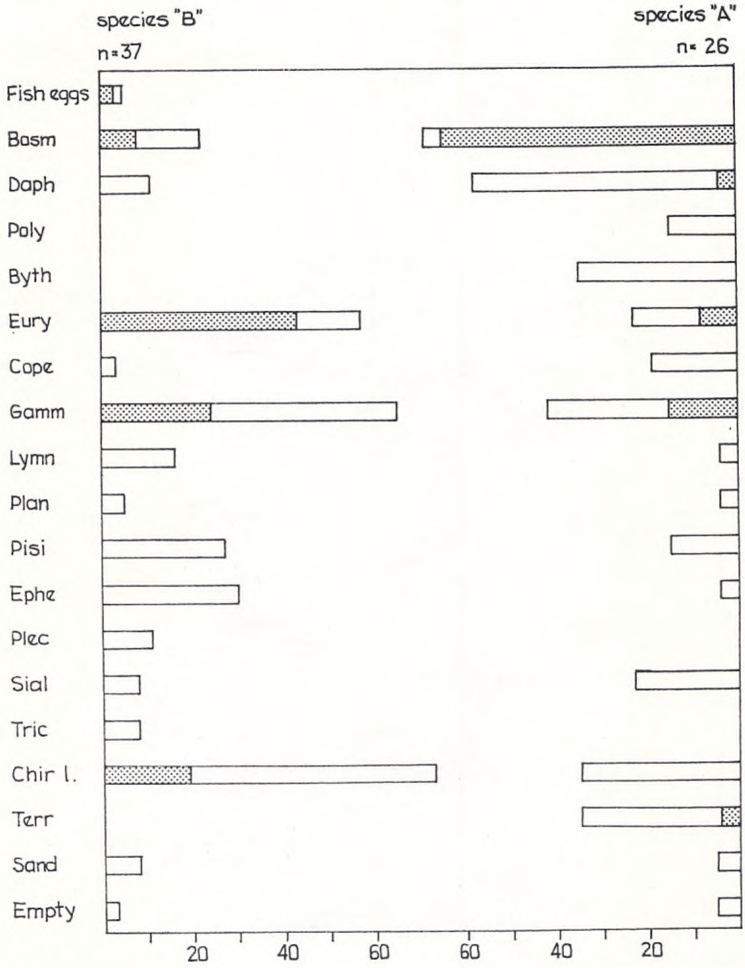

Fig. 10. The food of char caught in Sept.—Oct. 1973. □=frequency of food items ($^0/_0$), ▨=dominating food items ($^0/_0$). Bosm=*Bosmina*, Daph=*Daphnia*, Poly=*Polyphemus*, Byth=*Bythotrephes*. (See also Fig. 8.)

($X^2 = 8.78$, $p < 0.01$) and in char "A" in the samples from the summer and autumn 1973 compared with the winter sample from 1970—71 ($X^2 = 5.11$, $p < 0.05$).

Diphyllobothrium ditremum was very common in both species, Table 8, but the intensity of infection was higher in the "A" char. As the distribution of the parasite in the fish population was overdispersed, the non-parametric Mann-Whitney U-test has been used to test for differences in central tendency (SIEGEL 1956).

As the intensity of infection with *D. ditremum* was increasing with age of fish the test has also been carried out including only one or two age groups (Table 9). Even in these cases the "A" char showed a higher intensity of infection.

This parasite too had increased from the winter 1970—71 to the autumn 1973 in both "B" ($z = 1.97$, $p < 0.05$) and "A" char ($z = 1.72$, $p < 0.05$).

The data, presented in Fig. 12, show a possible tendency for a seasonal cycle in *Eubothrium salvelini*. The incidence of infection was highest during autumn and winter, but some of the samples are too small for any conclusions to be based on them. All age groups of fish are included in the figure since there was no significant difference in incidence of infection between age-group 3+, which consisted almost entirely of species "B", and older fish. There was no significant difference in the incidence of infection between the two species of char.

The incidence of infection with *Cyathocephalus*

Table 7. *Incidence (%) and intensity ($\bar{x}$) of infection with Diphyllobothrium dendriticum at different times in the two species of char, age 4+ and older.*

time	species	n	% inf.	$\bar{x}$	s^2	max	Mann-Whitney U-test
Winter 1970—71	"B"	26	4	0.04	0.04	1	
	"A"	22	18	0.18	0.16	1	
Winter 1972—73	"B"	20	25	0.3	0.33	2	z=2.35
	"A"	29	55	1.1	1.95	5	$p < 0.01$
Summer 1973	"B"	6	17	0.2	0.41	1	z=2.05
	"A"	22	64	1.2	1.90	4	p=0.02
Autumn 1973	"B"	26	42	0.5	0.34	2	
	"A"	26	38	0.7	1.02	3	

Table 8. *Incidence and intensity of infection with Diphyllobothrium ditremum at different times in the two species of char, age 4+ and older.*

time	species	n	% inf.	$\bar{x}$	s^2	range	Mann-Whitney U-test
Winter 1970—71	"B"	26	88	22.9	930.7	0—122	z=1.88
	"A"	22	100	39.0	2681.4	1—252	$p < 0.05$
Winter 1972—73	"B"	20	95	31.0	1612.5	0—148	z=1.84
	"A"	29	100	50.1	1491.0	1—125	$p < 0.05$
Summer 1973	"B"	6	(100)	(69.8)	1319.8	15—120	
	"A"	22	100	62.3	2456.9	1—185	
Autumn 1973	"B"	26	100	35.0	1055.1	1—122	z=1.94
	"A"	26	100	61.0	2379.9	2—144	$p < 0.05$

truncatus was higher in the "B" char than in the "A" char, in the samples from the summer (Fisher exact probability test, $p < 0.01$) and autumn ($X^2 = 4.07$, $p < 0.05$) 1973 (Fig. 13). The "A" char showed a high incidence only during the winter. Since there was no difference in incidence of infection between age-class 3+ and older fish, all age groups of fish are included in the figure.

Vik (1954, 1958) showed that trout taken by net were more heavily infected with *C. truncatus* than trout taken by otter, which could explain the low incidence of infection in "B" char in March 1973, since these fish were caught by bobbing.

There was a positive correlation between intensity of infection with *C. truncatus* and occurrence of *Gammarus* in the stomach content ($r = 0.62$, $p < 0.01$ and $r = 0.35$, $p < 0.01$ in the samples from the winter 1972—73 and autumn 1973, respectively) and a negative correlation between intensity of infection and occurrence of

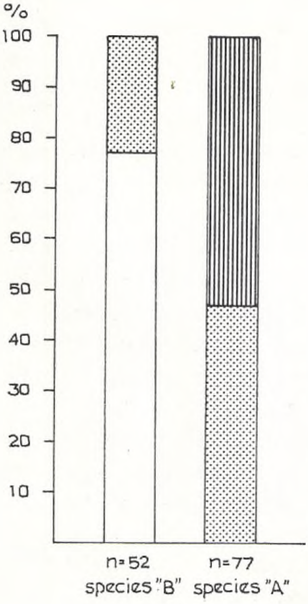

Fig. 11. Flesh colour of char from Lake Fättjaure of age ≥ 4+. □=white, ⁙=slightly pink ||||=pink.

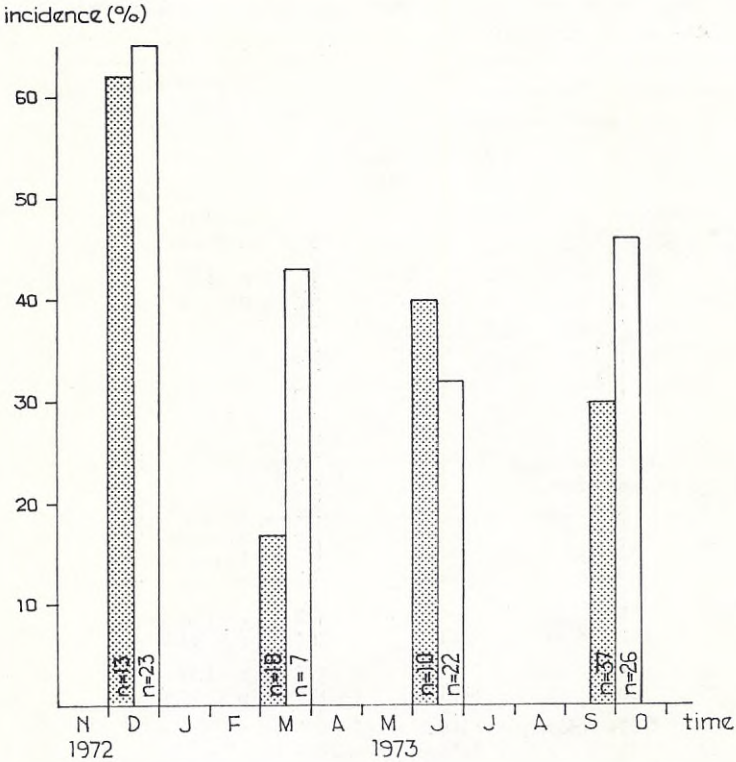

Fig. 12. Incidence of infection with *Eubothrium salvelini* at different seasons. All ages of fish included. ⁘= species "B", ☐=species "A".

Cladocera ($r = -0.30$, $p < 0.05$, autumn 1973).

Fig. 14 shows the incidence and intensity of infection with *Proteocephalus sp.* during different seasons. There was an obvious seasonal cycle in both with a maximum in the autumn. There was no correlation between the age of fish and the incidence of infection.

The "A" char was more heavily infected with *Proteocephalus sp.* than the "B" char. The difference was significant both in the winter 1972—73 ($X^2 = 6.81$, $p < 0.01$) and in the autumn 1973 ($X^2 = 10.49$, $p < 0.01$).

There was a positive correlation between intensity of infection with *Proteocephalus sp.* and occurrence of *Cladocera* in the stomach content during the autumn 1973 ($r = 0.34$, $p < 0.01$).

Crepidostomum metoecus was investigated only during the winter 1972—73. Thirty-two per cent of char "B" and 48 % of char "A" were infected. The difference is not significant.

Salmincola edwardsii occurred at a fairly low level of infection in both chars (Table 10). There was, however, an overall tendency for "A" char to be more infected (all samples, age of fish $\geq 4+$, $X^2 = 5.76$, $p < 0.02$) and in the winter 1970—71 the difference was significant. Since the youngest fish was less infected, age group 3+ is excluded from the table.

Ecological "distance" between the species during different seasons

The program-system SIMCA was also used to get a measure of the "distance" between the species during different seasons as measured by the most discriminating "ecological" variables (*i.e.* parasites and food items).

The most discriminating "ecological" variables during the autumn 1973 were DEN with discriminating power=2.8, CYAT=1.9, PROT=1.7, *Cladocera* (CLAD)=2.1, *Eurycercus* (EURY)=5.8, *Chironomidae* larvae (CHIR)=2.6 and fly nymphs (NYMP)=2.6. The fish were classified using these variables, except DEN, which was used in the original classification. The "distance"

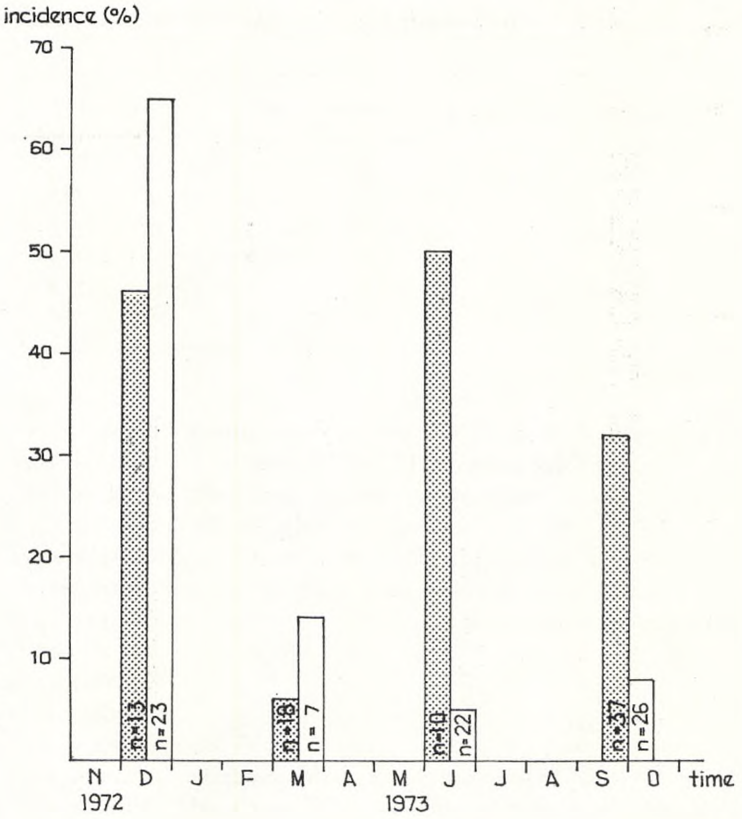

Fig. 13. Incidence of infection with *Cyathocephalus truncatus* at different seasons. All ages of fish included. ░=species "B", □=species "A".

between the species was highly significant (F= 2.36, df=90, 90, $p < 0.005$). Forty-eight (76 %) of the char were classified to the correct class, 10 (16 %) could belong to both classes and only 5 (8 %) were placed in the wrong class. If the fish, classified as possibly belonging to both classes, were placed in the "closest" class, 55 (87 %) were classified to the correct class.

During the winter 1972—73 most of the "ecological" variables had a low discriminating power. The most discriminating were CYAT=1.6, PROT =2.1, GAMM=2.3, CHIR=1.6 and DIT=2.0.

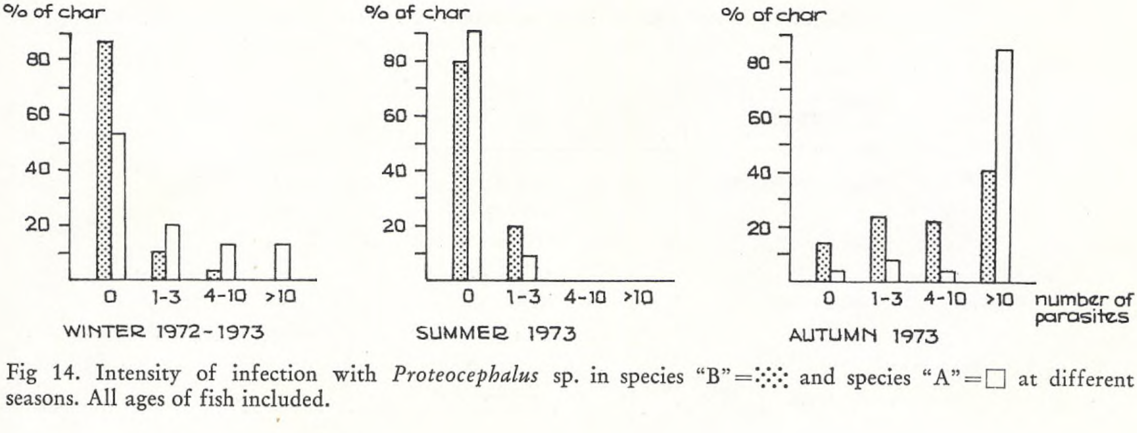

Fig 14. Intensity of infection with *Proteocephalus* sp. in species "B"=░ and species "A"=□ at different seasons. All ages of fish included.

Table 9. *Intensity of infection with Diphyllobothrium ditremum in some age-groups of the two species of char.*

time	species	age	n	$\bar{x}$	range	Mann-Whitney U-test
Winter 1970—71	"B"	4+	7	9.9	0—35	$U=9$
	"A"	4+	6	29.5	1—63	$p=0.05$
Autumn 1973	"B"	4+5+	18	25.2	1—85	$U=61.5$
	"A"	4+5+	12	53.2	5—131	$p=0.05$
Winter 1972—73	"B"	5+	12	27.8	3—148	$z=1.33$
	"A"	5+	22	46.5	1—121	$p=0.09$

The "distance" between the species, as measured by these variables except DIT, which was used in the original classification, was not significant ($F=1.18$, df$=90$, 90). Accordingly only 16 (26 $^0/_0$) of the char were classified correctly, 41 (67 $^0/_0$) could belong to both classes and 4 (7 $^0/_0$) were placed in the wrong class.

IV DISCUSSION

Nilsson (1960) found that char and trout became progressively more segregated into different food niches during the ice-free season. In September and October the segregation was most marked, the char concentrating almost exclusively on *Cladocera* and the trout on bottom animals. The same trend seems to be true for the two species of char in Lake Fättjaure.

In the winter there is no great difference in their food habits. During the summer, however, there is an increasing segregation and in the autumn they occupy two distinctly separated food niches. The difference, as compared with char and trout, is that both chars concentrate on *Cladocera* during September—October the T_S dwarf on the planktonic *Bosmina* and *Daphnia*, and the T_F dwarf on the semibenthic *Eurycercus* but also on *Chironomidae* larvae and fly nymphs. *Gammarus* seems to be utilized by both types even in the autumn. Nilsson and Filipsson (1971) found a similar food segregation during the autumn between the two species of char in Lake Övre Björkvattnet. They used a volumetric method for the analysis of stomach content but according to Nilsson (1955) there is practically no difference between the "volumetric" and the "dominance" methods.

During the winter when the two species of char occupy roughly the same food niche the more benthic form (T_F) suffers from food shortage, which perhaps could be one explanation of its

Table 10. *Incidence and intensity of infection with Salmincola edwardsii at different seasons in the two species of char, age 4+ and older.*

time	species	n	$^0/_0$ inf.	$\bar{x}$	s^2	max
Winter 1970—71	"B"	26	15	0.2	0.34	2
	"A"	22	50	0.8	1.04	4
Winter 1972—73	"B"	20	20	0.2	0.17	1
	"A"	29	34	0.6	1.9	7
Summer 1973	"B"	6	17	0.3	0.82	2
	"A"	22	32	0.4	0.44	2
Autumn 1973	"B"	26	19	0.4	0.81	3
	"A"	26	27	0.3	0.40	2

slower growth rate. Also, the T_F char concentrates more on *Chironomidae* larvae, whereas the T_S char concentrates on gammarids, which are more substantial food items.

A similar conclusion was arrived at by NILSSON and FILIPSSON (1971) concerning the dwarf char (T_F) in Lake Övre Björkvattnet. This identical ecological response of the positively identified dwarf in Lake Övre Björkvattnet and the proposed benthic dwarf (T_F) in the Fättjaure water system is further evidence of their homology.

The difference between the chars in feeding ecology is further reflected in their parasite faunas. The T_F dwarf is more heavily infected with *Cyathocephalus truncatus,* using *Gammarus* as its intermediate host, during the summer and autumn, while the T_S dwarf is more heavily infected with parasites using planktonic copepods as intermediate hosts, especially *Diphyllobothrium dendriticum, D. ditremum* and *Proteocephalus* sp.

The difference in intensity of infection with *Diphyllobothrium* is present throughout the year, while the difference in infection with *Proteocephalus sp.* is most marked during the autumn and winter. This is because the plerocercoids of *Diphyllobothrium* remain for a long time (probably the fish's whole life span) in the fish. *Proteocephalus sp.* on the other hand show a marked seasonal cycle (KENNEDY and HINE 1969, LEN and BORGSTRÖM 1973), with a maximum during the autumn correlated with the greater importance of planktonic crustaceans as food during that season. PETERSSON (1971 a) found that whitefish species (*Coregonus spp.*) with a high number of gillrakers, and thus predominantly plankton-feeding, were more heavily infected with *Proteocephalus sp.* than those with a low number.

The greater difference in rate of infection with C. *truncatus* during the summer and autumn than during the rest of the year can be explained by the more pronounced food segregation during that time and by the relatively short life-span of *C. truncatus* (up to 55 days according to VIK (1958)). PETERSSON (1971 b) found that whitefish species with low numbers of gillrakers were more infected with *C. truncatus.*

It seems as if the seasonal cycle of *C. truncatus* is different in the two species. In the T_F dwarf the incidence of infection is relatively high throughout the year except for the late winter, correlated with the lesser importance of *Gammarus* as a food item during that time. In the T_S dwarf the incidence is very high in the winter, when *Gammarus* is an important food item, but low during the rest of the year.

The T_S dwarf also shows a tendency to be more infected with *Crepidostomum metoecus,* which has *Gammarus* as the intermediate host, during the winter. THOMAS (1958) and AWACHIE (1968) showed that this parasite has a seasonal cycle with maximum abundance in the fish during the winter. *Crepidostomum suecicum* NYBELIN 1932 (=*C. metoecus* (HOPKINS 1934)) was found in *Salvelinus alpinus* in Sweden by NYBELIN (1933).

The absence of a significant difference in infection with *Eubothrium salvelini,* which has *Cyclops* sp. as the first intermediate host (BOYCE 1974), might partly be explained by the fact that it has a longer life-span than *C. truncatus* and *Proteocephalus* (up to two years according to SMITH (1973)). This should reduce the possible difference during the time of maximum food segregation.

VIK (1963) indicated a possible tendency for an increased infection of trout (*Salmo trutta* L.) with *E. crassum* in the autumn. This trend is present also in Lake Fättjaure, especially in the pelagic T_S dwarf, and may be explained by the great importance of planktonic crustaceans as food during that time of the year.

Salmincola edwardsii has a direct life-cycle (KABATA and COUSENS 1973) and it is hard to find any reason for a difference in the level of infection between the two chars.

In Lake Korsvattnet the slow growing "dwarf char" was found to be planktivorous (NILSSON 1955) and BYLUND (1973) found the "small char" in Lake Inarinjärvi more infected with plerocercoids of *D. ditremum.* In these cases, however, like in Lake St. Rösjön (ANDERSON *et al.* 1971), the "big char" is more fast growing compared to the "big" T_S char in Lake Fättjaure, and has apparently occupied a different food niche, being a predator. KLEMETSEN and ØSTBYE (1967), in Lake Finsevatn, and SKRESLET (1973), in Lake Nordlaguna, found that the "big char" were in a better condition than the "small char", but the "big char" in these lakes were fish-eating and attained lengths up to 60 cm.

The methods of pattern recognition used in the present study to classify the chars seem very promising. The chars in Lake Fättjaure are fairly well separated in their growth rate and most of them can be classified using the variables length and age only. During the autumn (1973) when they were well segregated in their choice of food, approximately 8 out of 10 char could be placed in the right class using 6 "ecological" variables. This means that in the case of two sympatric populations of char with approximately the same growth rate the methods might be even more valuable, especially when combined with gene frequency analysis.

The Fättjaure water system is, so far, the only known case where two species of Arctic char that normally occur as dwarfs in combination with normal pelagic char are found sympatrically without the presence of a normal char. Since the two chars are well separated in one of the lakes (Lake Fättjaure) on the basis of gene frequency, growth rate, parasites and feeding ecology it seems safe to assume that the rate of gene flow between the species is low indeed. On the other hand, comparison with frequency data from adjacent regions shows marked differences emanating from introgression, which then must have occurred over a long period of time. Also, it is interesting to note that hybridization has proceeded at a different pace in the three interconnected lakes.

Obviously, one of the usually benthic dwarfs (T_S) has been more successful as a plankton feeder, and this selective advantage has rendered a better growth rate possible, analogous to the situation for the normal char. This ability to readily switch over to a more pelagic life sheds light on the allopatric population in Lake Torrön previously described by NYMAN (1972).

The population in Lake Torrön was previously denominated by a question mark, since it occupied the "frequency region" of a T_S dwarf but grew and lived like a normal pelagic char. Obviously, this char when living allopatrically prefers the pelagic region. This hypothesis is further substantiated by data from Lake Namsvattnet in Norway (NYMAN, unpublished data) where the allopatric char present has the same properities as the char in Lake Torrön. This observation is very important from a practical point of view, since the char from Lake Torrön is widely used as brood stock. Evidently it should be restricted to stocking in lakes where no normal char exist to sustain its good growth potential.

Thus two dwarfed forms of Arctic char live sympatricallly in the three lakes studied, segregated in a manner similar to a normal char/dwarfed char relationship (NILSSON and FILIPSSON 1971). Since hybridization between the two has progressed at a different rate in the three lakes, some biological implications of practical interest may be elucidated. In Fig. 6 it is evident that there is most variation in growth potential in the least altered lake, Lake Fättjaure, and with increasing introgression the variability decreases, at the same time as the possibility to discern the two chars contributing is reduced. The extreme is Lower Fättjaure Lake where not only the gene frequencies of fast and slow growing fish are almost identical, but the growth diagram forms a homogeneous cluster. The average length of the fish is, however, not significantly changed by introgression (Lake Fättjaure 19.8 cm, Lower Fättjaure Lake 19.5 cm and Lake Borkajaure 20.3 cm). On the other hand there seems to be a pronounced impact by the rate at which hybridization has occurred with regard to the size distribution.

		percentage of fish	
		≥ 22 cm	≥ 25 cm
Lake Fättjaure	(1973)	48 %	11 %
Lake Borkajaure	(1973)	33 %	6 %
Lower Fättjaure Lake	(1973)	18 %	2 %

In this lake system hybridization between two char species has had a very negative impact on fish with a good growth rate. There seems to be a direct negative correlation between rate of introgression and presence of large fish. The practical problems are easy to realize. Arctic char smaller than 22 cm are hardly of any value commercially, small fish are less attractive to anglers, and last but not least, flesh colour — which is indicative of flesh quality — is most vivid in the large fish, hence the fish present after introgression has occurred offer a poorer quality to the human consumer.

It still remains to find out whether these negative results of introgression are common rules in long-term char hybridization.

There is, however, a direct parallel case described in whitefish (SVÄRDSON 1970) where introgression has changed the original species and where the variability of the discriminating character is negatively correlated with introgression — like the growth pattern in these char. Introgression is dependent on the local environment and may be initiated by acts of man (*e.g.* selective fishing, destruction of spawning areas by water level regulation, introduction of new species etc.). "This factor thus enters the evolutionary process and destroys the effects of speciation in the past . . ." (SVÄRDSON 1970).

V. SUMMARY

A lake system in southern Swedish Lapland has been found to harbour two sympatric species of Arctic char. To find out the optimal set of parameters for discrimination between the two species and for classifying individual fish to species, multivariate data analysis with methods of pattern recognition was attempted. Parasites and food items proved valuable.

Species determination, gene flow and introgression discussions are based on allele frequency data from a blood serum esterase polymorphism. It is shown that both species are dwarfed forms and that hybridization has proceeded at a different rate in the three lakes studied. With increasing introgression the difference in length — age distribution between the two species is reduced.

Special attention has been paid to qualitative and quantitative data on the parasite faunas and food habits during different seasons. One species is shown to be more pelagic in its food habits, the other more benthic. The food segregation is most marked in the autumn. This is also reflected in the parasite faunas.

Several biological and management implications of the findings are discussed.

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The Body-Scale Length Relation on the Oulu River Population of *Coregonus lavaretus* (Linné) *s.str.*

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I. INTRODUCTION

Though the well-known work of C. SEGERSTRÅLE (1933) supplied an excellent pointer for the use of empirical methods in the back-calculation of the fish growth, this method subsequently remained more or less ignored by Finnish ichthyologists. Nor were the new methods (HILE 1950, VOVK 1955, SHENTYAKOVA 1966) used very extensively. The requirement for a local body-scale relation for every fish population (LINDROTH 1963, SHENTYAKOVA 1966) has not been fulfilled in whitefish studies in Finland; instead a body-scale relation from Central Europe (EINSELE 1943) has tended to be used. In view of the urgent need for a body-scale relation for Finnish whitefish populations, work towards this aim was begun by the authors in 1965. In addition, the present result of body-scale relation for the sea-spawning whitefish from the Gulf of Bothnia is now also available (VALTONEN and VALTONEN 1975).

II. MATERIALS

The work concerns the species *Coregonus lavaretus* (LINNÉ) *s.str.* The material was gathered by two methods. First, young individuals, fry, fingerlings and yearlings were obtained from the Oulujoki Oy's hatchery at Montta. Roe fertilized from spawning fish at the river mouth at Oulu was specially raised during the summer of 1965 to obtain fry and fingerlings. 135 fingerlings and 45 yearlings (age 1 year, gathered on 9.10.1974 from Montta) were used in the determination of the body-scale relation. Secondly, 438 spawning individuals were gathered randomly from the fishermen's hoop-net catch at Kuusisaari in the river mouth during the period 15.—31.10.1965. The species was ascertained by counting the gillraker number in a sample of whitefish spawning in the Oulu river and in the hatchery-grown fish.

The results were:

	n	x̄	S.E.
Spawning in the river	95	29.08	0.23
Hatchery fish, age group 1	45	28.93	0.30
Hatchery fish, age group 0	30	28.47	0.37

An additional sample of 39 young *Coregonus lavaretus* living in the sea was obtained from around the island of Ulkokrunni, approx. 55 km north-west of Oulu. Fishes were identified by the method of VALTONEN (1976). It was not possible to determine whether these fish belonged precisely to the Oulu river population.

III. METHODS

An empirical body-scale relation was obtained from the material using the methods of SEGERSTRÅLE (1933), VOVK (1955) and SHENTYAKOVA (1966). In the last mentioned method the most refined statistical analysis is used. Since EINSELE (1943) restricted his body-scale ratio on certain scales between the pelvic fins (Fig. 11 in EINSELE

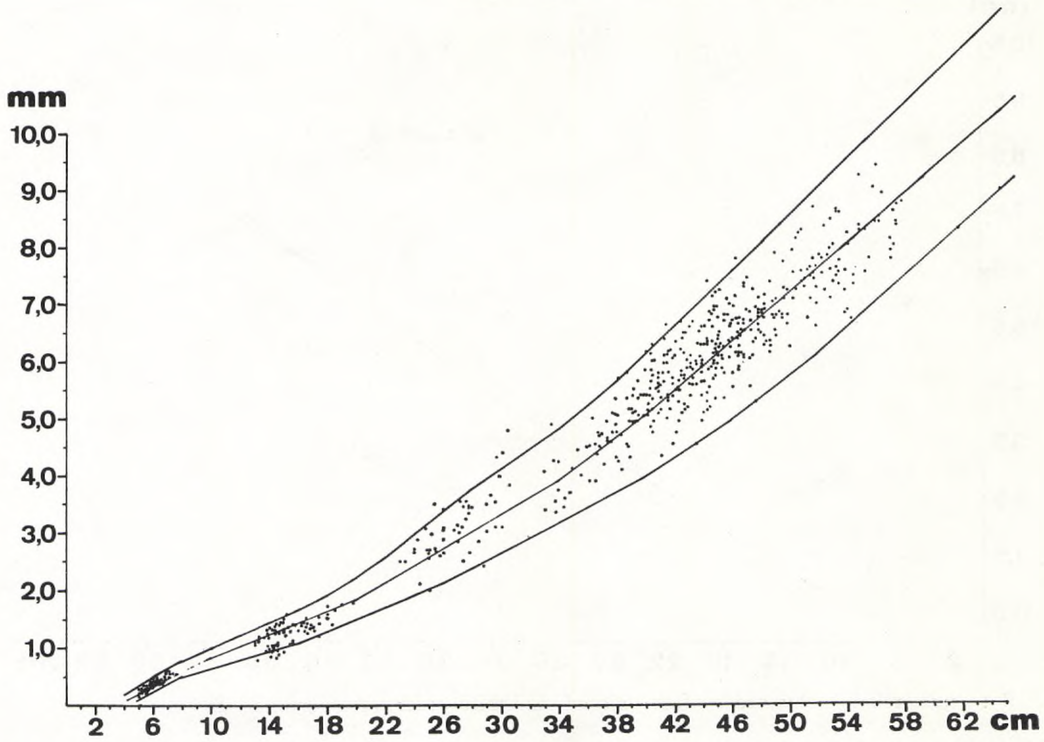

Fig. 1. Empirical curve for body-scale length relation after VOVK.

1943, cf. TESCH 1968) it was necessary to establish this Fennoscandian whitefish body-scale relation for these same scales, 12 in number. Even so, to obtain more accuracy for the back-calculation of growth, scales, once regenerated, were not accepted for this purpose (*cf.* LINDROTH 1963). These scales are also useless for the back-calculation of fish growth. The maximal oral length was measured from all unregenerated scales and their means was counted. It was also determined whether the middle ones of EINSELE's key scales were larger than the lateral ones. The material was used for an empirical body-scale relation. The statistical analyses were carried out using SURVO-1971, a computation system developed by the University of Tampere. This was very useful, especially when step-by-step polynomial regressions were required. In this paper results are given only for the methods of VOVK (1955) and SHENTYAKOVA (1966). The chief interest lies in the results obtained using third-degree polynomial regression. On the basis of this, the information required for a useful back-calculation device, the Carlander-Smith nomograph (HILE 1970) is given.

Fish length was measured as total length (LAEVASTU 1965) to the nearest millimetre.

IV. RESULTS

VOVK's *method*

The empirical description obtained by VOVK's method is given in Fig. 1. A nomograph (HILE 1970) was also drawn by this method, and was succesfully used on the authors' own material gathered from the Gulf of Bothnia and also for that presented by JÄRVI (1928). Since the statistical analysis of the empirical material confirms the results, it has not been thought necessary to present detailed data for back-calculation using VOVK's method.

Regression analyses

The statistical basis for the use of this method is now included in most routine data-processing

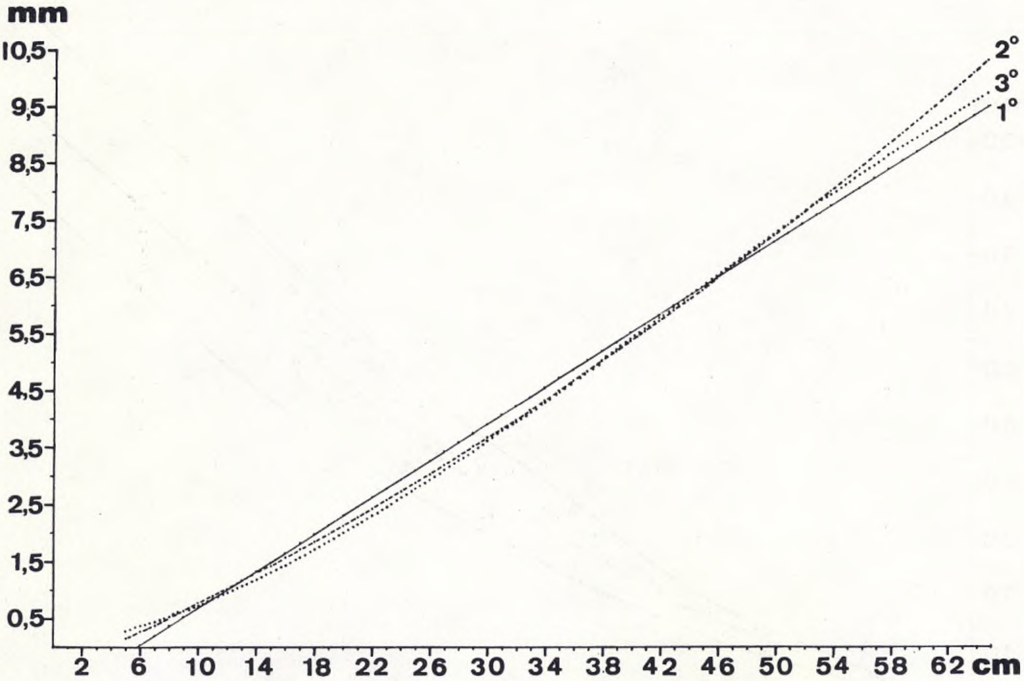

Fig. 2. Body-scale relation obtained by first-, second- and third-order regression analyses.

programmes including the SURVO-1971 programme developed at the University of Tampere, Finland. This renders the programming phase extremely simple, and also enables one to determine automatically the point at which a higher polynomial equation fails to give any better description of the correlation, in this case that between the fish and its scale. In the present whitefish population the polynomial of the third order was found to give the best results. The equations for the linear relation and for regressions of second- and third-order polynomials were as follows:

$y = -0.9171 + 0.01610x$
$y = -0.4218 + 0.01112x + 0.0000084x^2$
$y = -0.0353 + 0.00475x + 0.0000321x^2 -$
$- 0.000000025x^3$

y = length of oral part of the scale in mm.
x = total length of the fish in mm.

The regressions are shown in Fig. 2. The results obtained from the third-order equation and used for the computation of the linear nomograph are given in Table 1, to an accuracy of 1 mm in fish length. It would serve no purpose to print the figure of the nomograph partly because of small errors in the printed text but above all because it would have to be abbreviated to an unpractical extent. HILE (1970) gives sufficiently good advice for the construction and use of a nomograph.

Evaluations of EINSELE'S *scale*

A special study was made in order to establish whether the key scale used by EINSELE (1943, *cf.* TESCH 1968) was as large in the median row as in the side rows. It is well known that the length-breadth relationship of scales changes considerably when scales from the ventral rows are compared with the lateral scales (*cf.* LINDROTH 1963). Measurements show a difference of only 0.08 mm in the mean oral length between the median-row and the side-row scales (in 438 fishes), amounting to approx. 1.5 % of the mean oral length. The scales in the median row were somewhat longer, but the difference was of no statistical significance. The comparison with EINSELE'S body-scale length relation presented in Fig. 3 suggests that the use

Table 1. *Corresponding oral scale lengths for each length of fish in mm, from a third-order polynomial regression curve.*

fish mm	scale mm	fish mm	scale mm	fish mm	scale mm	fish mm	scale mm	fish mm	scale mm	fish mm	scale mm
50	0.279	105	0.791	160	1.446	215	2.226	270	3.101	325	4.047
51	0.281	106	0.801	161	1.458	216	2.241	271	3.116	326	4.064
52	0.295	107	0.812	162	1.472	217	2.256	272	3.133	327	4.082
53	0.302	108	0.824	163	1.485	218	2.270	273	3.150	328	4.100
54	0.311	109	0.834	164	1.498	219	2.286	274	3.166	329	4.119
55	0.320	110	0.843	165	1.510	220	2.301	275	3.182	330	4.138
56	0.328	111	0.855	166	1.524	221	2.316	276	3.199	331	4.154
57	0.336	112	0.865	167	1.537	222	2.332	277	3.216	332	4.172
58	0.345	113	0.876	168	1.550	223	2.346	278	3.233	333	4.189
59	0.354	114	0.889	169	1.565	224	2.362	279	3.250	334	4.208
60	0.360	115	0.900	170	1.579	225	2.377	280	3.269	335	4.226
61	0.370	116	0.910	171	1.591	226	2.394	281	3.284	336	4.244
62	0.380	117	0.921	172	1.605	227	2.408	282	3.301	337	4.262
63	0.388	118	0.932	173	1.620	228	2.424	283	3.318	338	4.280
64	0.396	119	0.944	174	1.635	229	2.440	284	3.335	339	4.299
65	0.405	120	0.955	175	1.647	230	2.455	285	3.353	340	4.316
66	0.412	121	0.966	176	1.662	231	2.469	286	3.369	341	4.334
67	0.421	122	0.977	177	1.676	232	2.485	287	3.386	342	4.351
68	0.430	123	0.990	178	1.690	233	2.500	288	3.404	343	4.370
69	0.437	124	1.001	179	1.705	234	2.516	289	3.420	344	4.389
70	0.446	125	1.014	180	1.717	235	2.536	290	3.438	345	4.407
71	0.455	126	1.025	181	1.730	236	2.549	291	3.454	346	4.425
72	0.465	127	1.036	182	1.745	237	2.565	292	3.471	347	4.443
73	0.474	128	1.047	183	1.759	238	2.580	293	3.488	348	4.460
74	0.484	129	1.058	184	1.772	239	2.595	294	3.506	349	4.479
75	0.492	130	1.071	185	1.788	240	2.612	295	3.524	350	4.498
76	0.501	131	1.083	186	1.802	241	2.626	296	3.540	351	4.516
77	0.511	132	1.095	187	1.815	242	2.644	297	3.557	352	4.534
78	0.520	133	1.106	188	1.830	243	2.569	298	3.575	353	4.552
79	0.529	134	1.119	189	1.845	244	2.675	299	3.592	354	4.571
80	0.538	135	1.131	190	1.857	245	2.691	300	3.610	355	4.589
81	0.549	136	1.144	191	1.873	246	2.707	301	3.627	356	4.606
82	0.559	137	1.155	192	1.887	247	2.724	302	3.644	357	4.626
83	0.568	138	1.167	193	1.902	248	2.740	303	3.661	358	4.642
84	0.577	139	1.180	194	1.916	249	2.756	304	3.689	359	4.660
85	0.586	140	1.192	195	1.931	250	2.773	305	3.697	360	4.679
86	0.596	141	1.204	195	1.946	251	2.787	306	3.714	361	4.696
87	0.606	142	1.217	197	1.960	252	2.804	307	3.732	362	4.714
88	0.616	143	1.230	198	1.975	253	2.820	308	3.749	363	4.733
89	0.626	144	1.243	199	1.990	254	2.836	309	3.768	364	4.750
90	0.635	145	1.255	200	2.002	255	2.852	310	3.784	365	4.768
91	0.645	146	1.268	201	2.018	256	2.869	311	3.802	366	4.786
92	0.655	147	1.281	202	2.033	257	2.885	312	3.820	367	4.804
93	0.666	148	1.294	203	2.047	258	2.901	313	3.837	368	4.823
94	0.676	149	1.306	204	2.063	259	2.918	314	3.854	369	4.840
95	0.686	150	1.317	205	2.078	260	2.935	315	3.872	370	4.860
96	0.697	151	1.331	206	2.092	261	2.950	316	3.889	371	4.880
97	0.707	152	1.344	207	2.107	262	2.966	317	3.907	372	4.899
98	0.718	153	1.357	208	2.122	263	2.983	318	3.924	373	4.918
99	0.729	154	1.370	209	2.139	264	3.000	319	3.942	374	4.935
100	0.736	155	1.383	210	2.150	265	3.017	320	3.960	375	4.953
101	0.749	156	1.396	211	2.165	266	3.034	321	3.977	376	4.970
102	0.759	157	1.408	212	2.181	267	3.050	322	3.994	377	4.988
103	0.770	158	1.420	213	2.199	268	3.066	323	4.011	378	5.006
104	0.780	159	1.433	214	2.212	269	3.085	324	4.029	379	5.025

fish mm	scale mm	fish mm	scale mm	fish mm	scale mm	fish mm	scale mm	fish mm	scale mm	fish mm	scale mm
380	5.044	426	5.894	471	6.726	517	7.562	562	8.355	608	9.126
381	5.061	427	5.913	472	6.745	518	7.581	563	8.371	609	9.141
382	5.079	428	5.931	473	6.763	519	7.599	564	8.389		
383	5.097	429	5.950	474	6.781			565	8.406	610	9.157
384	5.116			475	6.798	520	7.618	566	8.423	611	9.174
385	5.134	430	5.968	476	6.816	521	7.635	567	8.440	612	9.190
386	5.152	431	5.986	477	6.835	522	7.652	568	8.456	613	9.205
387	5.171	432	6.004	478	6.854	523	7.671	569	8.475	614	9.222
388	5.190	433	6.023	479	6.871	524	7.689			615	9.237
389	5.209	434	6.042			525	7.707	570	8.493	616	9.254
		435	6.061	480	6.892	526	7.725	571	8.510	617	9.269
390	5.228	436	6.080	481	6.909	527	7.743	572	8.526	618	9.285
391	5.246	437	6.099	482	6.927	528	7.760	573	8.545	619	9.300
392	5.264	438	6.117	483	6.946	529	7.779	574	8.561		
393	5.283	439	6.136	484	6.964			575	8.579	620	9.316
394	5.301			485	6.982	530	7.794	576	8.595	621	9.331
395	5.319	440	6.153	486	7.000	531	7.813	577	8.612	622	9.347
396	5.337	441	6.173	487	7.019	532	7.830	578	8.628	623	9.362
397	5.356	442	6.193	488	7.036	533	7.848	579	8.646	624	9.379
398	5.375	443	6.209	489	7.055	534	7.866			625	9.394
399	5.394	444	6.229			535	7.884	580	8.663	626	9.410
		445	6.247	490	7.073	536	7.900	581	8.680	627	9.425
400	5.412	446	6.265	491	7.090	537	7.919	582	8.697	628	9.441
401	5.430	447	6.285	492	7.109	538	7.937	583	8.714	629	9.456
402	5.449	448	6.302	493	7.128	539	7.954	584	8.730		
403	5.467	449	6.320	494	7.146			585	8.747	630	9.472
404	5.486			495	7.165	540	7.973	586	8.764	631	9.488
405	5.504	450	6.339	496	7.183	541	7.991	587	8.780	632	9.502
406	5.523	451	6.357	497	7.201	542	8.009	588	8.797	633	9.518
407	5.542	452	6.376	498	7.220	543	8.026	589	8.814	634	9.534
408	5.560	453	6.395	499	7.239	544	8.044			635	9.549
409	5.579	454	6.414			545	8.060	590	8.830	636	9.564
		455	6.433	500	7.257	546	8.078	591	8.846	637	9.580
410	5.597	456	6.450	501	7.274	547	8.096	592	8.864	638	9.595
411	5.617	457	6.469	502	7.293	548	8.113	593	8.880	639	9.611
412	5.636	458	6.487	503	7.310	549	8.130	594	8.897		
413	5.654	459	6.506	504	7.328			595	8.913	640	9.626
414	5.673			505	7.347	550	8.148	596	8.930	641	9.641
415	5.692	460	6.523	506	7.365	551	8.164	597	8.946	642	9.656
416	5.709	461	6.543	507	7.384	552	8.181	598	8.962	643	9.671
417	5.729	462	6.562	508	7.401	553	8.199	599	8.979	644	9.686
418	5.746	463	6.579	509	7.419	554	8.216			645	9.701
419	5.765	464	6.598			555	8.234	600	8.994	646	9.716
		465	6.617	510	7.438	556	8.251	601	9.011	647	9.731
420	5.782	466	6.636	511	7.454	557	8.269	602	9.028	648	9.746
421	5.801	467	6.654	512	7.473	558	8.286	603	9.044	649	9.761
422	5.820	468	6.672	513	7.490	559	8.304	604	9.060	650	9.776
423	5.839	469	6.691	514	7.509			605	9.077		
424	5.857			515	7.526	560	8.322	606	9.094		
425	5.875	470	6.708	516	7.545	561	8.338	607	9.110		

in Finland of Einsele's relation from Central Europe was not so unwise as one might have expected.

V. DISCUSSION AND SUMMARY

Shentyakova (1966; *cf.* Lindroth 1963) shows clearly the need for a body-scale relation in any thorough study of a fish population. This has now been achieved for the whitefish, *Coregonus lavaretus* (Linné) *s.str.* population in the Oulu river. The work is based on empirical material, which must be regarded as the only reliable method (Shentyakova 1966, *cf.* Hile 1970). Moden statistical methods described by Schindowski & Tesch (1957) and Shentyakova (1966)

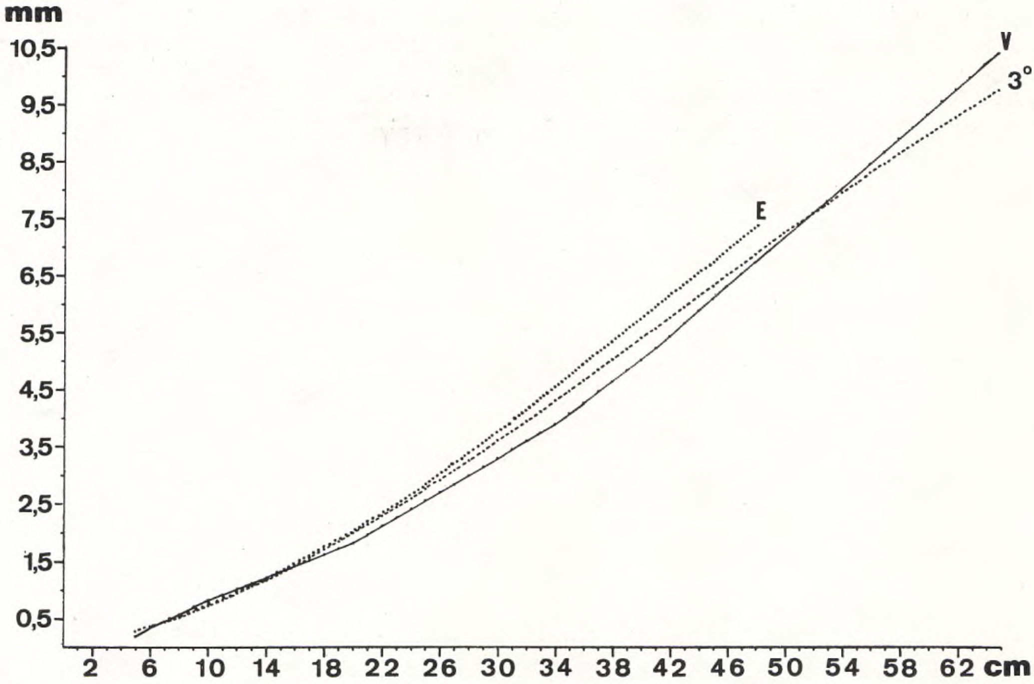

Fig. 3. Body-scale relation of whitefish from Central Europe (E., Einsele 1943) and from the Oulu river by method of Vovk (V) and by third-order regression analysis (3°).

were used in the analysis. The body-scale length ratio based on the third-order regression equation was found to be the most suitable for the back-caculation of fish growth in this population. A table of fish and scale lengths necessary for the construction of a linear nomograph (Hile 1970) for the work is given. The results are equally suited to fully automatic processing by computer. It was very interesting to note the wide difference (approx. 6 cm) in the back-calculation results between the lengths obtained by Järvi (1928) and by the present method for the same fish in the Gulf of Bothnia at the age of one year. Such differences have already been observed by Segerstråle (1933). It is quite obvious that the difference is mainly due to Lee's phenomenon. This is to be found in Järvi's results, mainly because of his simple back-calculation method.

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Estimates of a Population of Spawning Perch (*Perca fluviatilis* L.) and of the Efficiency of Trap and Gill-Net Fishing

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I. INTRODUCTION

The reasons why stunted perch populations occur were examined by ALM (1946) who also showed that perch populations could be reduced substantially by intensive fishing with traps, gillnets and other gear. In Norway fishing with unbaited traps during the spawning season has been a common method to reduce perch populations in small lakes and tarns since SØMME (1939) demonstrated that great numbers of perch could cheaply be caught in this way. The trap is a passive gear, but in contrast to fish caught on gillnets, perch are not permanently caught in a trap but can be seen to swim in and out of the funnel. Consequently frequent lifting will increase the catch substantially, and so will frequent moving of the traps to new places (SØMME 1939). Often, but not always, traps fished during the spawning period catch mainly male perch.

Little is known about the fishing mortality on perch populations caused by known fishing efforts with different kinds of gear. However, the reduction of the numeral density of the perch population in Lake Windermere to about 3% by intensive fishing with traps and other gear (LE CREN 1958) indicates a very high fishing mortality. LE CREN (1962) estimated the fishing mortality due to traps in 1941 as roughly $\hat{F}=1.52$ for male perch in Windermere. For River Vistula where perch were not regarded attractive for the fishery BACKIEL (1971) gave a very tentative estimate of only $\hat{F}=0.19$ for perch aged 7 years or more.

As emphasized by BAGENAL (1972) estimating perch populations solely from trap catches is difficult because of the great variances in catch between traps, between places (beats), between days (lifts) and the interactions between these variables. Of course this does not necessarily mean that perch population estimation based on trap fishing in combination with marking is hopeless. If the marked and unmarked members of the population under study behave in the same way, and the fishing is done randomly over the whole lake, reasonably accurate estimates can still be obtained. One way to check the reliability of the method is to test if other independent estimates, for instance by rotenone treatment, give comparable results (JENSEN 1974). Another check — this time with gill nets — is demonstrated in this paper.

II. MATERIALS AND METHODS

Lake Øyungen is a small (0.465 km^2) oligotrophic lake, altitude 283 m, situated in a forest area some 15 km north of Oslo, Norway. The fish species are brown trout, char, perch and minnow (*Phoxinus*). The lake is popular among sport fishermen and some gill-netting is also done. Øyungen is regularly stocked with fingerling brown trout and the perch population kept down by fishing with $^1/_2$ inch mesh perch traps in the spawning period. In connection with studies of perch predation on trout fingerlings we attempted to estimate the size of the population of spawning perch and the fishing mortality caused by certain efforts with traps and gill nets.

The lake was continuously fished with 19 unbaited $^1/_2$ inch perch traps from the evening of

April 30 to May 15, 1974. 13 of the traps were made of nylon and 6 of steelthread ("wire-mesh"). The traps were distributed along the whole shore of the lake, but never deeper than 5—6 m as the perch in Øyungen spawns in shallow water. The traps were lifted twice per day on May 1—11 and once per day May 12—15. After each lifting the trap was moved to a new place. All fish (except 10 killed by accident) were immediately after capture tagged below the front of the first dorsal with Floy FD-67 F flag tags (for description see Dell 1968). The flags had in advance been cut away to ensure a tagging method which would not increase the catchability of perch on gill nets. Series of different tag colours were used. On the last days the fish were marked by cutting away the anal fin. Recaptured, previously tagged perch were released without addition of new tags or marks.

Experimental fishing with gill nets was done September 14—16, 1974 and again on May 25—26 1975. The nets were about 25 m long and made of spun nylon with mesh sizes (knot to nearest knot) 24, 26 and 29 mm. 11 nets of each mesh were used. The nets were set one and one randomly along the lake shore and moved to new places each day. The effort in September was 78 gill-net nights. During the second night's fishing in May, 9 of the nets were stolen, so the fishing effort in May was only 57 gill-net nights. All perch caught on the gill nets were killed.

III. POPULATION ESTIMATES FROM THE TRAP EXPERIMENTS

Table 1 shows the daily trap catches, numbers of perch tagged or marked and the recaptures. 4,667 fish were tagged or marked and 1,165 recaptures were made during the trap fishing. Nearly the whole catch consisted of spawning males; only 30 females were tagged. We can obviously only estimate the population of spawning males from these data.

Table 2 gives daily Schnabel and Petersen population estimates (Ricker 1975). After 8 May the Petersen estimates increase considerably. The increase in the Schnabel estimates is more moderate because these estimates are strongly influenced by all previous recaptures and catches.

The third column in Table 1 shows the mean number of perch caught per trap in the first haul each day. The catches decrease quickly after May 9. The reason for this decrease in catchability is probably that gradually the males are spent and lose interest in the traps.

It is quite possible that we to the catchable part of the population have a continuous inflow of maturing males and a continuous outflow (loss of interest in traps) of spent males, and this could seriously bias our estimates. However, substantial changes of this kind could be expected to result in differences in recapture between the different tag colours. As for instance, all Lilacs were tagged on May 1—3 and all Whites on May 6—10, we could expect that on May 11—15 the proportions of recaptured Lilacs would be smaller than the proportions of recaptured Whites. The daily recapture proportions for each colour are listed in Table 1. The proportions are decreasing with time, but apparently there is no clear difference between colours. One way to separate the variation due to time (date of recapture) is to apply a two-way analysis of variance without replication (Sokal and Rohlf 1969). Each proportion p_i was transformed to arc. sin $\sqrt{p_i}$ and the transformed data analysed. The results are shown in Table 3. The Anova compares all 5 colours in the last 5 fishing days. There is a difference between colours significant at the 5% level. Much of this difference, however, is caused by differences between the two last colours Grey and White. An a posteriori test of the differences between all 5 means is also shown in Table 3. Only the differences (White-Grey) and (Green-Grey) are significant at the 5 % level.

However, in spite of the transformation we may still seriously have violated assumptions on which analyses of variance are based. The non-parametric Friedman's method for randomized blocks (Sokal and Rohlf 1969) was therefore tried. The differences in recapture between colours were found not significant ($X^2 = 5.82$; d.f. $= 3$).

Unfortunately the grey and white tags look so much alike that we can not exclude the possibility that some of the recaptured Greys have been listed as Whites and vice versa. We can avoid bias from this by pooling Grey and White. When this is done, there is no significant difference between

Table 1. *Daily catch, number marked (m), number recaptured (r) and fraction recaptured (r/m).*

Date	Catch	Catch per trap	Lilac			Green			Yellow			Grey			White			Fin-cut	
			m	r	r/m	m	r	r/m	m	r	r/m	m	r	r/m	m	r	r/m	m	r
1.5	98	4.9	96	1															
2.5	538	23.9	525	10															
3.5	361	13.6	59	26		271	5												
4.5	752	27.9		43	0.063	394	27		283	5									
5.5	580	28.9		49	0.072		33	0.050	214	28		252	1						
6.5	611	27.9		52	0.076		34	0.051		40	0.080	442	15		28	0			
7.5	340	15.3		21	0.031		24	0.036		10	0.020		31	0.045	253	0			
8.5	663	26.5		46	0.068		52	0.078		29	0.058		43	0.062	478	15			
9.5	553	25.5		34	0.050		34	0.051		18	0.036		27	0.039	409	31			
10.5	412	16.8		23	0.034		21	0.032		18	0.036		19	0.027	298	33			
11.5	320	15.1		15	0.022		21	0.032		14	0.028		12	0.017		27	0.018	225	6
12.5	269	14.2		8	0.012		10	0.015		6	0.012		7	0.010		34	0.023	193	11
13.5	199	10.5		4	0.006		5	0.008		5	0.010		8	0.012		23	0.016	143	11
14.5	87	4.6		1	0.001		3	0.005		4	0.008		0	0		9	0.006	60	8
15.5	59	3.1		1	0.001		1	0.002		1	0.002		0	0		5	0.003	44	7
Total	5,842		680	334	0.49	665	270	0.41	497	178	0.36	694	163	0.23	1466	177	0.12	665	43

Table 2. Estimates of number of spawning males.

Date	Schnabel estimates							Daily Petersen estimates					
	Lilac	Green	Yellow	Grey	White	Fin-cut	Pooled	Lilac	Green	Yellow	Grey	White	Pooled
2.5	4,695						4,695						
3.5	7,455						6,567						
4.5	9,718	7,278					8,476	11,637					11,637
5.5	9,089	9,664	5,660				8,494	7,902	11,364				9,415
6.5	8,775	10,482	6,780	9,623			8,717	7,852	11,628	7,419			8,876
7.5	9,006	10,268	8,061	8,296			9,006	10,540	9,071	15,407	7,395		9,940
8.5	9,153	9,724	8,947	9,445	12,239		9,308	9,607	8,331	11,000	10,473		9,053
9.5	9,382	9,905	9,850	10,546	13,097		9,923	10,763	10,526	14,491	13,731		12,324
10.5	9,553	10,197	10,041	11,175	13,710		10,363	11,702	12,484	10,803	14,331		12,773
11.5	9,822	10,233	10,158	11,769	14,634		10,662	13,643	9,703	10,636	17,136	16,807	14,274
12.5	10,139	10,491	10,601	12,442	13,902	5,044	10,968	20,400	16,323	19,170	23,423	11,309	16,372
13.5	10,424	10,837	10,873	12,679	13,732	6,248	11,204	27,200	22,167	16,567	15,422	12,217	17,400
14.5	10,570	10,892	10,872	13,049	13,834	6,210	11,305	29,920	14,630	(8,747)		12,901	19,565
15.5	10,658	10,999	10,978	13,300	13,854	6,030	11,473	(20,400)	(19,950)	(14,910)		14,660	26,680

Table 3. *Comparisons of transformed r/m means.*

	d.f	Mean square	F_s
Between days of recapture 11.5—15.5	4	35.44	26.25***
Between 5 colurs	4	5.67	4.20*
Rest (Error)	16	1.35	

Student—Newman—Keuls test:

$$s_{\bar{x}}=\sqrt{\frac{1.35}{5}}=0.5196$$

k	2	3	4	5
$Q_{0.05}$	2.998	3.649	4.046	4.333
LSR	1.558	1.896	2.102	2.251

	Grey	Lilac	Green	Yellow	White
Mean:	3.90	4.58	5.81	5.87	6.52

k=5:	White	—Grey	=2.62	Significant
k=4:	White	—Lilac	=1.94	Not significant
	Yellow	—Grey	=1.97	Not significant
k=3:	White	—Green	=0.71	Not significant
	Yellow	—Lilac	=1.29	Not significant
	Green	—Grey	=1.91	Significant
k=2:	White	—Yellow	=0.65	Not significant
	Yellow	—Green	=0.06	Not significant
	Green	—Lilac	=1.23	Not significant
	Lilac	—Grey	=0.68	Not significant

colours, but we have lost one degree of freedom so the test is less sensitive.

Possible differences in recapture rates between dates of tagging were thus too small to be detected by the methods that were used. One explanation is that nearly all adult males participated in the spawning from about May 5—6, hence after this time there was no substantial difference in catchability between tagged and untagged male adults.

Through the whole spring small numbers of juvenile and spent perch also enter the traps. When the catchability of the spent males dcreases towards the end of the spawning, an increasing fraction of the catch will consist of untagged juveniles, and this will cause a rise in the population estimates. The day with the biggest catch, and probably the culmination of the spawning period, was May 8, and we shall use this day's estimates as our best estimates of the population of spawning males. The Petersen estimates on this day vary for the different colours between $N_P=8{,}331$ and $N_P=11{,}000$, and for all colours pooled $N_P=9{,}053$ with 95 % confidence interval 8,044—10,281. The corresponding Schnabel estimate is $N_S=9{,}308$ with approximate 95 % interval 8,970—9,680.

IV. ESTIMATES FROM GILL-NET FISHING

Data from the experimental gill-net fishing is shown in Table 4. An unknown, but probably small number of tagged and untagged perch had been removed by fishermen after the tagging, so we can hardly use the data for population estimates, but we can check the fraction of marked fish among the males. The per cent recaptured, fin-cut perch is suspiciously low, probably because of increased mortality due to this method of marking. Further, the fin-cuts were not used to obtain our best estimate, so we leave the fin-cuts out.

Of our estimated population in May of 8,000—10,000 spawning males 4,002 or 40—50 % were tagged with coloured tags. In the gill-net catch in September the same year a fraction of the males of 303/596 or 50.8 % (approximate 95 % confidence interval 46—55%) carried coloured tags. In the gill-net catches in May the next year 42/91 or 46.2 % (approximate 95 % interval 36—56 % of the males carired coloured tags. The excellent agreement between the three independent estimates of the proportion of tagged males confirms the population estimate and does also indicate that tag losses, post-tagging mortality and recruitment can not have been substantial.

Of the 30 tagged females 16 were recaptured by our gill-net fishing. Apparently a substantial proportion of the population of spawning females was later caught in our gill nets.

V. MANAGEMENT CONSIDERATIONS

The populations of more or less stunted perch that are so commonly found in lakes in the Scandinavian forests compete seriously for food with trout and other valuable fish species. Stocking of such lakes with fingerling trout are often disappointing,

Table 4. *Perch caught on gill nets in Lake Øyungen autumn 1974 and spring 1975.*

	Un-tagged	Lilac	Green	Yellow	Grey	White	Fin-cut	Total
Males:								
No. tagged spring 1974 ..	—	680	665	497	694	1466	665	4667
No. captured autumn 1974	293	71	68	57	59	48	3	599
% recaptured autumn 1974	—	10.4	10.2	11.5	8.5	3.3	0.5	—
No. captured spring 1975..	49	7	9	7	7	12	2	93
% recaptured spring 1975	—	1.03	1.35	1.41	1.01	0.82	0.30	—
Females:								
No. tagged spring 1974 ...	—	5	3	2	3	15	2	30
No. captured autumn 1974	841	2	1	1	2	6	—	853
No. captured spring 1975	353	1	1	—	1	1	—	357

and great numbers of fingerlings can be found in the perch stomachs immediately after stocking. Perch traps are often used to reduce stunted perch populations.

The experiments cited indicate that in a small lake continuous fishing through the 14 days' spawning period with approximately 0.4 traps per hectare lake surface caught 40 %—50 % of all spawning males (corresponding fishing mortalities for spawning males F=0.51—0.69). When they are not delayed by tagging and recording, two men in a small boat can easily lift, empty and move 40—50 traps 2—3 times daily. The figures indicate that a substantial fraction (tentatively about $^1/_2$) of the population of adult female perch can be caught by a yearly fishing effort of magnitude 3 gill-net nights per hectare lake surface, provided that the mesh size is adequate.

In big, deep lakes where the lake area per meter of shore line is bigger, and where the spawning period of perch lasts longer, other fishing efforts per hectare will be needed to obtain corresponding fishing mortalities.

VI. SUMMARY

In a 46.5 hectare oligotrophic forest lake near Oslo, Norway, the population of spawning male perch was estimated by means of tagging — recapture of perch caught in wire-mesh traps. The estimated fraction of tagged adult males/untagged adult males was later controlled twice by experimental gill-net fishing and found correct.

Continuous fishing through the 14 days' spawning period with 0.4 traps per hectare lifted twice to once daily caught 40—50 % of all spawning male perch.

The traps caught an insignificant fraction of the adult female perch. The recapture figures indicate that a substantial proportion (tentatively $^1/_2$) of the population of adult females were caught by a fishing effort of about 3 gill-net nights per hectare lake area.

VII. ACKNOWLEDGMENTS

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The Growth and Year-Class Strength of Perch (*Perca fluviatilis* L.) in Some Baltic Archipelagoes, with Special Reference to Temperature

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I. INTRODUCTION

The perch (*Perca fluviatilis* L.) is one of the commonest fishes in the Baltic archipelagoes. Yet only scant information is available on its age distribution and growth in these waters. The main aim of this paper is to describe the growth of perch along the Swedish coast of the central Baltic. The study is part of an extensive fishery-biological investigation and is being carried out in three separate areas. The year-to-year variations in growth rates between the areas are compared and are related to the temperature conditions. A study is being made of means of year classes and the growth of individuals. The correlation between the strength of year classes and the temperature is also being investigated.

The distance between the annual rings on the opercular bone in the gill cover has been used to back-calculate the growth. Annuli on the operculum were observed by ARNOLD as early as 1913. In 1929, SVETOVIDOV showed that the growth of the operculum does not bear a linear relationship to the length increment of the body, but decreases in relation to increasing size. LE CREN (1947) has calculated a formula describing this "allometric growth" for perch in Lake Windermere in northwestern England. A corresponding study was made by AGNEDAL (1968) for Lake Erken in eastern Sweden. The method used by these authors was adopted in the present study.

In investigations covering a large number of fish species, a relationship was established between growth and year-class strength, on the one hand, and the temperature level in different years, on the other. As regards perch, the only detailed analysis in this field is by LE CREN (1958), who studied the effects of temperature and population density on growth in Windermere.

A more extensive analysis of the material treated in this paper has been presented in Swedish (NEUMAN 1974 a).

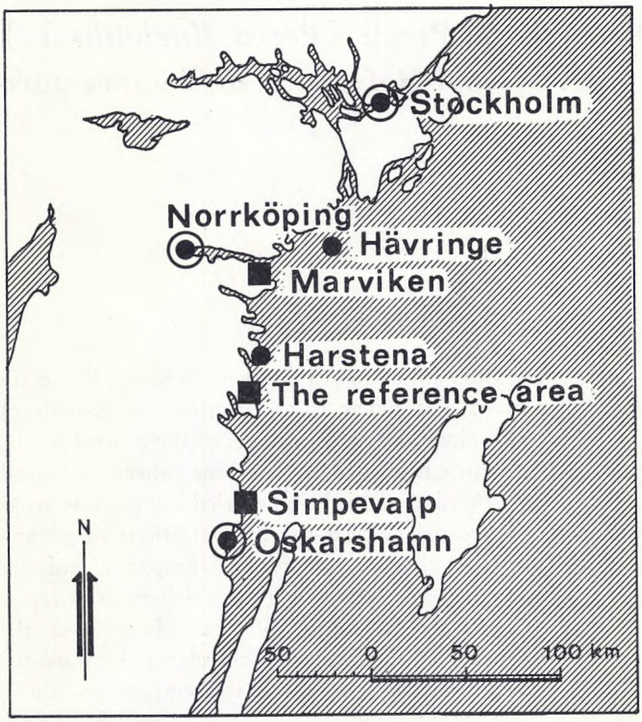

Fig. 1. The investigation areas.

II. MATERIAL AND METHODS

(a) The investigation areas

Gill covers of perch were collected in three archipelago areas (Fig.1). In two of these, Marviken and Simpevarp, thermal power stations are situated. The material presented here, however, was collected before the plants started operating. The third area lies between Marviken and Simpevarp and serves as a reference.

Marviken is sheltered from the open sea and is to some extent affected by the adjacent estuary of the River Motala ström. In Simpevarp, on the other hand, the archipelago is very narrow and a great deal of the perch is sampled from localities in direct contact with the open sea. The conditions at the reference area are intermediate in these respects. During the 1960s the mean surface salinities were 6.2, 7.0 and 7.1 ‰ in Marviken, the reference area and Simpevarp, respectively. The limnic element in the flora and fauna is more marked in Marviken than in the other areas. The summer temperature can reach 25°C in shallow bays, but the summer mean surface temperature outside Simpevarp is only 15°C.

(b) Collection and analysis of the operculae

In most years since 1963 samples of 200 perch have been collected in each area. The perch were taken from gill nets of different mesh sizes used for test fishing. In 1965 no samples were collected in Simpevarp. In 1970, the last sampling year in the present context, the number of samples was doubled and in Marviken and Simpevarp a large proportion of the samples was taken from big fyke nets. The operculars have almost exclusively been collected in May and June. Samples have often been taken of the whole night's catch. When selections were made, the aim was to get a sample with a size distribution corresponding to the one in the catch.

The method described by Le Cren (1947) was used in analysing the operculum. The distances between the annuli were measured by means of a projector (x16). Total length and back-calculated lengths were measured to the nearest whole or half centimetre below. As a first step in the computing, an addition of 0.2 cm was made to all length data (the correct class centre of 0.25 would have occupied too much space on the punched cards). While most of LE CREN's calculations express growth as the increment in weight, the present calculations used length data only.

Most of the operculars were read without much difficulty. In many of them, however, the first annuli were often very weakly developed and were difficult to identify. In several cases it was difficult to distinguish false rings from the real ones, as the whole opercular had a diffuse character. Because of this, nearly 15 per cent of the collected material had to be discarded.

In all, 4,066 fish were successfully analysed, one third or 1,375 being males. As the finest meshes of the gill nets used had a mesh bar of 21 mm, only a few perch younger than three years of age were caught. Fish more than 11 years old rarely occur and were excluded from most statistical analyses for technical reasons.

(c) The relationship between length of body and length of opercular

LE CREN (1947 and 1958) describes the non-linear relation between the length of the body and the operculum by the following formula: $F = 22.76\ B^{0.876}$, where F is the total length of the fish and B the opercular length.

AGNEDAL (1968) did corresponding work on perch from Lake Erken in eastern Sweden. He arrived at the equation $F = 19.45\ B^{0.8610}$. He also found fairly similar values for perch from the Baltic. As the aim of the present study is to compare years and areas rather than to establish the exact and absolute values of the growth, possible systematic errors in the back-calculation are of minor importance. For this reason, the formula of AGNEDAL is considered to be fully adequate for use in these calculations.

(d) Environmental factors

The collected operculars give information — by back-calculation — on the growth of perch back to the end of the 1940s. Unfortunately, measurements of temperature were not made in these coastal areas until the beginning of the investigation, and this made it difficult to find links between growth and water temperature. In the absence of more representative values, the daily measurements from the lightship at Hävringe have been used. This lightship was anchored 39 km east of Marviken and 7 km outside the outer skerries (Fig. 1) but after the 1967 season it was removed. Monthly hydrographic observations in Marviken and Simpevarp began in 1962. The covariation between the water temperatures in these areas and the one at Hävringe was examined by regression analysis, which included the months from April to October and covered the depths 0 m, 5—6 m and 15—16 m. All the relations were found to be significantly correlated. On the basis of these values, the monthly averages of surface water temperatures at Hävringe from June to September were chosen as a temperature index. In 1968 and 1969 there were no observations at Hävringe and the measurements in Marviken were used instead, with the result that one measurement represents a whole month. The variations in the strengths of year classes were explained by testing the monthly averages of air temperatures from May to September at Harstena, about 26 km north-east of the reference area (Fig. 1).

III. RESULTS

A. Dimensioning of year classes

Many writers, e.g. ALM (1952) and LE CREN (1955), have observed marked fluctuations in the strengths of year classes of perch. Such fluctuations may also be seen in the present material and they have been analysed below for possible covariation between the areas and the relationship between year-class strength and temperature.

(a) Inter-area relationship on year-class strength

SVÄRDSON (1961), among others, designed models in order to estimate the relative year-class strength by means of the age distributions in the catches. A similar model is also used below in the analysis of the effect of temperature on year-class strength, but these methods are imperfect, since the standardizations performed make the values included dependent on each other. For a comparison between the three areas, however, such standardizations are not necessary. The methods of collection were the same between years and areas, and the representation of birth years in relation to each

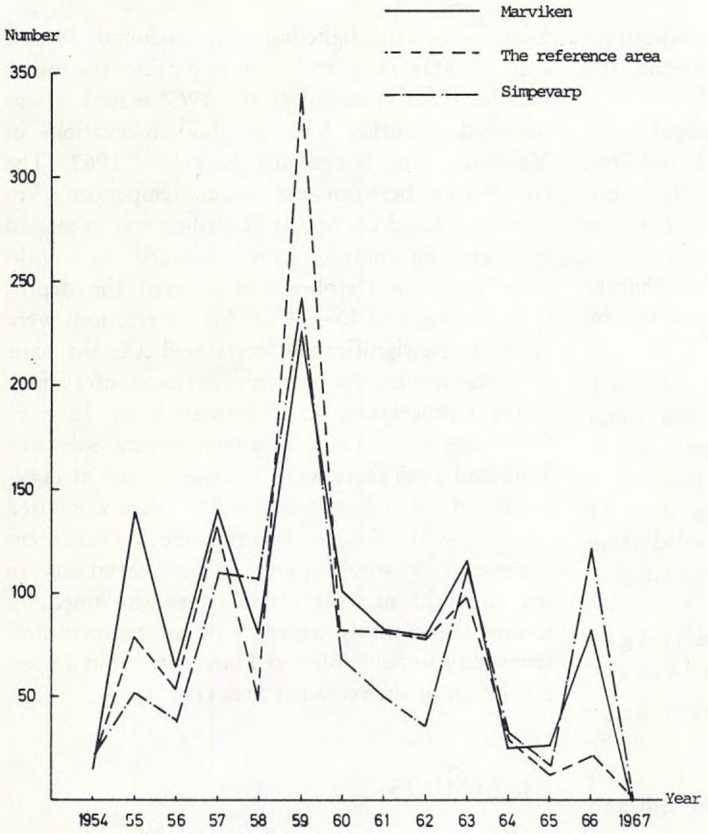

Fig. 2. The distribution on birth years of the catches 1963—69.

other is unimportant in this context. By excluding 1970, with its differing standards of collection, it is possible to make direct comparisons of the distribution over birth years in the three areas (Fig. 2). It can be seen that the areas are strikingly alike in this respect. The similarity has been statistically tested with an analysis of rank sums, which shows that the correlation between Marviken and the two other sampling stations is significant at the 1 % level and between Simpevarp and the reference area is significant at the 5 % level.

(b) Calculations of year-class strength

The year classes must be made comparable before an analysis of the relationship between temperature and strength of year class can be attempted. This has been done by the method described by SVÄRDSON (1961) and KEMPE (1962), slightly modified. The number of age samples of a year class from a certain year of catch is weighed against the total catch in the year in question and against the distribution over age-at-capture of the whole material. The mean of the values thus obtained for a year class denotes the relative strength of that particular year class. With the support of the comparison between areas made above, these were combined in the calculation. The year classes 1954—64 and the catch years 1963—69 were included, the catch in 1970 being omitted as not representative. Fish caught at ages of less than three years or more than 11 years have been excluded, as they are very few in number. The results of the calculations can be seen in Fig. 3.

As mentioned earlier, the method of standardization gives an artificial dependence between the year classes. A more direct method is to study the real number of caught individuals of different year classes. This requires a standardization of fishing technique and intensity, which can easily be done with the catches of the test fishing that

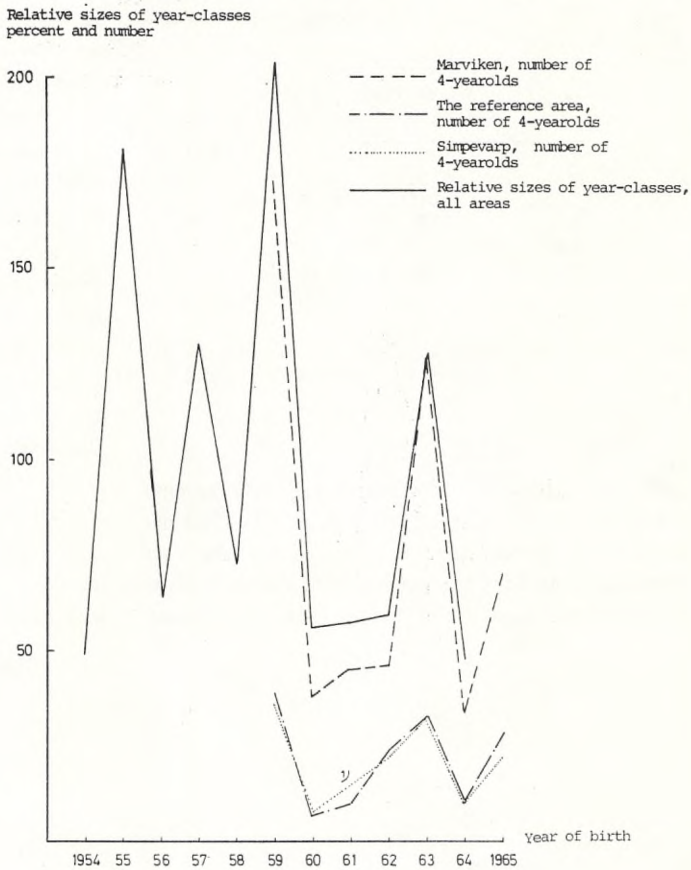

Fig 3. Relative sizes of year-classes.

1) No fishing in Simpevarp in 1965

gave the growth material. In 1965, however, no test fishing was carried out in the Simpevarp area. The analysis was confined to the catches of May and June, since the growth samples were taken from these catches. Only one age group at a time can be treated by this method. The fourth year was chosen as being the youngest sufficiently represented age-at-capture. The number of caught four-year olds has been calculated by multiplying the total catch of the months by the proportion of the four-year olds for the year in question. In doing so, the proportion which is valid for the whole material has been assumed to apply to all three areas. It should not be too hazardous to take for granted the same age distribution in the total catch as in the age-determined sample, since the samples from Simpevarp and the reference area included the largest proportion of the catch, and in Marviken it forms a large part of it. The values for each separate area have been related to the standardized values (Fig. 3), which are applicable to the whole material. As can be seen, there is good agreement. Apart from the fact that only one year at a time can be treated by the direct method, the result is dependent on factors irrelevant in this context, such as the influence of environmental factors on the size of the catch. Therefore, standardized values were used for the analysis of the temperature effect.

(c) Temperature effect on year-class strength

The year classes have been related both to montly average temperatures of surface water at Hävringe from May to September and to the corre-

Table 1. *The correlation between year-class strength and temperature.*

Month	Water temp. r	Air temp. r
May	(0.01)	(—0.33)
June	(—0.15)	(—0.22)
July	0.75	0.89
Aug.	0.92	0.92
Sept.	0.62	(0.30)

The correlation coefficients within parentheses are not significant, the others are significant on the 5 %-level.

sponding values of air temperature at Harstena (se Material and Methods II (d), p. 53). The use of the air temperature is justified by the fact that spawn and fry are generally found in shallow and sheltered bays where the air temperature may be more representative than the water temperature at Hävringe. Separate regression analyses were made for the different months (see Table 1). The August and July temperatures seem to be the most essential for the dimensioning of the year classes, air and water temperatures being of about equal importance in this respect.

The effect of temperature may be directly physiological, or the supply of food, zooplankton, may increase owing to high temperature (Smyly 1952). Smyly examined the food of perch fry in Lake Windermere and established that the supply of the most important preys, *Bosmina* and *Diaptomus*, and the intake of food both reach a minimum in July. This could possibly be accentuated in a cold year and cause high mortality.

A pilot investigation into the food of perch fry during the critical months of July and August was carried out at Simpevarp. The contents of

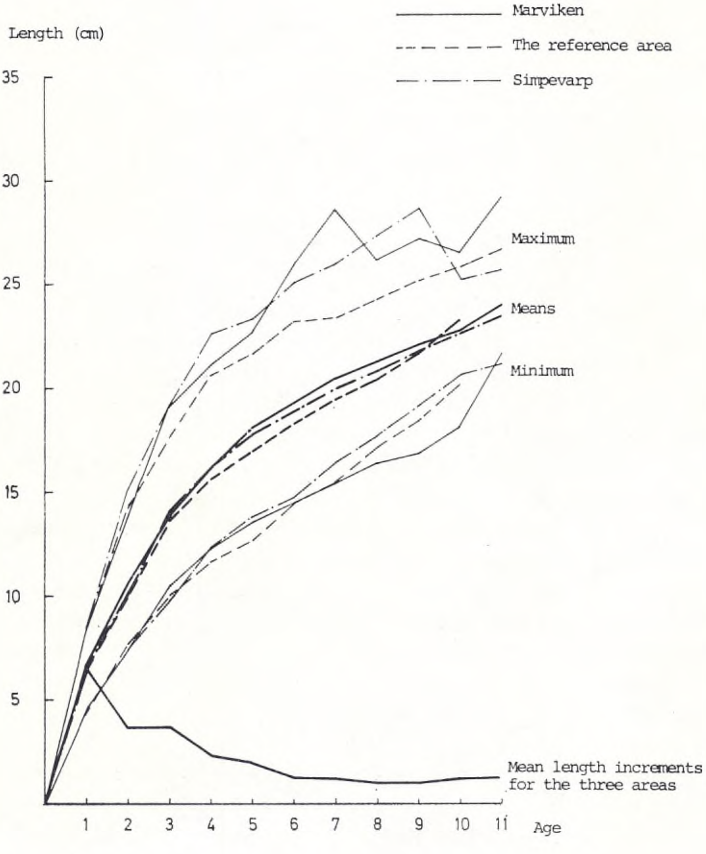

Fig. 4 a. The mean growth of females.

124 stomachs were analysed (25 from 1970, 24 from 1971 and 75 from 1973). A clear predominance of copepods was found in all cases. The dominating species seems to be *Acartia tonsa* but in 1971 *Eurytemora* was also well represented. Hessle and Wallin (1934) report that the number of copepods in the Baltic archipelagoes is positively correlated to temperature during the summer, and that in a cold summer the maximum density can be shifted from June-July to the late summer and autumn. The temperature dependence of the copepods may possibly indirectly influence the survival of perch fry.

B The mean growth

(a) The growth of Baltic perch

A preliminary estimation of the growth of perch in the coastal waters examined was reached by calculating the mean values of all lengths for the first 11 years of life. The two sexes were considered separately. The results are illustrated in Fig. 4. The good agreement between the mean values of the three areas is remarkable, as the biotopes show marked differences (Neuman 1974 b).

The values reported here were compared with corresponding values from other investigations. Unfortunately, the supply of such material from the Baltic is sparse. Nilsson (1921) collected gill covers from Lake Mälaren, the archipelago north of Stockholm, and from several stations along the Gulf of Bothnia. From Nilsson's material, the females from Sandön off Luleå, the most northerly sampling station, were selected for comparison with other archipelagoes. Before the material could be used it was necessary to make a number of transformations (see Neuman 1974 a). Other in-

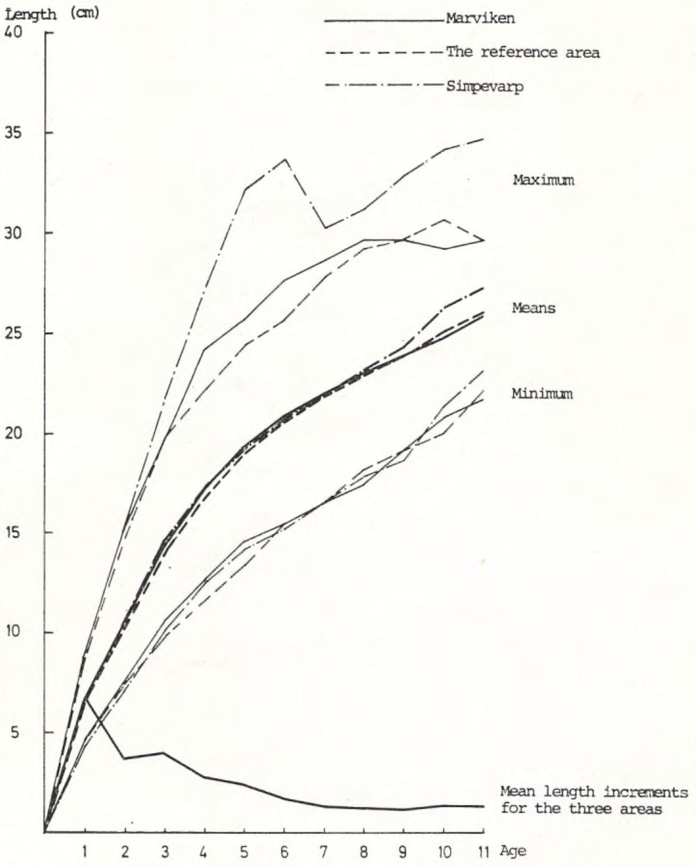

Fig. 4 b. The mean growth of males.

Table 2. *The growth rate of female perch.*

Age	1	2	3	4	5	6	7	8	9	10	11
Marviken—Simpevarp	6.7	10.3	14.3	17.1	19.2	20.8	22.0	23.0	24.0	25.4	26.4
Erken	6.8	10.8	13.3	15.3	17.2	19.9	22.4	24.9	27.4	29.3	—
Öregrundsgrepen	6.1	9.8	13.2	16.3	19.1	21.3	22.0	23.0	24.2	25.4	26.7
Pellinge	4.7	7.9	10.6	13.2	—	—	18.9	20.0	19.9	21.9	24.2
Sandön, Luleå	6.0	9.9	13.3	16.2	18.8	21.5	23.6	26.0	28.5	—	—

vestigations in similar waters have been made by BERGSTRAND (unpublished) in Öregrundsgrepen (110 km north of Stockholm) and by SEGERSTRÅLE (1948) in Pellinge (60 km east of Helsinki).

In Table 2 the growth of females in Marviken—Simpevarp is compared with that in Pellinge, Öregrundsgrepen and the archipelago of Luleå. Values from Lake Erken, 65 km north of Stockholm, has also been entered, since this material (AGNEDAL 1968) is the most extensive available from Scandinavian lakes. The first impression obtained from the table is that the growth rates are alike, with the exception of SEGERSTRÅLE's. The good growth in the archipelago of Luleå is sur-

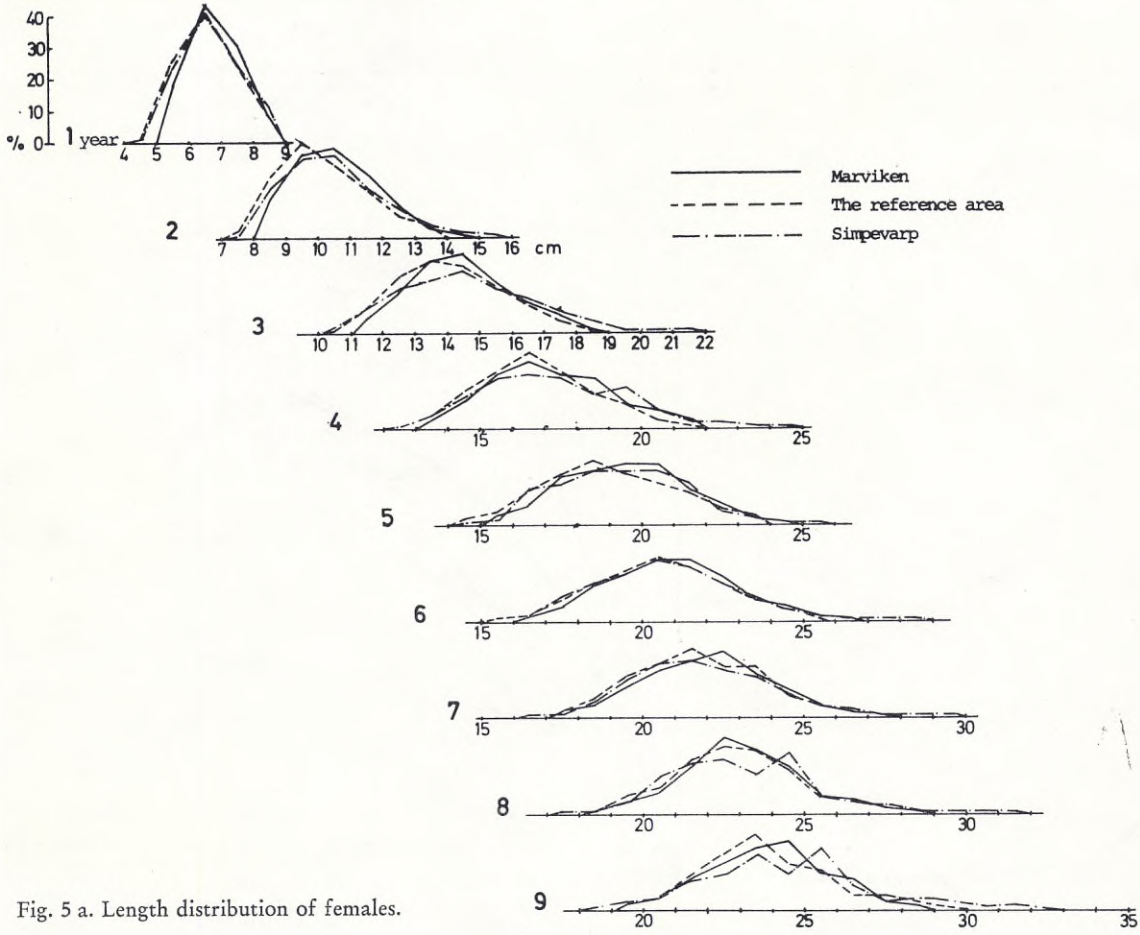

Fig. 5 a. Length distribution of females.

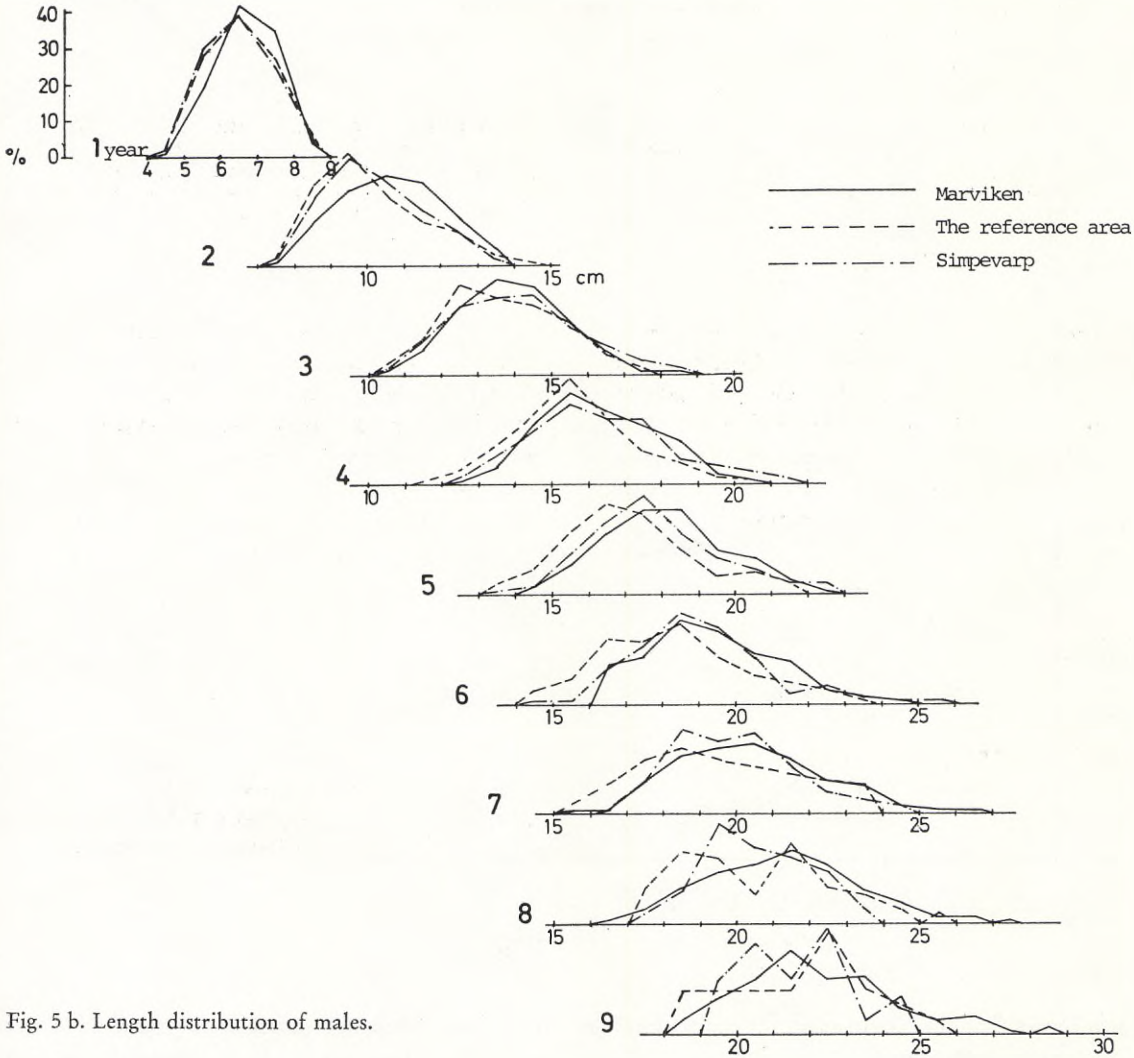

Fig. 5 b. Length distribution of males.

prising, considering the fact that the growth season there may be expected to be short. The fact that the material is sparse and the transformations inexact can hardly provide the entire explanation. An equal growth rate independent of the latitude can be noticed through the whole of NILSSON's material, from Lake Mälaren to Luleå. It is reasonable to assume that the values of this investigation must be comparable with one another. To sum up, the sparse information available indicates that the growth of perch is similar in different parts of the Baltic.

(b) Length distribution within age

The mean growth of perch has been established to be very similar in the three archipelago areas in question. On the whole this also applies to the standard deviation around these values (NEUMAN 1974 a). Fig. 5 gives the dispersion based on the distribution over length classes with a class width of 1 cm. The values have been expressed as percentage distributions so as to put them on a more comparable basis. Once again there is a striking similarity between the three areas. Fig. 5

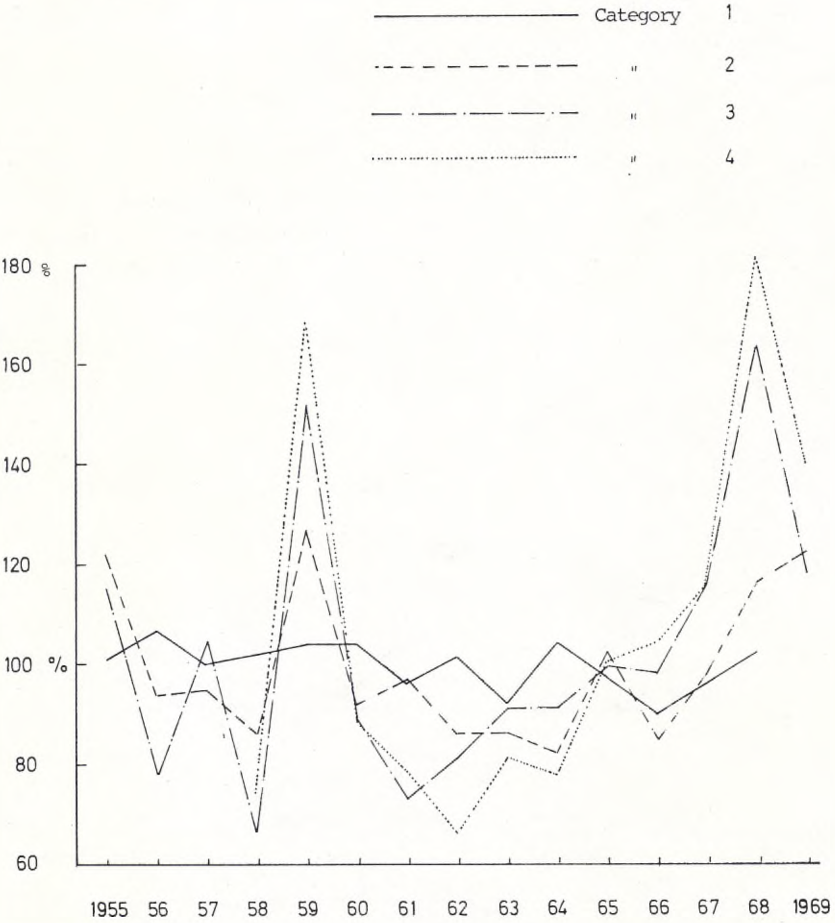

Fig. 6 Relative growth of females from Simpevarp.

also shows that the length observations within age are approximately normally distributed.

C. *The variations of growth between years*

Mean growth has been shown to be relatively well descibed as a simple function of age (Le Cren 1958). However, it is not possible to apply this fact to individual growth (Neuman 1974 a), which may be due to individual qualities and the changing environmental conditions in different years. In order to analyse the significance of the changing environment, the annual growth of each individual has been expressed as a percentage of the average for each sex and for the age in question in the whole material. This made possible the comparison of growth data for all ages and both sexes. In order to make the material easier to handle, the growth observations of the first 11 years of life were combined into four age categories, *viz.* the growth in the first year (category 1), the second year (2), the third to fifth years (3) and, finally, the growth in the sixth to eleventh years (4).

The mean relative growth of females in Simpevarp is illustrated in Fig. 6. The differences between the years are seen to increase with age; category 4 varies between 66 and 181 % of the normal value. Before looking for an explanation, we should consider the relationship between variations of the different age categories, the sexes and the areas. The following analyses are based on the mean values of the year classes.

Table 3. *The correlation between growth (females) of category 3 and categories 1, 2 and 4.*

Category	Marviken		Simpevarp	
	r	level of significance	r	level of significance
1	0.28	—	0.09	—
2	0.85	1 %	0.77	1 %
4	0.98	1 %	0.97	1 %

(a) A comparison between the relative growths of the age categories

For the females of Marviken and Simpevarp, the relationship between the age categories was examined by a regression analysis, in which category 3 was related to the others one by one. The result is demonstrated in Table 3. LE CREN's (1958) observation of the similarity in the variations in growth of the adults is here confirmed. The variations in the second year also resemble the older ones, while the first year shows no correlation.

The deviation of the first year could be due to the difficulty of establishing accurately the position of the first annual ring, as mentioned in Material and Methods. An error involving the first ring would have a similar effect on length increment of the second year. However, high correlation between this length increment and that in category 3 does not indicate that this source of error would be serious. The fluctuations around the mean value of the first year are also remarkably small. The standard deviation (NEUMAN 1974 a) increases with age, in spite of the fact that the considerably larger length increment during the first year in fact promotes a larger dispersion.

The smallness of the variations between individuals of the same year class and between year classes indicates that the growth of the first year is not influenced so strongly by the variation of environmental factors between years as is the growth at higher ages. Moreover, the imperfect covariation with older fish suggests that the dependence of environmental factors is of a different nature in the first year.

Table 4. *The correlation between growth of males and females (Simpevarp).*

Category	r	Level of significance
All	0.88	1 %
1	0.56	5 %
2	0.70	1 %
3	0.93	1 %
4	0.90	1 %

(b) Relative growth of males and females

It is reasonable to assume that variations in the relative growth of the two sexes are similar from year to year (*cf.* LE CREN 1958). However, regression analysis has been made on the Simpevarp material (Table 4). For all age categories the correlations are significant at least at the 5 % level. This enabled the two sexes to be combined into one group when making comparisons between the areas.

(c) Relative growth in the different areas

A regression analysis of the relationship between the fluctuations of growth over years was made in pairs between the areas, both sexes being treated together. The results are shown in Table 5, where all the age categories are positively correlated. The fact that the correlation coefficients are relatively low for the first two years

Table 5. *The correlation between growth in the three areas.*

Category	Marviken—Simpevarp	Marviken—Reference area	Simpevarp—Reference area
	r	r	r
All	0.87	0.88	0.80
1	0.41*	0.57	0.63
2	0.65	0.65	0.57
3	0.91	0.90	0.83
4	0.91	0.93	0.86

* Significant on the 5 %-level, the others in the 1 %-level.

Table 6. *The correlation between growth and temperature.*

Category	Month	r	Level of significance
1	Aug.	0.48	—
2	Aug.	0.67	5 %
3	Sept.	0.73	5 %
4	Sept.	0.78	5 %

may indicate that the biotopes of the fry are more influenced by local variations than are those of the adults.

D. Growth in relation to temperature

In the search for a relationship between growth and temperature, the growth observations were grouped into the age categories described above. The temperature data are described in Material and Methods (II (d)). Since growth data on males and females were created by standardization around separate values, they should not be treated together. As the greater part of the material consists of females, most analyses of the relationship between growth and temperature have been restricted to this sex. Moreover, the few fish born before 1953 have been excluded and the analyses thus cover the year classes from 1953 to 1968. The comparison between the fluctuations of growth in the three areas showed weaker relationships for the first two years of life and therefore the analysis of the fluctuations was restricted to material from Marviken, on account of its location near Hävringe. The correlation growth-temperature was studied by means of multiple regression analyses.

(a) Growth in relation to the temperature at Hävringe

The results of the regression analyses are demonstrated in Table 6, showing the correlation coefficients for the months first selected. August is the most important month for the year-to-year variations in growth in the first two years and September is the most important month for adults. The correlations are significant, with the exception of the first year. The fact that year-to-year fluctuations of growth increase with age (Fig. 6) is evidently connected with an age-dependent relationship between growth and temperature.

(b) Growth *versus* the temperature at Marviken

In spite of the good relationship between the temperatures at the Hävringe lightship and the temperatures in Marviken and Simpevarp (Material and Methods, II d), it is unfortunate that the temperature had to be quantified with such a remote place as Hävringe. The possibility of using the measurements in Marviken was tested for the category 4 females collected there. The correlation between relative annual growth and the temperature at a depth of 2 m was tested with a regression analysis for each month from June to October. The correlation coefficients obtained are —0.23, —0.48, 0.58, 0.83 and, in October, 0.10. Only the September value is significant at the 5 % level. The variations in growth due to temperature seem to be mainly dependent on conditions in September and probably also August. This must be evidence that the greatest part of the annual length increment takes place at that time. The high correlation coefficient, which agrees with the corresponding values from Hävringe, indicates that a single monthly measurement of temperature may be used as a basis for the quantification of the temperature.

(c) The growth of individuals

A multiple regression analysis was carried out for the years 1958—69, with all individual observations on both males and females in the oldest group as dependent variables and the observations at Hävringe as independent ones. The highest coefficients refer to August (0.48) and September (0.47). However, the correlations are not significant, which must be due to the influence of the individual dispersion.

E. Individual variations in growth

Field studies on the growth of fish are generally limited to an analysis of the mean growth of large groups, the fluctuations of which may often

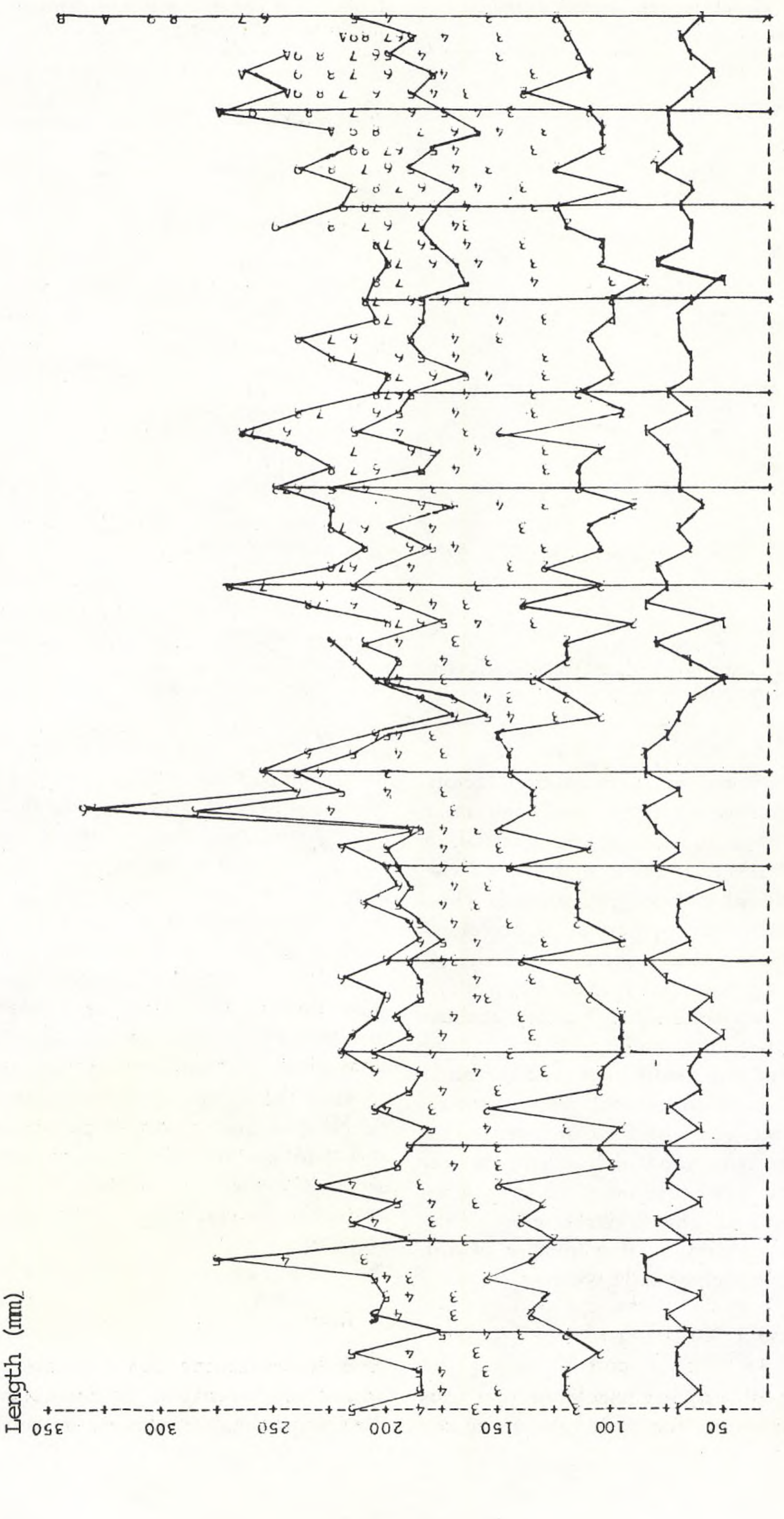

Fig. 7. Individual growth of females from Simpevarp born in 1958.

Table 7. *The correlation between growth of individuals in two consecutive years.*

Age Birth year	1	2	3	4	5	6	7	8
1953		0	0	–	+	0	0	+
1954		+	–	–	+	+	0	0
1955		0	–	0	0	0	0	+
1956		0	–	–	0	0	+	0
1957		0	–	0	–	+	+	+
1958		0	–	0	+	+	0	+
1959		0	0	+	+	+	+	+
1960		0	–	+	0	+	0	0
1961		0	0	+	+	0	+	0
1962		0	0	+	0	+	0	+
1963		+	+	+	+	+	+	
1964		0	0	+	+	0		
1965		0	0	0	0			
1966		+	0	+				
1967		+	0					
1968		0						
Per cent positive correlations		25	6	50	58	58	45	60 %
Per cent negative correlations		0	40	21	8	0	0	0 %

+ represents significant (5 %) positive correlations, – negative, and 0 non-significant relations.

Table 8. *The correlation between growth of individuals in two years with one year in between.*

Age Birth year	1—3	2—4	3—5	5—7
1953	0	0	–	0
1954	0	0	0	0
1955	–	0	0	–
1956	–	+	+	0
1957	–	0	–	0
1958	–	–	0	0
1959	–	–	0	0
1960	–	–	0	0
1961	–	–	0	0
1962	0	–	0	+
1963	0	–	0	0
1964	0	0	0	
1965	0	0	–	
1966	0	0		
1967	0			
1968	0			
Per cent positive correlations	0	7	8	9
Per cent negative correlations	44	43	23	9

be successfully related to environmental factors. The correlation between temperature and mean growth, established in the present material, is considerably weakened if the growths of individual fish are included as dependent variables (D (c) p. 62). Naturally, the variation in hereditary qualities and the choice of habitat may counteract the effects of environmental factors, which affect the population as a whole. If hereditary qualities have a dominating influence in this respect, one would expect the same individuals to have better than average growth for several years in succession. The same effect would be obtained if the fish kept to the same good or bad habitats year after year. The first question to answer when analysing individual growth is therefore: Does the population contain a large number of fish with permanently good or bad growth?

(a) Increment in length of individuals

The lengths of all analysed females of year class 1958 from Simpevarp for each year up to the year of capture were plotted by computer (Fig. 7) to provide a visual background to the discussion on the growth of separate individuals. The diagram immediately shows that the question above can be answered in the negative, *i.e.* the population does not contain large numbers of fish with permanently good or bad growth. A similar investigation of year class 1959 gave the same result. The few individuals that are either considerably larger or smaller than the others at a certain age have, as a rule, reached their differing position during one or two years at the most. In fact, the picture gives an impression of considerable individual dispersion of growth at all ages and not only in some occasional extreme case where there is a wide divergence from the average of the year class.

(b) The relationship between the growth of individuals in two or tree successive years

As mentioned above, Fig. 7 indicates that there is no lifelong positive or negative deviation from the mean annual growth of the perch examined.

Table 9. *Relative mean growth versus the percentage deviation.*

Age	2	3	4	5	6	7	8
Year							
1956	84—19	—	—	—	—	—	—
1958	88—22	75—19	81—29	66—14	—	—	—
1961	—	82—22	89—37	85—33	88—32	88—40	71—30
1962	—	81—20	90—35	68—22	79—32	85—46	75—28
1959	123—33	137—17	150—13	159—6	173—9	—	—
1968	123—29	151—5	165—10	127—11	177—7	132—12	194—6
1969	128—13	—	131—19	126—17	130—21	157—12	—

The left-hand value denotes the mean growth, the right-hand value denotes individuals with a growth deviating in the opposite direction.

The fact that a small deviation might occur in two or perhaps three consecutive years cannot be excluded, however, without a statistical analysis. Such an analysis was carried out for the total number of females included in the data base, *i.e.* all those born in the period 1953—68 and caught at an age of not more than 11 years. The different year classes were treated separately in the analysis. The correlation coefficient for the length increment of the individuals in two consecutive years was calculated from the mean value of each year and year class. Thus, a positive coefficient denotes that the same individuals in both years tend to differ in the same way from the mean values in question, a negative coefficient shows that good growth in one year is followed by poor growth in relation to other fish of the same age during the second year, and *vice versa.* The relationship was analysed for the consecutive years from the first to the eighth year of life. In addition to this, corresponding analyses were made for the first *versus* the third year, the second *versus* the fourth, the third *versus* the fifth, and the fifth *versus* the seventh year. The presence of correlations significant on the 5 % level is summarized in Tables 7 and 8.

The results in Tables 7 and 8 show that the positive correlations are dominant for consecutive years, while the negative correlations are dominant for two years with one intervening year. The fact that postitive correlations are rare for several years in succession may partly be statistically explained. The individuals that previously grew fast have little possibility of experiencing conditions that are still more favourable, but tend to be subjected to a deterioration of conditions, while the opposite applies to the individuals who previously grew slowly. This phenomenon is called "regression fallacy". As regards two consecutive years it is interesting to note that the proportion of positive correlations increases with age. The relationship between the first and the second year is, however, an exception in this respect. It could possibly be explained by the fact that differences in the size of the individuals would probably be more important for the choice of food at that age than at a higher age. Fast-growing individuals may change to bigger prey earlier; this, as a rule, gives a better relationship between catch effort and contents of energy.

To sum up, Tables 7 and 8 show that most individuals do not, as regards growth, deviate from the mean value of the year class in the same direction for more than two years in succession. The probability that genetic factors control the growth of individuals in any conclusive way therefore seems to be remote.

(c) Growth of individuals *versus* mean growth of the year classes

In Table 9 a selection of the best and poorest mean growths have been related to the proportion of individuals with a poorer or better growth than the average of the whole material. The first year has been excluded, as it gave very small differences between calendar years. The table shows a remarkably high proportion of fish with a growth differing from that of the majority. This is

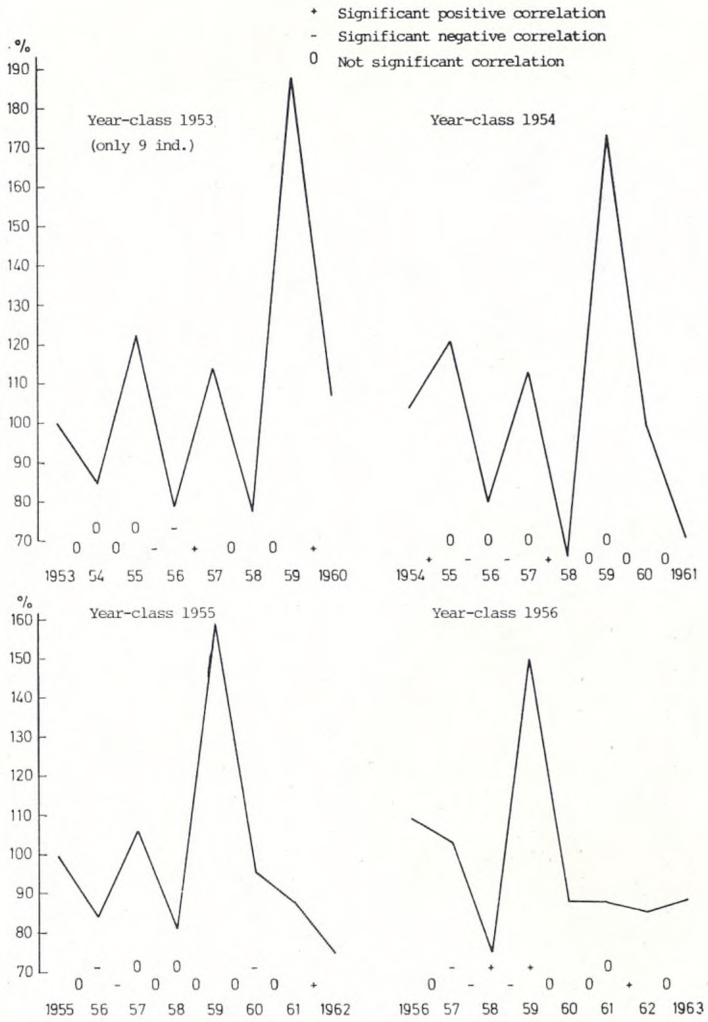

Fig. 8 a.

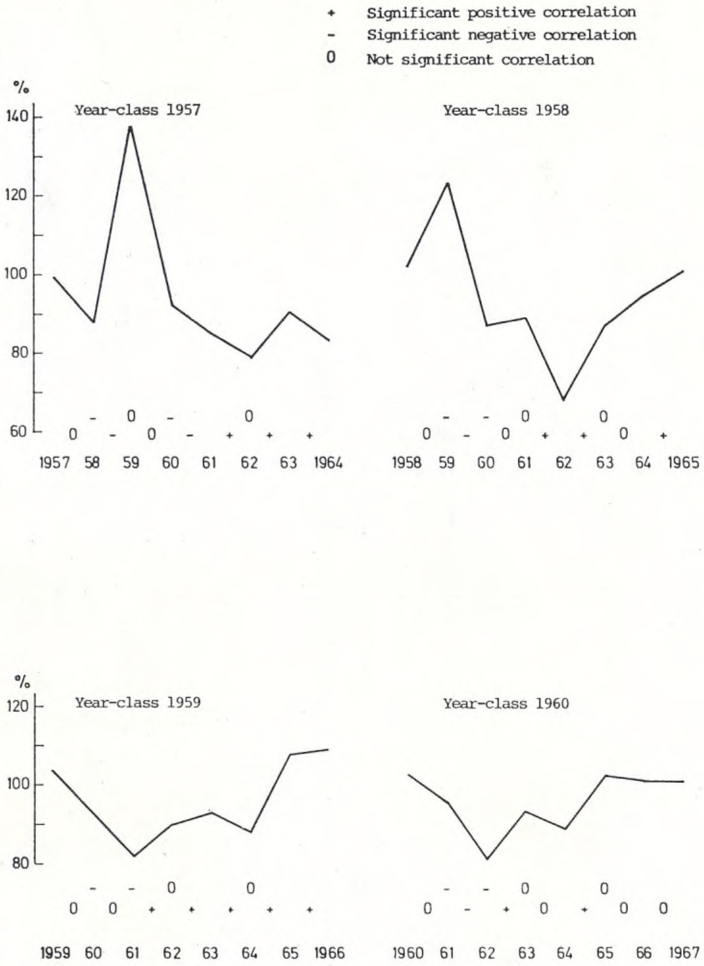

Fig. 8 b.

Fig. 8 The correlation between the growth of individuals in different years in relation to the mean growth of the year-class.

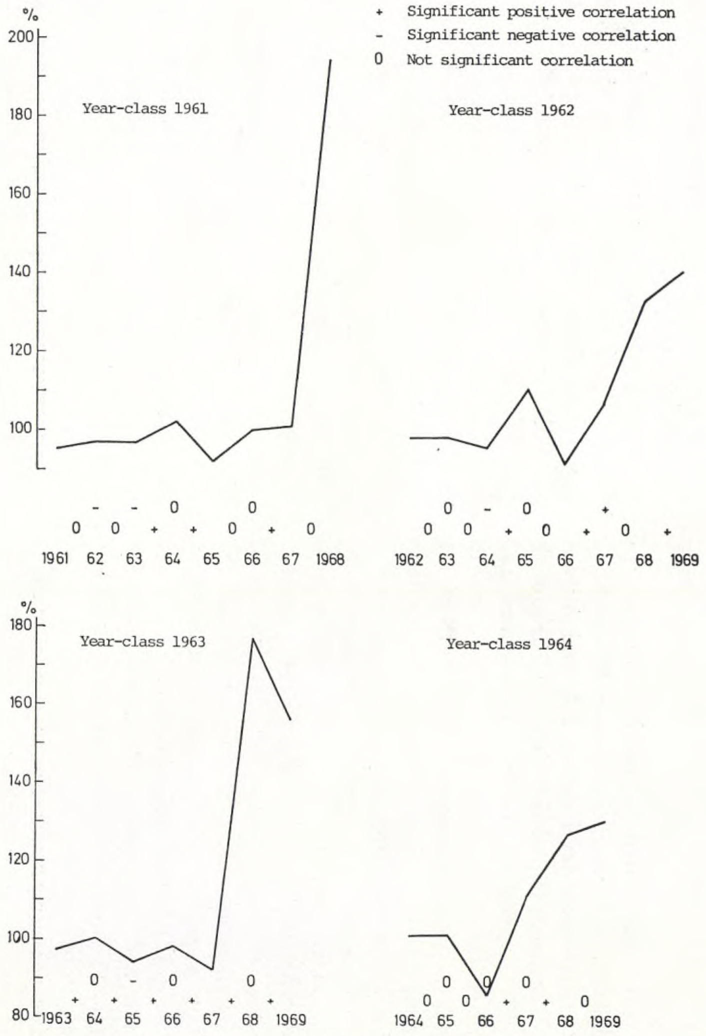

Fig. 8 c.

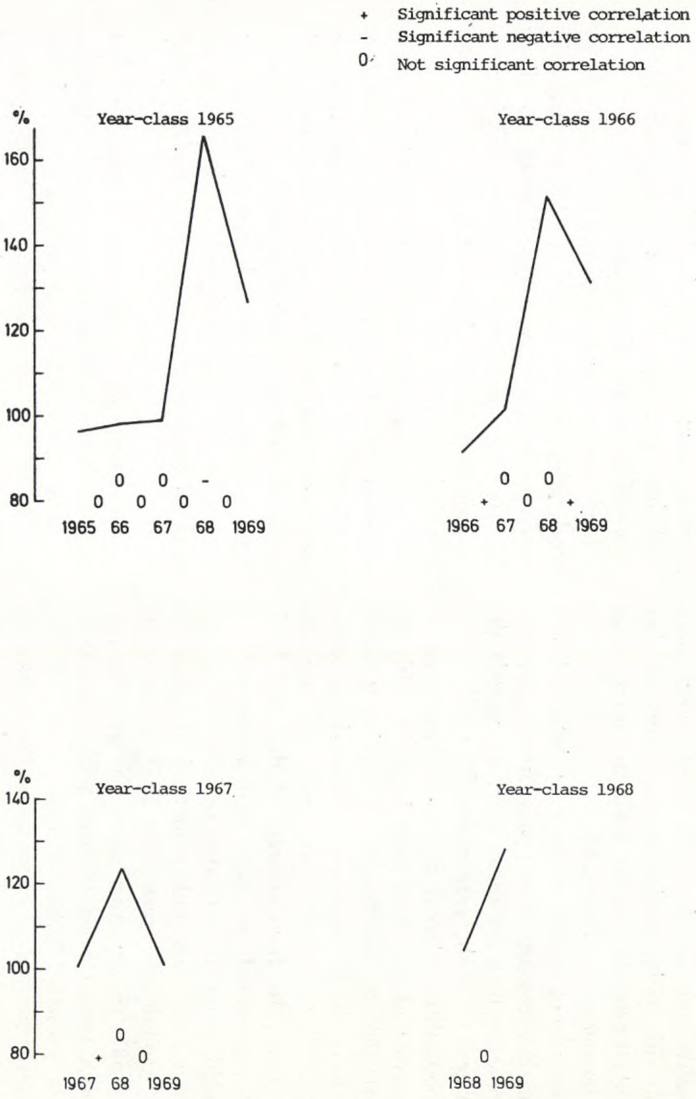

Fig. 8 d.

Fig. 8 The correlation between the growth of individuals in different years in relation to the mean growth of the year-class.

especially true of the bad years. When seen against this background, it is not surprising that individual growths give no significant correlations with temperature (D (c) p. 62).

It may be of interest to compare the correlation of length increments in two consecutive years with the relation between these years as regards the mean growth of the year classes. This will reveal the possibilities offered by the environment. A comparison of this kind may be made with the aid of Fig. 8, which gives the relative mean growths of the different year classes (all the areas, females only). Symbols of the individual relationships have also been entered. If the 1953 birth year, represented by only nine individuals, is excluded, there is only one positive correlation between two years with a marked difference in mean growth (the year class 1963 in the years 1967—68). In the other cases, the positive correlations appear between years with a relatively similar growth. Adjoining years with big differences instead give negative or not significant correlations. This circumstance will be discussed later.

IV. DISCUSSION

The year-class strength of perch in the investigated Baltic archipelagoes is positively correlated to the temperature level during July and August. This dependence is probably linked to the growth rate. The position of the fry *vis-à-vis* prey and predators should be improved by a high growth rate. The correlation between the growth of fry and temperature, probably positive, has not been established in the present material; the mean growth does not vary very much between years. This is evident from Fig. 6, which should be compared with the dramatic changes of year-class sizes seen in Fig. 3. A probable explanation is that temperature regulates the number of fry reaching a growth rate necessary for survival; specimens that grow too slowly will succumb (RICKER and FOERSTER 1948, LINDSTRÖM 1962 and others). A negative correlation growth-density could also be supposed. A high survival rate may increase the competition for food and space to the extent that it neutralizes the positive effect of temperature on growth. This competition is probably accentuated by a higher density of cyprinid fry in warm summers.

High temperatures may stimulate growth by accelerating the metabolism and by increasing the supply of food. LE CREN (1958) considers it likely that the direct physiological effect of temperature on growth dominates, because all age groups react in a similar way in spite of the different choice of food. The fact that the largest perch are most dependent on temperature speaks in favour of LE CREN's opinion. If variations in the supply of food were vital in this respect, the young perch ought to show a greater dependence on temperature, since the plankton is influenced to a greater extent by the environmental conditions of the year in question than is the older prey of adult perch.

The amplitude of the year-to-year variations in growth and their correlation with temperature increase with age. It seems to be a universal fact, so far as fish are concerned, that the balance between anabolic and catabolic processes tends to swing to the latter with increasing size (BRETT 1970, among others). URSIN (1963) has shown that the decline in condition of Norway pout (*Gadus esmarcki* NILSSON) during the winter increases with the length of the fish. In consequence, an increasing amount of energy is needed for the fish to regain its condition during the growing season, and this results in the effective growing season being shorter. It is reasonable to assume that the unfavourable balance of large fish between anabolic and catabolic processes and their shorter period of growth will make them more dependent on environmental factors during this period. This is probably reflected in the age-dependent correlation between length increment and temperature. The later start of the growth in length may explain why the perch fry seem to grow best in August, whereas September is the best month for adults. This may also be a result of the spawning. LE CREN (1951) showed that the negative effect of spawning was the reason why mature perch did not reach optimal condition until September, while the immature ones reach it in August.

Temperature strongly influences the mean growth of a year class. This relationship, however, may be changed for some individuals by other factors. Thus in years with very good or very poor growth for the year class as a whole, a tenth to a third of the examined individuals might differ to the opposite extreme. Several writers have used two different models to describe individual growth. These are discussed by BERG (1970). One such model, "compensatory growth", deals with species of whitefish, while the so-called hierarchy of size is exemplified by the trout (BROWN 1946). Compensatory growth means that those fish which grew better than others of the same age at the beginning of their lives, later show a poorer growth, and *vice versa*. For trout, on the other hand, the differences of size increase with age, a circumstance which, according to BERG (1970), is typical of solitary predatory fish. Greater length gives these a chance of catching larger prey and defending good territories. As regards shoal fish, on the other hand, the social organization would give a more homogeneous distribution of the available food, to the advantage of all the individuals of the shoal. ALM (1946) studied perch in small ponds and observed individual growths similar to the "trout model". In the present material there is a similar tendency for two consecutive years, while over several years rather compensatory growth is dominant.

The growth rate is by no means a simple unambiguous character, but is the result of a complex combination of factors, *e.g.* several environmental factors and individual qualities such as hunting skill, activity and metabolic efficiency (LINDSTRÖM 1971). Apart from the fact that the individuals have different qualifications for growing in the same environment, they stay in different habitats, they often choose different kinds of prey and are on the whole confronted by the world around them in different ways. This is especially the case in the archipelagoes with their varied topography and often rapidly changing hydrographical conditions. It is natural that a combination of individual qualities and, *e.g.* habitat, which in one year will give a particular individual a better growth than the others of the same year class should also be successful in a following similar period, while on the other hand a drastically changed temperature, for instance, breaks such a relationship. This might explain the observation that positive correlations between growths of individuals in two consecutive years primarily appear if the years are similar as regards mean growth and, consequently, probably also the environmental factors, at least during late summer. A deeper understanding of these causal connections might be reached by relating individual growth to shoal membership. If the shoals have a fairly constant composition over a fairly long period, their members may be expected to have been subjected to similar environmental conditions. This approach might also reveal possible trends towards compensatory growth within the shoal.

V. SUMMARY

The effect of natural temperature variations on the yearly length increment and year-class strength of perch (*Perca fluviatilis* L.) was studied in three areas along the Baltic coast of Sweden. From 1963—70 operculae from about 200 perch from each area were sampled yearly for age determination and back calculation of growth. The relative strengths of year classes were calculated from the age composition of catches.

1. The three areas were found to be almost identical as regards mean growth rate, variation of growth between years and variation between the relative strengths of year classes.

2. The mean annual growth was found to be positively correlated to the water temperature in August for the second year of life and to that in September for the adults. There is no significant correlation for the first year.

3. The strengths of year classes showed covariation with both the water and the air temperature in July and August.

4. The year-to-year variation in growth and its dependence on temperature increased markedly with age.

5. The correlation between growth and temperature dropped below the level of significance if the mean values of year classes were replaced by the length increments of single individuals in the analysis.

6. The individual dispersion was so large that, even in a year with a markedly good or markedly bad growth for the year class as a

whole, from one-tenth to one-third of the individuals may differ to the opposite extreme.

7. Individual deviations from the mean value of a year class seldom occur in the same direction more than two years in succession.

8. Individual growths often tended to differ in the same direction for two consecutive years. This tendency was much more pronounced if the two years were similar as regards the mean growth of the year class.

VI. ACKNOWLEDGMENTS

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Mercury Levels in Biota from Mörrum River during a 10 Year Clean-Up Period

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I. INTRODUCTION

In order to study the changes in mercury levels in biota from a flowing water system after mercury discharge had ceased, biological material from Mörrum river was collected in 1965 and has been collected each year since 1967 in the first week of July, and analysed for mercury. The material was collected at 11 localities and it consisted of aquatic plants, invertebrates and vertebrates representing different niches as well as different habitats covering a broad part of the ecosystem investigated. This has made it possible to study the mercury levels in different species in relation to their habitat and position in the nourishment web.

Mörrum river is one of the largest rivers in southern Sweden, see Fig. 1. Up to 1965 a paper-mill on Mörrum river had an annual consumption of phenyl mercury acetate of approximately 1 ton. In 1965 the use of mercury ceased and a "cleaning up" of the river was expected to start.

The water exchange is rapid, only a few days for the entire river. Normally the water flow reaches a maximum during the spring thaw. Data on the monthly water flow is presented in Fig. 2.

Since only very small amounts of water are added to the river downstream from the paper-mill there is no further significant dilution of the discharge during the transport down to the coast. This is an advantage when making comparisons between the levels at different localities.

In the first investigation in 1965, a substantial increase in the mercury levels was found in organisms downstream from the paper-mill relative to those upstream (WESTERMARK *et al.* 1965, JOHNELS *et al.* 1967). The first report on a decrease in the mercury levels was given in 1969 (JOHNELS *et al.* 1969). This paper presents a summary of the data of the materials for the years 1965—74.

II. MATERIAL AND METHODS

Biological material

The following species were selected as being representative of the biota and were collected at the different localities. The aquatic species were collected at a depth of 0.5—1.5 m.

Plants

Watermoss (*Fontinalis antipyretica*) was collected on stones in rapids. The samples were shaken and rinsed in river water.

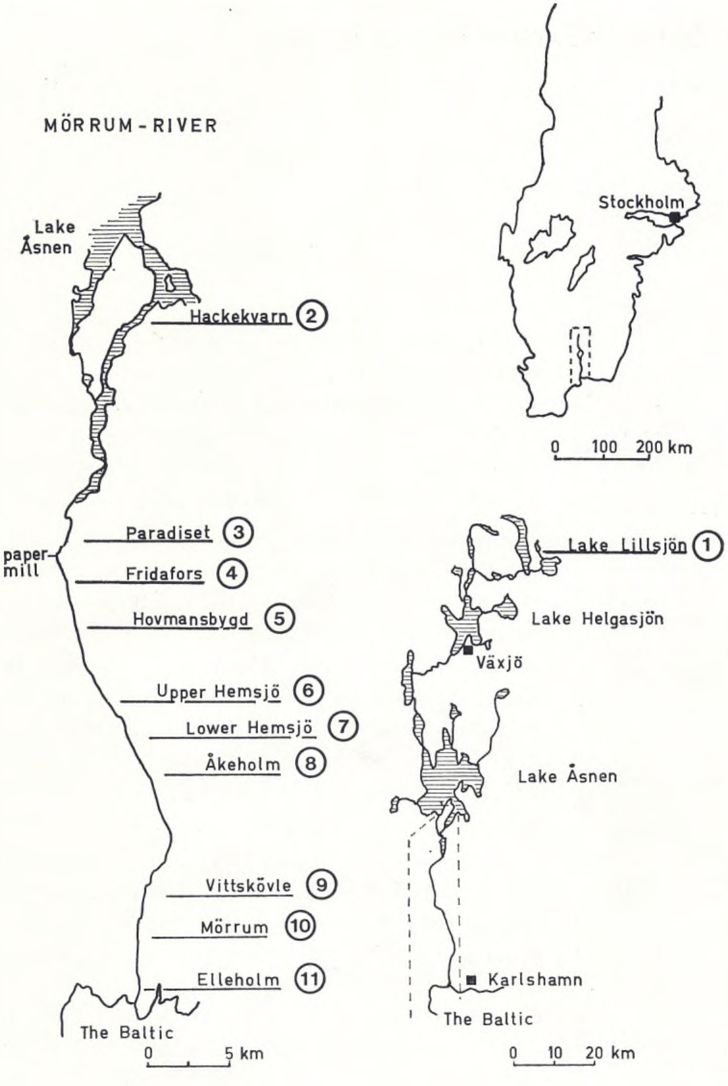

Fig 1. Map showing the geographical situation and the sampling localities along Mörrum river. Sampling localities have been underlined.

Invertebrates

90 % of the leeches sampled consisted of specimens belonging to *Erpobdellidae*. This percentage is in good accordance with what has been found previously in the same river (DAHM 1964). These animals feed on insect larvae, crustacea, and "worms" (PAWLOWSKI 1937, WESENBERG-LUND 1939, WHITEHEAD 1943).

The isopod *Asellus aquaticus* is found mainly on soft sediments in backwaters of the river and it feeds on plant material and detritus (WILLER 1917, WESENBERG-LUND 1939, GRUNER 1965).

Caddis fly larvae (*Hydropsyche pelucidula* and *H. instabilis*) were sampled on stones in rapids. The larvae are omnivorous and collect the organic drift of the river (WESENBERG-LUND 1913). In Mörrum river their food consists mainly of algae, plant material and detritus and during the summer algae and plant material are dominant (PERSSON 1972, PERSSON, pers. comm. 1975).

Dragon fly larvae (*Agrion splendens*) were collected on straws and rootlets by the bank of the river in flowing water. These larvae are carnivorous, feeding on invertebrates (POPOWA 1926/1927).

Imagines of dragon flies were also collected.

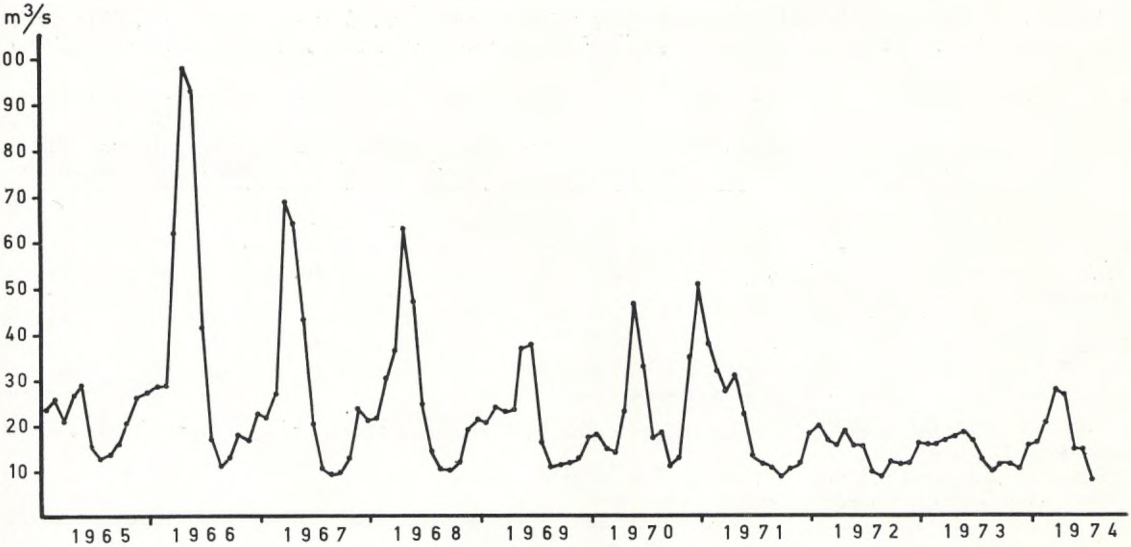

Fig 2. Monthly mean waterflow in Mörrum river during the investigation period. (Sydkraft 1975.)

However, the larvae are likely to be more stationary and representative of the locality than the flying imagines.

Alder fly larvae (*Sialis lutaria*) were collected in surface layers of soft sediments in backwaters of the river. This species is carnivorous, feeding on invertebrates (KIMMINS 1962), *Ephemeroptera — Trichopetera — Nematocera* larvae and *Oligocheata* (DU BOIS and GEIGY 1935).

The specimens were put into small glass bottles. At the end of the collection day the specimens were cleaned from sediment particles in order to reduce the contamination from that source. Afterwards they were kept frozen until the day of analysis. Since 1969 the water content in all samples has been determined.

About 5—15 specimens of each species or species group were pooled and analysed. For every species, locality and year, one analysis has been carried out.

Fish

Two month-old fry of cyprinid fishes were collected. Roughly 95 % of the samples consisted of roach or chub 10—20 mm long. Roughly 5 % belonging to the species *Gobio gobio*. However, comparison of mercury levels in the different species from the same localities and years show no difference in mercury levels.

Small roach (*Rutilus rutilus*) about one- or two-year old were collected in 1971 in order to form a basis for statistical calculations on the differences between different localities from the upper to the lower part of the river.

In order to make statistical calculations on differences between years, adult roach have been collected since 1968 from locality 6, which is a hydroelectric power-dam lake with a stationary population of roach with no possibilities of migration. About 20 fishes have been collected and analysed annually.

Pike (*Esox lucius*) from the same locality were sampled in 1965, 1968, 1969, 1971 and 1973.

For fish fry the same type of preparation was made as for invertebrates, which means that 5—15 specimens were homogenized together and analysed for mercury. For small and adult roach and pike, lateral muscle tissue was analysed from the specimens individually. The preparation was in accordance with a method previously described (JOHNELS *et al.* 1967).

Birds

Breeding white wagtail (*Motacilla alba*) or fledglings of the same species were shot on the river-

Table 1. *Characteristics of the various localities along Mörrum river at which specimens of the specific species were collected. Abbrevations used: r=rapids, f=flowing water, b=backwaters of the river, s=soft sediment, l=lake.*

	1 Lill-sjön[1]	2 Hacke-kvarn[2]	3 Para-diset[3]	4 Frida-fors	5 Hovmans-bygd	6 Upper Hemsjö	7 Lower Hemsjö	8 Åke-holm	9 Vitt-skövle	10 Mörrum	11 Elle-holm
Fontinalis	f	r	—	r	r	r	—	r	r	r	—
Erpobdellidae	f	f+r	s	r	r	r	s	r	r	r+s	s
Asellus aquaticus	f	f	s	b	r	f	s	b	b	b	s
Hydropsyche	f	r	—	r	r	r	—	r	r	r	—
Agrion larvae	f	f	f	r	r	r	f	r	f	r	s
Sialis	s	s	s	s	s	s	s	s	s	b	s
Fish fry	l	f	f	b	f	f	f	f	s	f	f

[1] Lake in a forest, free from local mercury pollution. The depth of visibility measured by a Secchi disc in summer varies between 2 and 4 metres.

[2] Water to some degree polluted from sewage plants of urbanized areas upstream.

[3] Lake above hydroelectric power dam, depth 2 metres.

bank. These birds feed on insects (Witherby *et al.* 1938).

Sampling localities

A short presentation of the hydrographic characteristics of the sampling sites at different localities and for different species is given in Table 1. The geographical situation of the river and the sampling localities are shown in Fig. 1.

Analytical method

The analyses were carried out using neutron activation analysis at the Isotope Technique Laboratory in Stockholm (Ljunggren *et al.* 1971). This means that all mercury values in this paper relate to the total amount of mercury found.

III. RESULTS AND DISCUSSION

Levels in relation to position in nourishment webs

The analytical data in this investigation have been used to study whether there is any correlation between mercury levels in different species and the position in the food chain or habitat of the species. All data from the three localities upstream from the paper-mill *i.e.* localities 1, 2 and 3, have been pooled within each species independent of collection year and locality. The mean levels of mercury have been calculated on a dry weight basis with a 95 % confidence interval. That meant that only material after 1969 could be used. The results are presented in Fig. 3. From this figure it is evident that there is no correlation between mercury level and habitat or trophic level. For instance, the lowest mercury level is found in the carnivorous alder fly larvae (*Sialis lutaria*). The sediment is this species' habitat. The highest level is found for another sediment invertebrate feeding on plants and detritus, the isopod (*Asellus aquaticus*). Furthermore, there is no difference between the caddis fly larvae (*Hydropsyche*) which feed mainly on algae and detritus and the carnivorous dragon fly larvae (*Agrion splendens*). Both species were collected in rapids. This means that there is no significant difference due to the position in the nourishment web or due to differences in substrate or habitat.

However, this may not apply within an area which is or has been seriously polluted by mercury. For instance, during the clean-up period it might be expected that the highest levels of mercury in the river would be found in soft sediments caused by a previous sedimentation of contaminated material including fibres. Since the levels found downstream from the paper-mill vary from locality to locality and from year to year, it is not possible to pool the figures of mercury levels within the different species due to the high

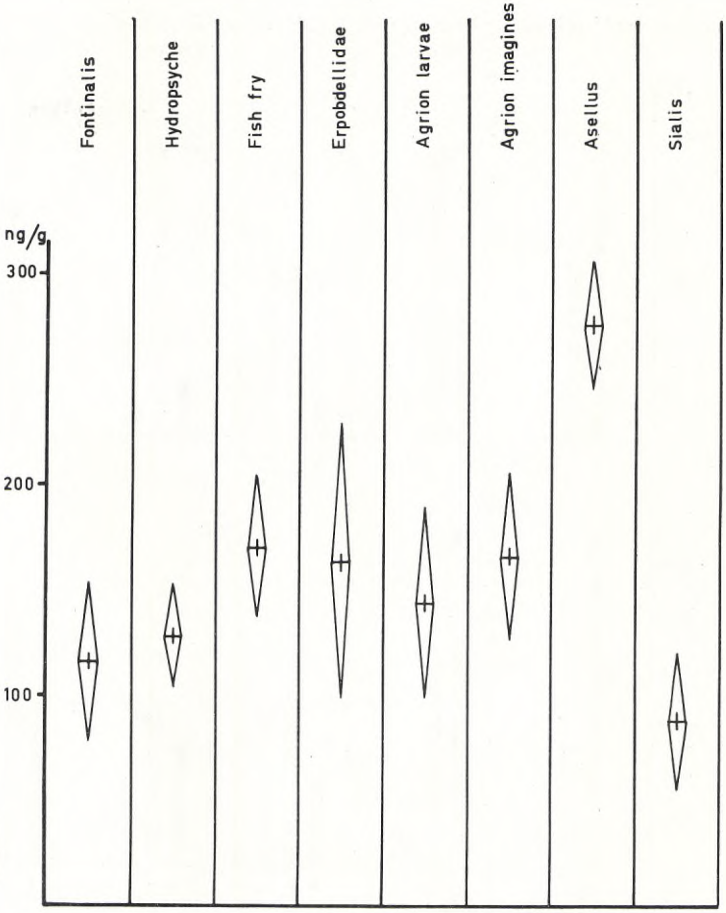

Fig 3. Mean levels of mercury and 95 % confidence intervals on dry weight basis in biota upstream from the paper-mill.

variability in levels during the period of investigation. Thus some sort of ratio evaluation system must be applied. In the clean areas the lowest levels were found in alder fly larvae (*Sialis lutaria*). Thus this species has been chosen as the reference species for the ratio evaluation for each locality and each year when calculating the ratios for the other species. The ratios have been divided into two main groups, one upstream and one downstream from the paper-mill. All data which have been used are from the years 1969—74, for which data calculated on a dry weight basis were available. The calculated ratios for the different species upstream and downstream from the paper-mill have been grouped into four classes depending on their numerical value. The classes are presented in Fig. 4. From this figure it is obvious that *Fontinalis* and *Hydropsyche* have approximately the same levels as *Sialis* or levels up to twice as high. Both upstream and downstream from the paper-mill the ratios are highest in *Asellus aquaticus*.

These data demonstrate that aquatic invertebrates show no correlation between the mercury levels and the trophic levels. This has already been shown by experimental data (HANNERZ 1968).

It is reasonable to believe that during the period after the discharge had ceased (1966—74), the mercury source in the river has been in the sediments. One might expect the highest levels to be found among invertebrates living on soft sediments. Nevertheless alder fly larvae (*Sialis lutaria*) which are predators and live on soft sediments generally show lower levels than other organisms.

It is also of interest that there seems to be no

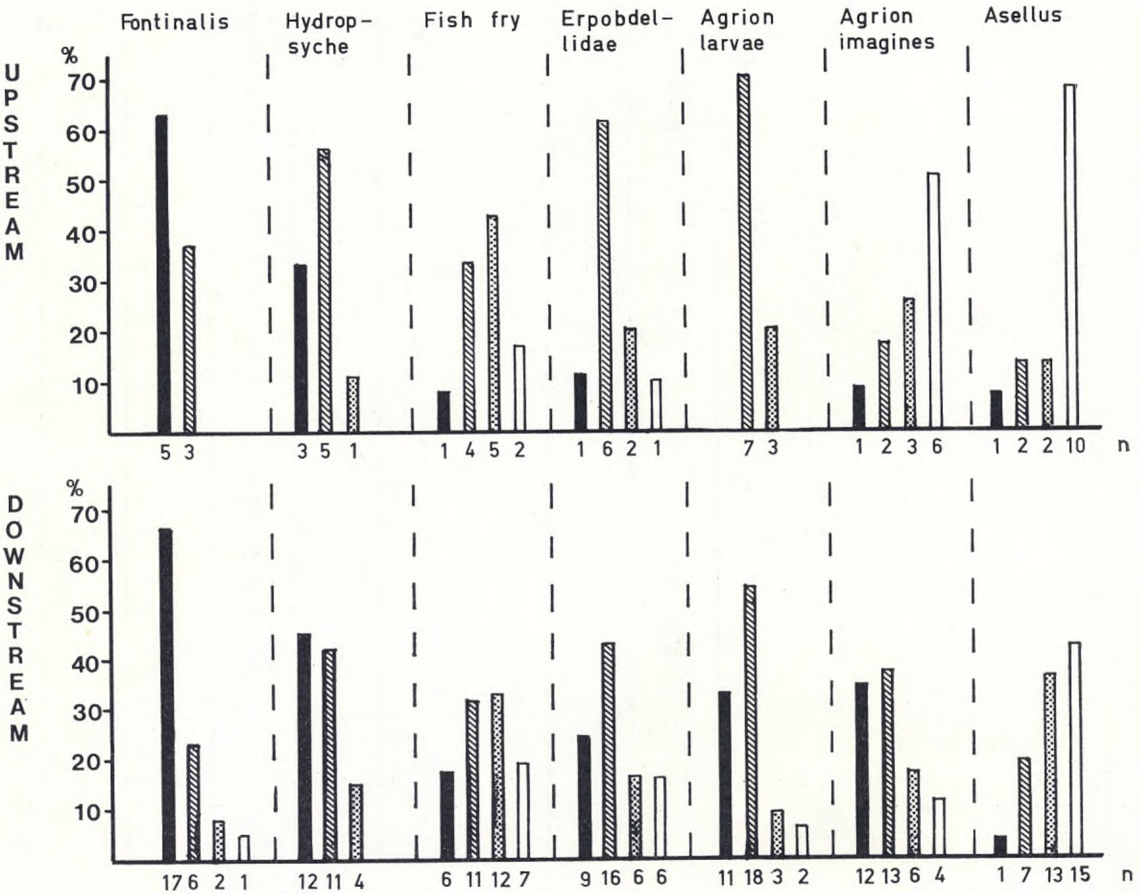

Fig 4. Percentage distribution of ratios between mercury levels in the dry tissue of different species upstream and downstream from the paper-mill. For each species the vertical scale indicates the percentage of observations giving mercury ratios (relative to *Sialis luteria*) within the following ranges: ≤ 1=black bar, > 1 ≤2=hatched bar, > 2 ≤ 3=dotted bar, > 3=white bar. n=number of observed ratios in the indicated range.

difference between the ratios in the unpolluted river upstream from the paper-mill and the polluted downstream river. Approximately the same distributions of ratios are found on both sides of the paper-mill (see Fig. 4).

It has been shown experimentally that organisms in slow-flowing water ponds have lower metabolic rates than those in swift waters (Fox and Simmonds 1933, Fox et al. 1935). In this investigation *Sialis lutaria* has generally been collected 1—2 cm deep in the soft sediments while other organisms were collected on the surface of hard and soft bottoms where the water exchange is comparatively good.

Asellus specimens generally show the highest ratio and since they feed partly on detritus the high ratio could be partly explained by detritus in the gasterointestinal tract as was found for tubificids and chironomids in highly contaminated areas (Jernelöv and Lann 1971). However, in this investigation, samples of surface sediment and *Asellus* from the same area in Lillsjön, see Fig. 1, were collected and compared over a four-year period. The mean level and standard error for sediment (dry weight) was 200 ± 41 ng/g and in *Asellus* (dry weight) 270 ± 26 ng/g. This means that in the uncontaminated area the mercury levels in *Asellus aquaticus* appears to be higher

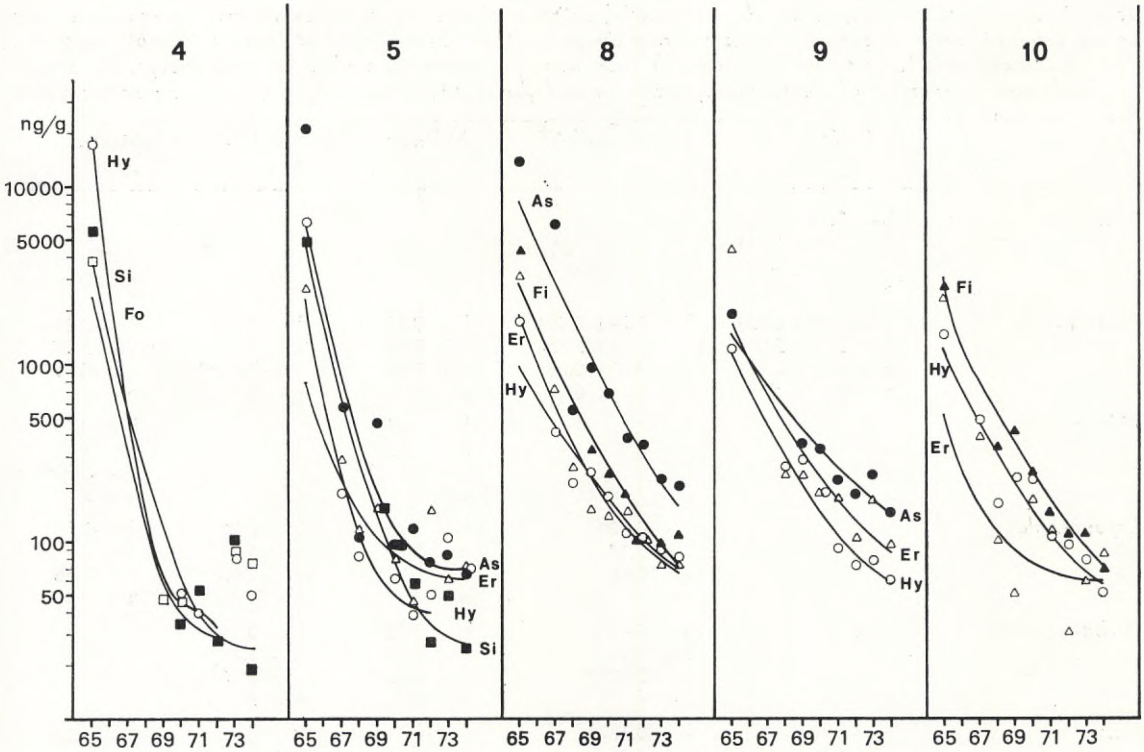

Fig 5. Levels of mercury (fresh tissue) in different species at various localities during the period 1965—74. The curves are based on calculations assuming exponential decrease of mercury. ○ Hy=*Hydropsyche*, ● As=*Asellus aquaticus*, □ Fo=*Fontinalis*, ■ Si=*Sialis*, △ Er=*Erpobdellidae*, ▲ Fi=Fish fry. Logarithmic scale. Compare with Table 2.

than in sediments. Furthermore, three samples of another crustacean, *Gammarus* sp. living at the bottom in rapids at locality 10 — where no sedimentation takes place — all show ratios > 3. The same condition was true for a sample of the planktonic crustacean *Daphnia* sp. from locality 5 — collected in a backwater of the river. Thus it seems likely that the intake of mercury directly from the water and the metabolic rate of the organism have a dominating influence on the various mercury levels found in aquatic organisms.

It is apparent that, among the organisms studied, the ratios for *Erpobdellidae* in particular and also *Agrion splendens*, both larvae and imagines show large variations, giving large 95 % confidence intervals, see Fig. 3. For *Agrion splendens* imagines, this might be due to the ability of the animal to migrate along the river. For *Erpobdellidae* the variation might be due to the irregularity in feeding habits and thus the metabolic rate (Whitehead 1943).

Levels in biota downstream from the paper-mill during the period 1965—74.

The analytical data are mostly from the period 1969—1974. However, a few data are available from 1965, 1967 and 1968. These sets of data representing a few species from a few localities are presented in Fig. 5. From the data plotted in the figure a very rapid decrease of mercury levels in biota since 1965 is quite obvious. Especially in the first two years there seems to have been a conspicuously rapid decrease of the levels. During the preparatory work it was apparent that at least some sets of data indicate an exponential decrease of the mercury levels. In order to investigate whether there is an exponential decrease of mercury in the river the logarithms of

Table 2. *Results of calculations on the exponential decrease of mercury in Mörrum river from measurements on the specified species at various localities during the period 1965–1974 (the period 1965–1972 within brackets). The calculations were based on mercury levels in fresh tissue. b=regression coefficient, a=intercept, r=correlation coefficient, n=number of observations. Significant at 5 per cent *, at 2 per cent **, at 1 per cent *** levels.*

	Fridafors 4	Hovmansbygd 5	Åkeholm 8	Vittskövle 9	Mörrum 10
Fontinalis	b=−0.18 (−0.52) a= 2.96 (4.03) r=−0.64 (−0.99) n= 5 (3)				
Hydropsyche	b=−0.36 (−0.75) a= 3.79 (5.03) r=−0.73 (−0.99) n= 5 (3)	b=−0.24 (−0.49) a= 2.98 (3.85) r=−0.61 (−0.88) ** n= 8 (6)	b=−0.17 a= 3.15 r=−0.96*** n= 9	b=−0.20 a= 3.25 r=−0.98*** n= 8	b=−0.21 a= 3.27 r=−0.95*** n= 9
Fish fry			b=−0.21 a= 3.65 r=−0.96*** n= 7		b=−0.19 a= 3.48 r=−0.98*** n= 8
Erpobdellidae		b=−0.30 a= 3.17 r=−0.66 n= 9	b=−0.25 a= 3.50 r=−0.97*** n= 9	b=−0.20 a= 3.43 r=−0.90*** n= 8	b=−0.32 a= 2.97 r=−0.56 n= 9
Asellus aquaticus		b=−0.41 a= 4.18 r=−0.90*** n= 9	b=−0.22 a= 4.12 r=−0.93*** n= 9	b=−0.14 a= 3.29 r=−0.96*** n= 7	
Sialis	b=−0.40 a= 4.00 r=−0.84* n= 6	b=−0.38 a= 4.05 r=−0.93*** n= 7			

the mercury levels minus mean background levels were correlated to the collection year, starting in 1965. The mean background levels were calculated from organisms at three localities (Nos. 1—3) upstream from the paper-mill. See also Fig. 3. The results of these correlations are presented in Table 2 from which it is evident that several localities and species show a significant exponential decrease. The curves in Fig. 5 are based upon the calculated line of the exponential decrease but the background levels have been added. The exponential decrease is very easily seen downstream from locality 8. At localities 4 and 5 the background levels were reached as early as about 1970 to 1972 which means that the last data of 1973 and 1974, with varying low levels, might have had a negative influence on the regression line. If the data of 1973 and 1974 are subtracted from those for *Hydropsyche* at locality 5 the correlation coefficient (r) gives a significant decrease.

Levels in biota during the period 1969—74

From the material presented above it is quite obvious that the levels have been significantly lower for the last few years in comparison to those for 1965 when the last mercury release took place. In order to study whether the levels were still decreasing in invertebrates during the years 1969 to 1974 the analytical data from this period have been plotted in a logarithmic-linear diagram to illustrate the trend for each individual species at each specific locality (Figs. 6, 7 and 8). All mercury levels have been calculated on a dry weight basis. In Fig. 6 organisms representing rapids and free living pelagical organisms are presented. Those organisms which represent soft bottoms are presented in Fig. 7. Finally in Fig. 8 *Agrion splendens* larvae and imagines and *Erpobdellidae* are shown. Since the levels for many of the species and localities show a tendency to decrease exponentially calculations for linear regression have been performed in the same way

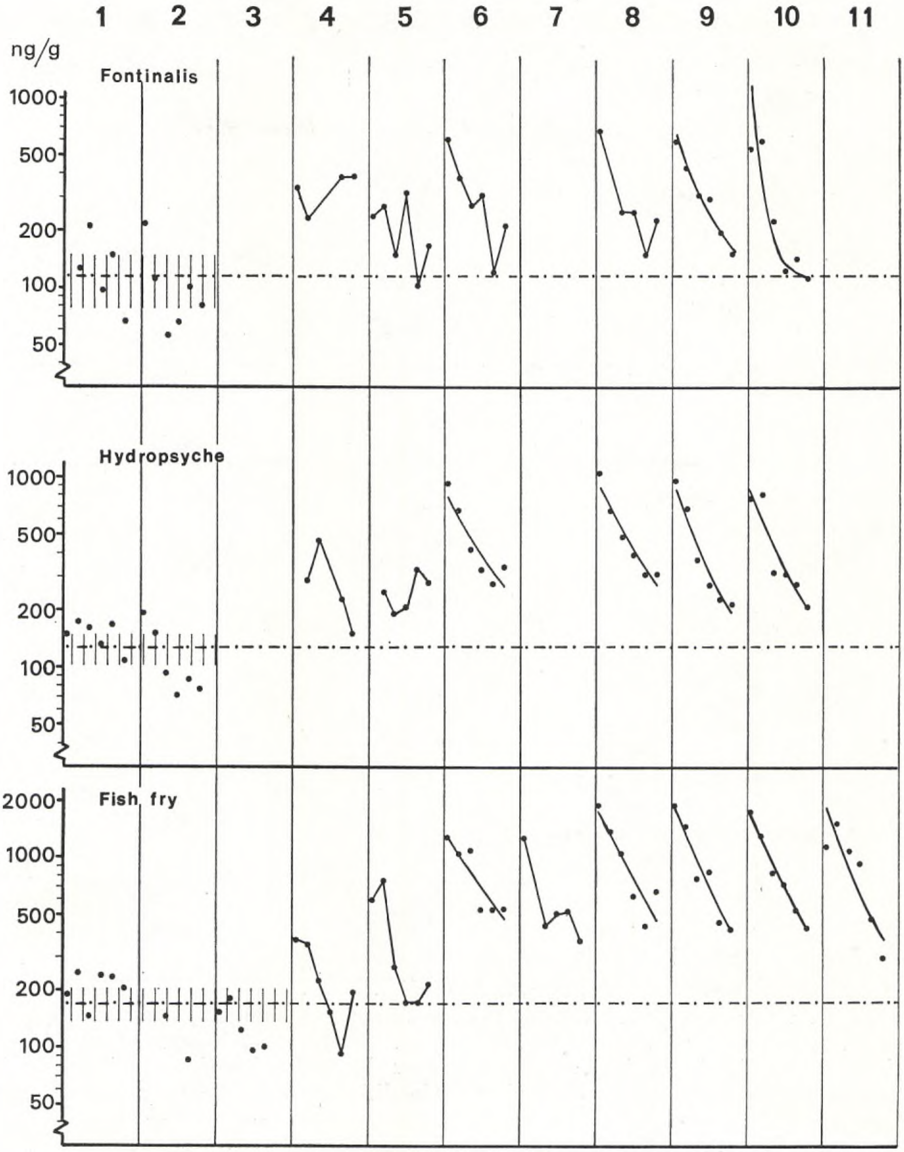

Fig 6. Levels of mercury (dry tissue) in organisms from rapids and pelagic fish fry. The localities have been arranged in the direction of the current. If the exponential decrease has been found significant (see Table 3) this curve has been drawn. Otherwise the line has been drawn between the level of single collection years. Mean background level and the 95 % confidence interval are given for localities upstream from the paper-mill. Logarithmic scale.

as for organisms from the period 1965—74, i.e. mercury levels minus background level for each collection year. Data from this calculation are shown in Table 3. It is quite obvious that for the lower part of the river the data for organisms living in rapids and pelagial organisms correspond very well to an exponential decrease of the levels. This refers to the species *Fontinalis*, *Hydropsyche*, and fish fry (Fig. 6). The organisms presented in Fig. 7 — *Asellus* and *Sialis*, live on soft bottoms and have values corresponding to an exponential decrease mainly in two localities — 5 and 8 — which are localities where quite visibly thick layers of sediments including fibre have been removed by the river during the investigated period. The values presented in Fig. 8 for *Agrion splendens*, larvae and imagines, and *Erpobdellidae* show considerable variability and no good correlation to an exponential decrease is found. However, from the figure it is clear that a

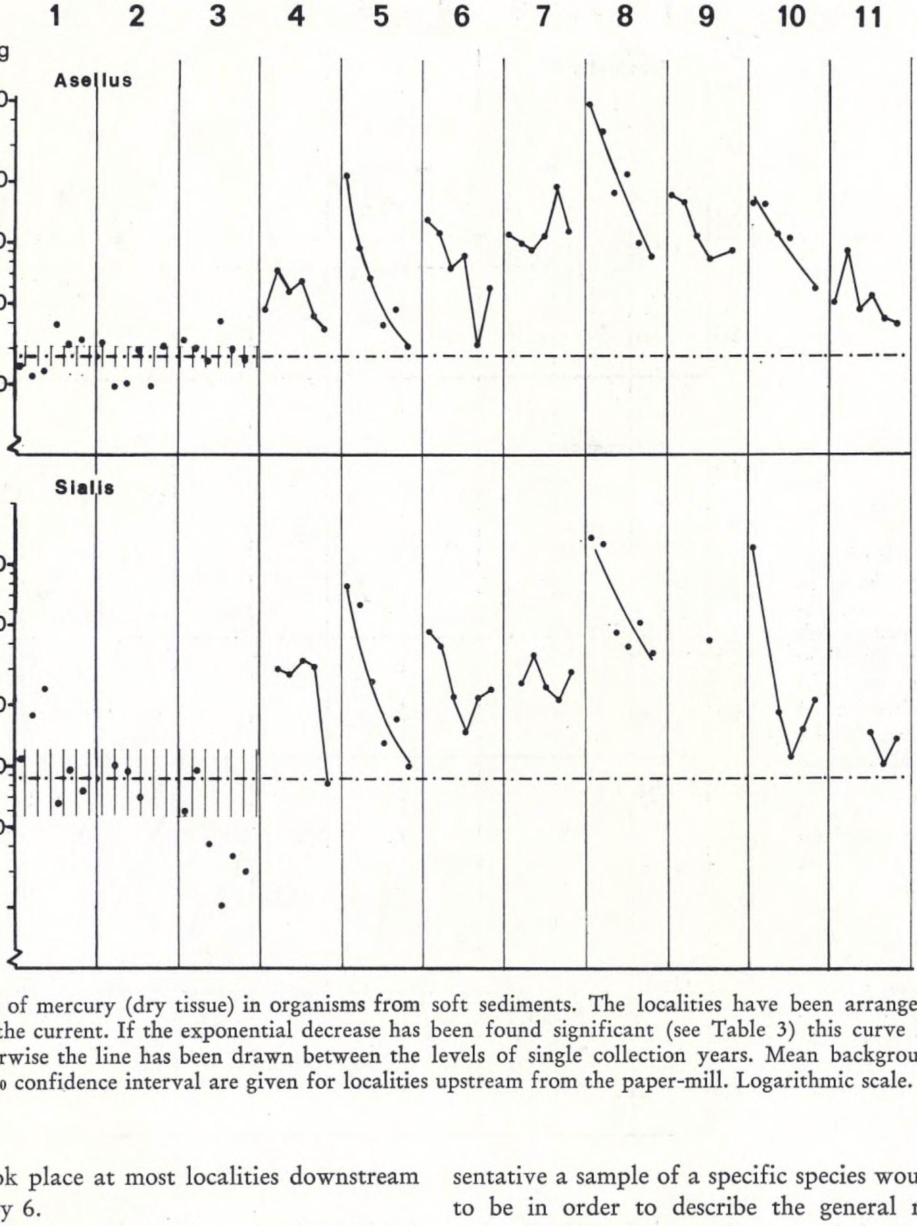

Fig 7. Levels of mercury (dry tissue) in organisms from soft sediments. The localities have been arranged in the direction of the current. If the exponential decrease has been found significant (see Table 3) this curve has been drawn. Otherwise the line has been drawn between the levels of single collection years. Mean background level and the 95 % confidence interval are given for localities upstream from the paper-mill. Logarithmic scale.

decrease took place at most localities downstream from locality 6.

Looking for a general tendency in the material — see Figs. 6, 7 and 8 — it seems that organisms from localities immediately downstream from the paper-mill reached the background levels during the last investigation period 1970—74. Thus no further decrease in the levels is to be expected.

It is conspicuous that the mercury levels found for different species showed no differences which could be related to ecological niches, habitats or substrates. However, in considering how representative a sample of a specific species would have to be in order to describe the general mercury contamination of a specific part of the river it is quite reasonable to believe that organisms on hard bottoms in flowing water or free swimming species in flowing water would be good test material. This is because their habitats represent environments with good water exchange. In the present material the data for species representing hard bottom fauna and free swimming species show good correlation to an exponential decrease, see Fig. 6. In organisms from soft sediments a

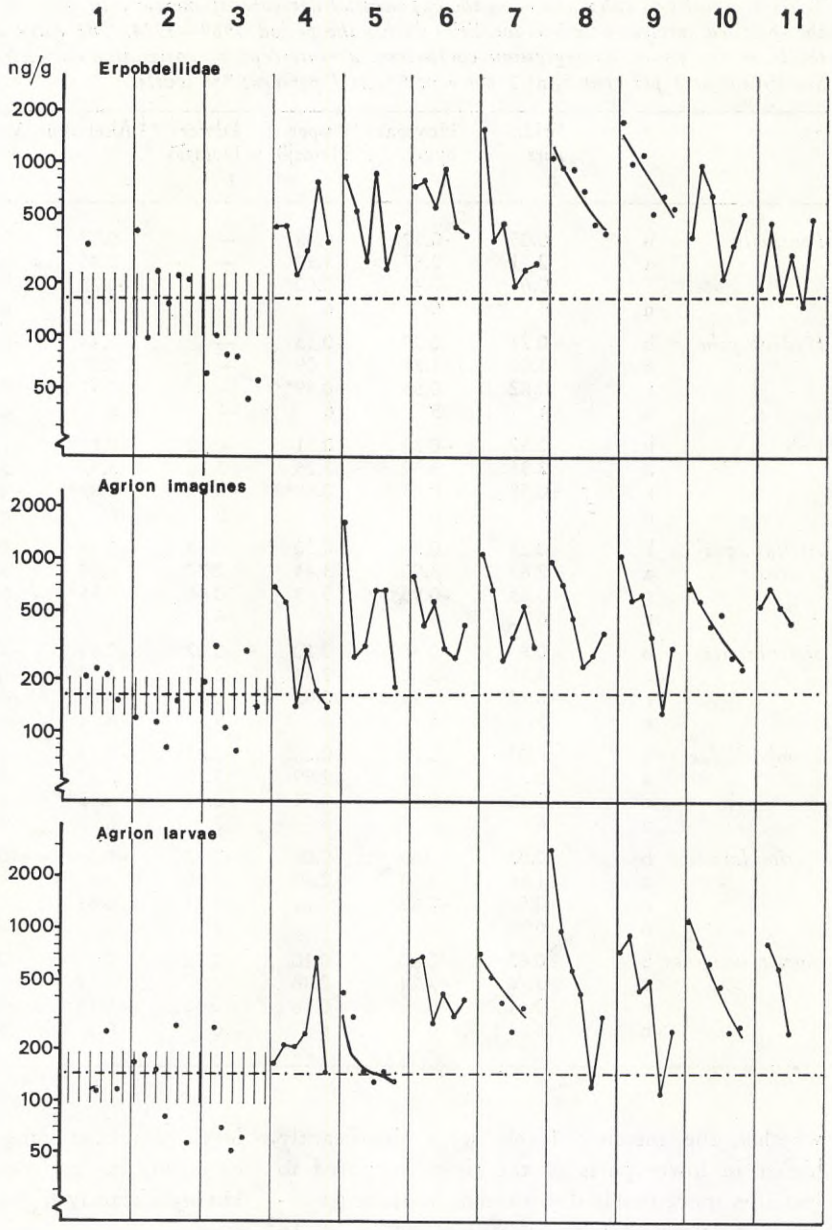

Fig. 8. Levels of mercury (dry tissue) in Agrion larvae and imagines and in *Erpobdellidae.* The localities have been arranged in the direction of the current. If the exponential decrease has been found significant (see Table 3) this curve has been drawn. Otherwise the line has been drawn between the levels of single collection years. Mean background level and the 95 % confidence interval are given for localities upstream from the paper-mill. Logarithmic scale.

higher variability is to be expected — and was in fact found, see Fig. 7 — since the mercury levels of the sediments will vary from place to place and since some movements of sediment will take place from one area to another between years.

It is also interesting to see that at one locality no decrease of the mercury levels seems to have occurred in organisms living in soft sediment such as *Asellus* and *Sialis.* This is at locality 7 which is a sedimentation area (Fig. 7).

Mercury levels in fish

Since gill-net-fishing on adult fish is difficult to carry out at many of the localities along the river, small roach one to two years old were sampled in 1971 using gill-nets. This was to see

Table 3. *Results of calculations on the exponential decrease of mercury in Mörrum river from measurements on the specified species at various localities during the period 1969—1974. The calculations were based on mercury levels in dry tissue. b=regression coefficient, a=intercept, r=correlation coefficient, n=number of observations. Significant at 5 per cent *, at 2 per cent **, at 1 per cent *** levels.*

		Fridafors 4	Hovmans bygd 5	Upper Hemsjö 6	Lower Hemsjö 7	Åkeholm 8	Vittskövle 9	Mörrum 10	Elleholm 11
Fontinalis	b	0.05	–0.32	–0.28	—	–0.17	–0.22	–0.61	—
	a	2.11	2.87	3.22	—	2.96	3.17	4.23	—
	r	0.61	–0.46	–0.60	—	–0.78	–0.97***	–0.91**	—
	n	4	6	6	—	5	6	6	—
Hydropsyche	b	–0.21	0.07	–0.13	—	–0.14	–0.21	–0.19	—
	a	3.09	1.71	3.09	—	3.18	3.30	3.21	—
	r	–0.82	0.53	–0.89**	—	–0.97***	–0.97***	–0.94***	—
	n	4	5	6	—	6	6	6	—
Fish fry	b	–0.57	–0.35	0.11	–0.12	–0.14	–0.18	–0.16	–0.19
	a	3.31	3.32	3.26	3.16	3.47	3.58	3.54	3.60
	r	–0.58	–0.73	–0.88**	–0.84	–0.89**	–0.97***	–0.99***	–0.89**
	n	6	6	6	5	6	6	6	6
Asellus aquaticus	b	–0.11	–0.34	–0.20	0.03	–0.18	–0.08	–0.12	–0.10
	a	2.83	3.90	3.44	2.77	4.00	3.28	3.41	2.77
	r	–0.65	–0.95***	–0.63	0.46	–0.96***	–0.85	–0.96***	–0.68
	n	6	6	6	6	6	5	5	6
Sialis luteria	b	–0.63	–0.35	–0.10	–0.02	–0.14	—	–0.21	–0.02
	a	4.86	3.62	2.64	2.33	3.33	—	3.05	1.63
	r	–0.70	–0.94***	–0.62	–0.21	–0.86*	—	–0.65	–0.06
	n	5	6	6	5	6	—	5	3
Erpobdellidae	b	0.02	–0.09	–0.08	–0.23	–0.13	–0.12	–0.06	–0.10
	a	2.22	2.83	2.99	3.22	3.27	3.34	2.65	1.64
	r	0.11	–0.41	–0.71	–0.74	–0.95***	–0.87*	–0.26	–0.12
	n	6	6	6	6	6	6	6	6
Agrion larvae	b	–0.03	–0.69	–0.08	–0.12	–0.33	–0.48	–0.20	–0.40
	a	1.86	3.63	2.80	2.98	3.97	4.03	3.43	4.08
	r	–0.08	–0.85*	–0.61	–0.84*	–0.81	–0.53	–0.96***	–0.95
	n	6	6	6	5	6	6	6	3
Agrion imagines	b	–0.63	–0.20	–0.10	–0.12	–0.16	–0.48	–0.17	–0.06
	a	3.76	3.24	2.86	2.97	3.12	4.00	3.10	2.76
	r	–0.61	–0.56	–0.66	–0.60	–0.75	–0.53	–0.93***	–0.63
	n	6	6	6	6	6	6	6	4

whether the mercury levels were significantly higher in lower parts of the river compared to localities immediately downstream from the paper-mill some years after the discharge had ceased. In Fig. 9 the mean mercury levels and the 95 % confidence interval for roach weighing 20 g are given. The mercury levels for 20 g weight have been calculated by the aid of regression analysis according to a method previously published (Grandell 1975). 20 g was chosen as the weight since it is a possible weight for one-to two-years-old roach and was a weight found in all catches along the river. As can be seen, the levels were the same upstream and downstream close to the paper-mill at localities 4 and 5, but significantly higher at localities further downstream.

In Fig. 10 a few analyses on pike from locality 6 are presented. Despite the small number of analytical data it is obvious and statistically proved ($p < 0.05$) that the levels have decreased between 1965 and 1970 at locality 6. The statistical calculations are based on a method presented by Radhakrishna Rao (1965).

At locality 6 adult roach have also been collected annually since 1968 and analysed for

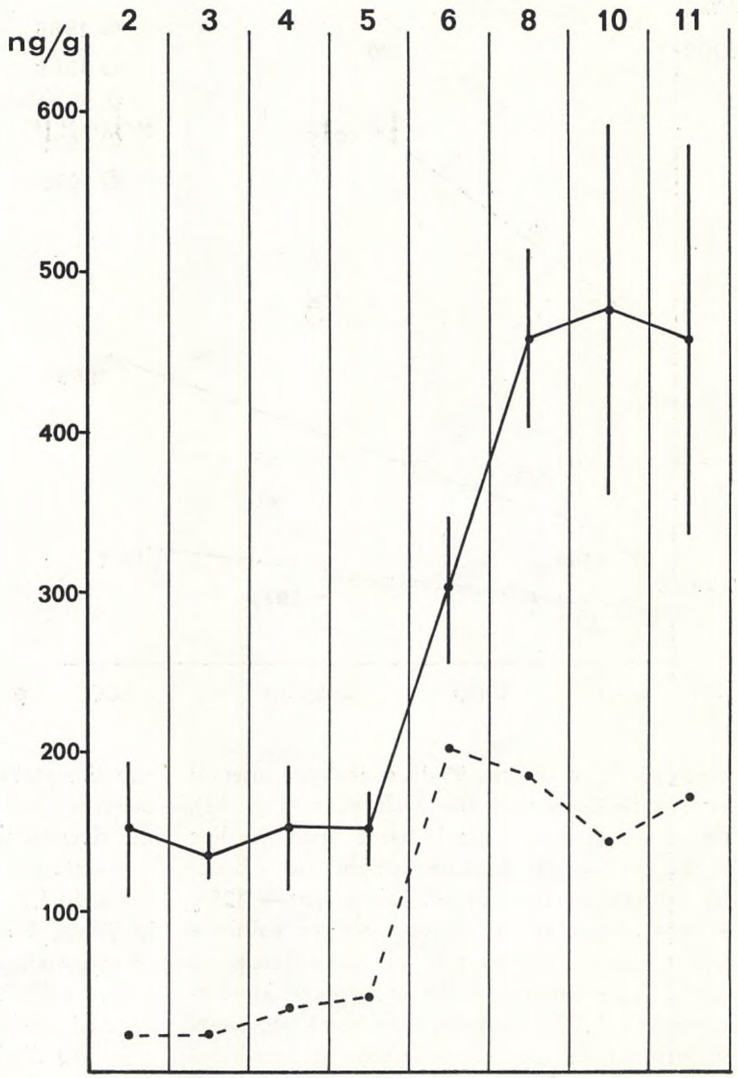

Fig 9. Calculated mean mercury levels and the 95 % confidence interval in the axial muscle of roach weighing 20 g. The material was collected in 1971. The mercury levels of homogenized 2 month-old fish fry of the same year is shown (broken line).

their mercury contents. Regression analysis has been carried out on this material and in Fig. 11 and Table 4 the regression lines are presented. From these it is apparent that the levels have decreased between 1968 and 1974. The differences are statistically significant ($p < 0.001$). The same statistical method has been used as in the case of pike.

In this material the correlation coefficients (r) are normally very high although in 1972 and 1973 the values of r are clearly lower than for the other years, see Table 4. These two years have small variations in waterflow while all the other years have distinct variations (Fig. 2). The low waterflow may have decreased the mixing of waterbodies within the river, especially within the sampling area — the lake above the hydroelectric power dam — giving differences in the exposure to mercury for the roach population during these two years, and this might explain the low correlation coefficients for the years 1972 and 1973.

In order to estimate the decrease of mercury in roach the levels for a standardized roach

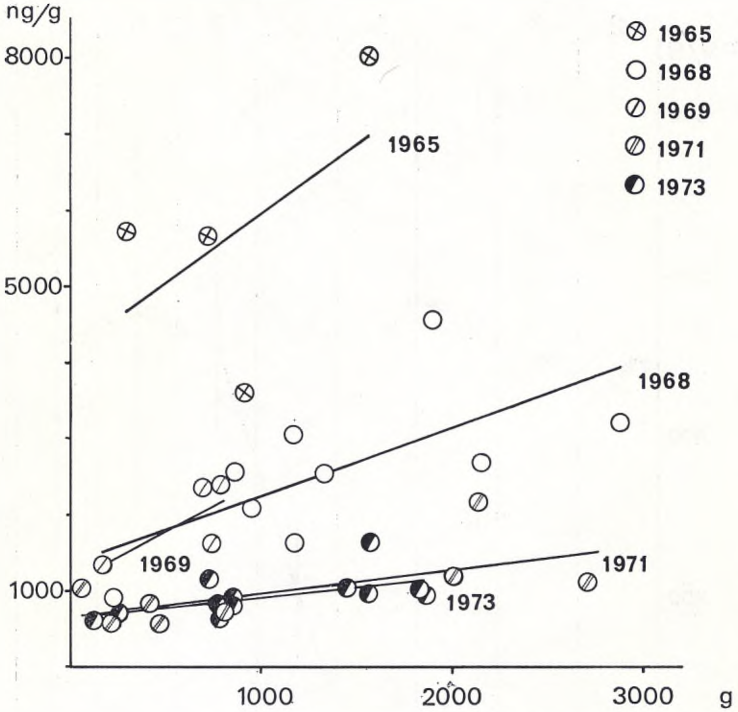

Fig 10. Mercury levels in the axial muscle of pike from the Upper Hemsjö hydroelectric power dam lake (6) collected during 1965—73. The lines of the correlation for mercury levels versus weight are given for the collection years individually (see Table 4).

weighing 125 g and the 95 % confidence interval have been calculated for each year (Fig. 12). The curve in this figure is based upon the line of the exponential decrease but the mean background level has been added. This weight — 125 g — was chosen as one possible weight within a weight interval common to all the investigated years. Determination of the background level at a weight of 125 g was made by using regression analysis on 21 specimens sampled at locality 3 upstream from the paper-mill. From the slope of the curve (the β value) it may be concluded that a 50 % decrease of the mercury levels in roach from locality 6 will take place during a period of about 2.5—3 years.

The time required for a 50 % mercury decrease in field collected adult roach from Mörrum river corresponds to the value found for the fish fry. Since the fish fry is only two-months old this material can be said more or less to represent the mercury decrease in the water. The β values also correspond to the half-life of mercury in fish based upon laboratory investigations previously reported (Järvenpää *et al.* 1970). The rather long half-life determined from the experimental data would seem to indicate a slower mercury decrease to 50 % in adult fish than in the river or the fish fry. Nevertheless, these two test materials show approximately the same time for a 50 % mercury decrease. (See the β values in Tables 3 and 4.) It was observed that roach of approximately the same weight, but born before and after the discharge had ceased, showed approximately the same mercury levels 3 years after the discharge had ceased. It was found in another area (Olsson 1976) that pike of similar weight but different age showed the same level of contamination when the mercury was generally decreasing.

Several reasons can be given for the rapid 50 % mercury decrease found in adult roach. Firstly, the experimental data are based on whole body measurements not taking account of the increase of body weight whereas the field data are based upon concentrations. Within one year the increase in weight of a fish such as roach will be 50—100 % and this will decrease the concentration but not the amount of mercury in the fish.

Secondly, the metabolic rate is of importance for mercury turnover (Fagerström and Åsell

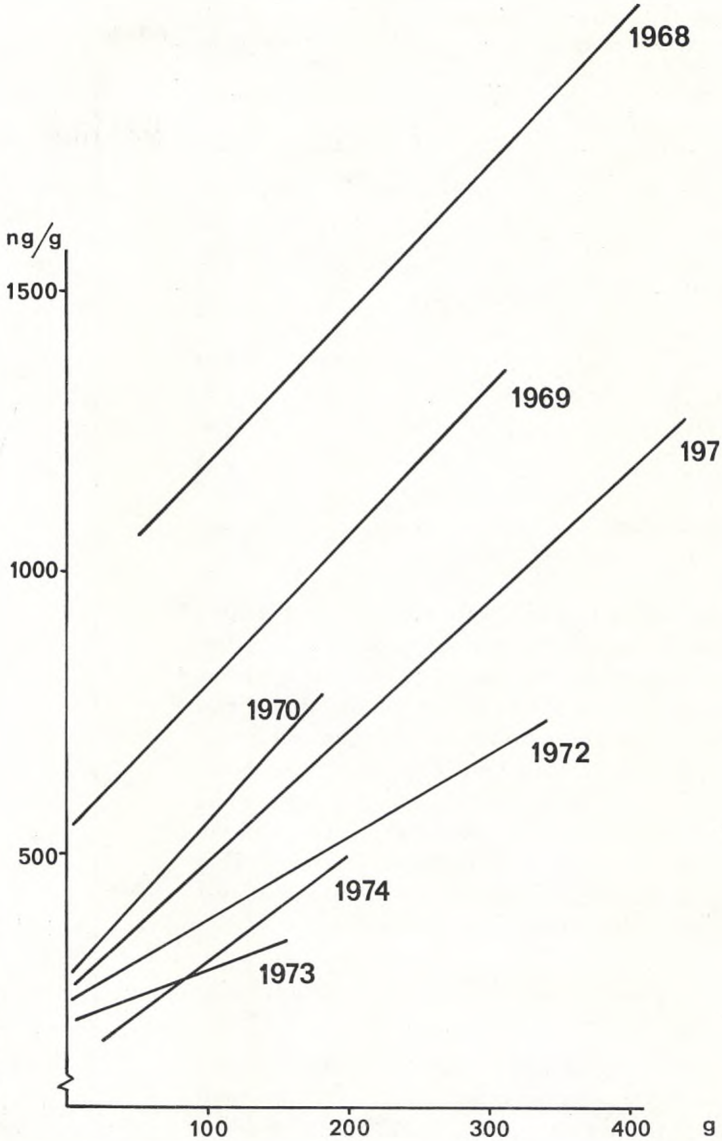

Fig 11. Lines of the correlation, mercury levels versus weight, in roach from the Upper Hemsjö hydroelectric power dam lake (6) during the period 1968—74 (see Table 4).

1973, Fagerström *et al.* 1974, de Freitas *et al.* 1975 and 1974, MacLeod and Pessah 1973). During a year the metabolic rate in natural conditions will differ from that during experimental conditions. Järvenpää and co-workers (1970) conclude that the half-life of mercury will decrease with increasing temperature. The investigation cited was carried out at a temperature of approximately 10°C whereas the metabolic rate in Mörrum river in summertime, when the temperature is about 20°C, can be expected to be twice as high.

It is also worth mentioning that fish in flowing water can be expected to have a higher metabolic rate than fish in aquariums and lakes where the fish do not have to move in order to compensate for water movements.

Mercury levels in birds upstream and downstream from the paper-mill.

To study whether increased mercury levels in aquatic insect larvae will cause increased mercury levels in insectivorous birds living close to the

Table 4. *Correlation of mercury levels versus weight in pike and roach in Upper Hemsjö hydroelectric power dam lake (6) for different years. n=number of specimens, b=regression coefficient, a=intercept, r=correlation coefficient.*

	Year	n	b	a	r
Roach	1968	12	2.67	933	0.93
	1969	24	2.66	539	0.86
	1970	16	2.79	283	0.92
	1971	29	2.31	255	0.95
	1972	51	1.47	236	0.69
	1973	21	0.96	201	0.49
	1974	23	1.88	122	0.93
Pike	1965	4	1.83	4130	0.54
	1968	9	0.86	1370	0.66
	1969	4	1.30	1150	0.73
	1971	8	0.32	663	0.63
	1973	12	0.28	641	0.60

river, white wagtails were collected at the river bank during the period 1967—68. As only a few specimens could be collected no division according to the locality has been carried out. Only two groups have been considered: upstream and downstream from the paper-mill. The results are shown in Fig. 13. The levels are higher among white wagtails downstream from the paper-mill in comparison with those collected upstream. Thus flying imagines of aquatic insects from the river influence the terrestrial environment.

Geographical changes of mercury contamination along the river.

In *Hydropsyche* and *Asellus* the highest mercury levels were generally found close to the paper-mill during the discharge period in 1965. This condition changed after the discharge had ceased and as early as in 1967 the highest levels were found further downstream. This condition still prevails in the river. From Figs. 14 and 15 it can be seen that the most rapid decrease in the level took place immediately downstream from the paper-mill. It is reasonable to believe that the original mercury source, the effluent water of the paper-mill, caused an immediate and severe accumulation of mercury in organisms in the water near the paper-mill when phenyl mercury — in more or less soluble form — was introduced together with other material including cellulose fibres. An uptake of mercury took place from aquatic solution to organic and biological matter. The longer the time or the further the distance from the source, the smaller the amount of dissolved mercury

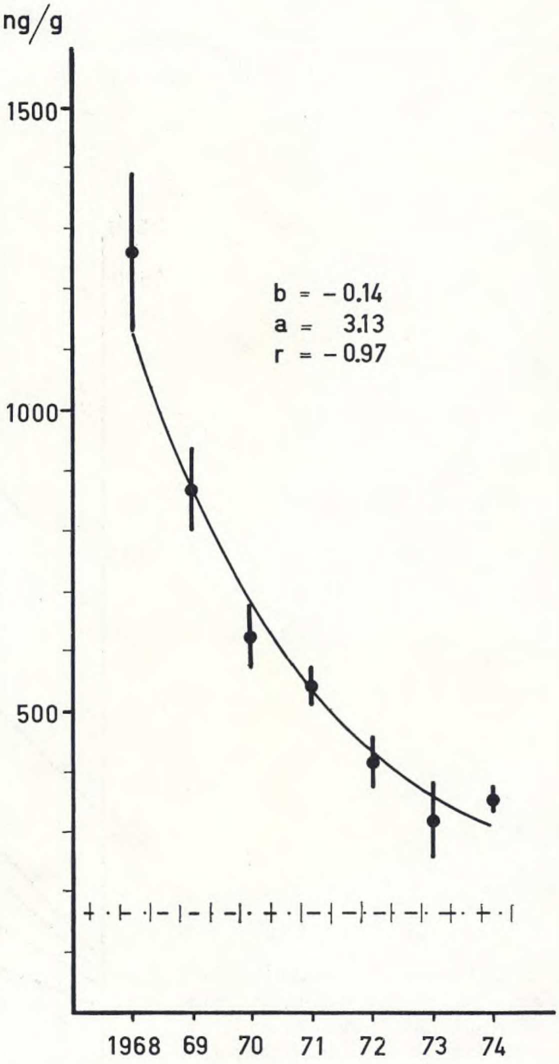

Fig 12. Calculated mean mercury levels in the axial muscle of roach weighing 125 g from the Upper Hemsjö hydroelectric power dam lake (6) during the period 1968—74. The 95 % confidence interval is shown. The line of exponential decrease and the background mercury level — calculated from fishes collected upstream the paper-mill — and its 95 % confidence interval are given. Significant at 1 per cent level. b=regression coefficient, a=intercept, r=correlation coefficient.

which was available for uptake since the mercury present was partly stored in living matter or on fibres and organic matter. This organic matter, dead or living, was partly deposited in the sediments and these were the prevailing conditions during the discharge period up to 1965. This may explain the lower levels found in lower parts of the river in comparison to areas closer to the paper-mill. After the mercury discharge from the paper-mill ceased, it would be expected that the mercury in the river would be found in the bottom sediments. Since the amount of water passing at the paper-mill is approximately the same as that at the mouth of the river, higher levels are to be expected further down the river. The reason for this is that more of the contaminated bottom sediments have been passed by the water lower down the river than by the water close to the paper-mill. This is of course a simplification of the situation in the river since local sedimentation areas will have more influence on the levels in the river water than areas deficient in sediment. An additional factor is that sedimentation of particles will have taken place in the river covering the mercury-laden sediments. However, the levels found in *Hydropsyche*, (Fig. 14) provide clear evidence that areas close to the paper-mill are now more or less free from the former mercury contamination. This is confirmed by the levels for *Asellus* (Fig. 15). However, for both species mercury levels above the background levels are still found further downstream although there too the levels show an annual decrease.

From the present material it is not possible to deduce any precise data on the time required for a 50 % decrease in the mercury levels for individual species at specific localities, but as a rough estimation based upon the slope of the curve, the β values, (see Tables 2 and 3) it can be said that the time required is between 1—2.5 years in benthic organisms. Only β values from curves with a statistical significance of 1 per cent or better have been considered.

IV. SUMMARY

In this investigation the mercury levels in biota upstream and downstream from a paper-mill have been studied. The investigation period covers both a mercury discharge period and a period after the discharge had ceased. The study was made in order to obtain representative data on the clean-up of the river. The results may be summarized as follows:

1. No correlation was found between mercury levels and the food or choice of habitat of the different species, *i.e.* no correlation to substrates or position in nourishment web was found.

2. The ratios between the mercury levels found in 8 different species are the same in uncontaminated areas as in contaminated areas.

3. The levels found in invertebrates seem to depend mainly on intake from the water and possibly also on the metabolic rate of the organism.

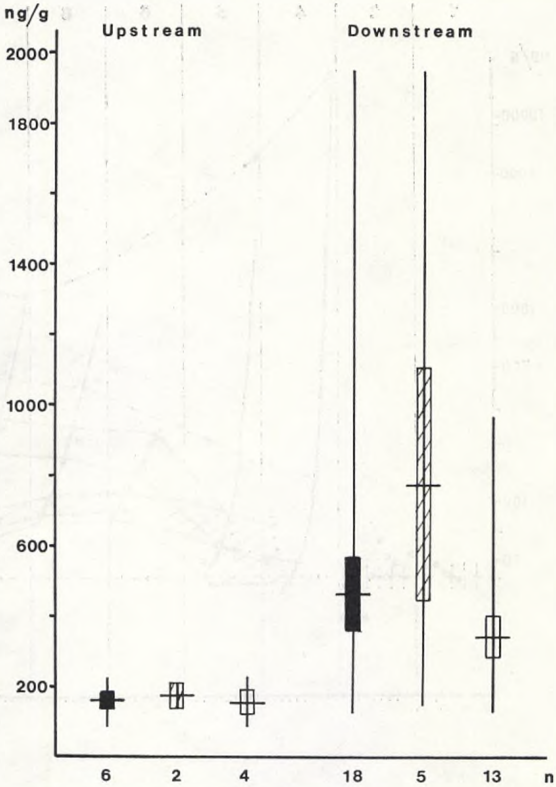

Fig 13. Levels of mercury in breast muscle of white wagtail collected upstream and downstream from the paper-mill. — mean level, ⊞ 95 % confidence interval, | range, ■ all specimens, ▨ adult birds, ☐ juvenile birds. n = number of specimens.

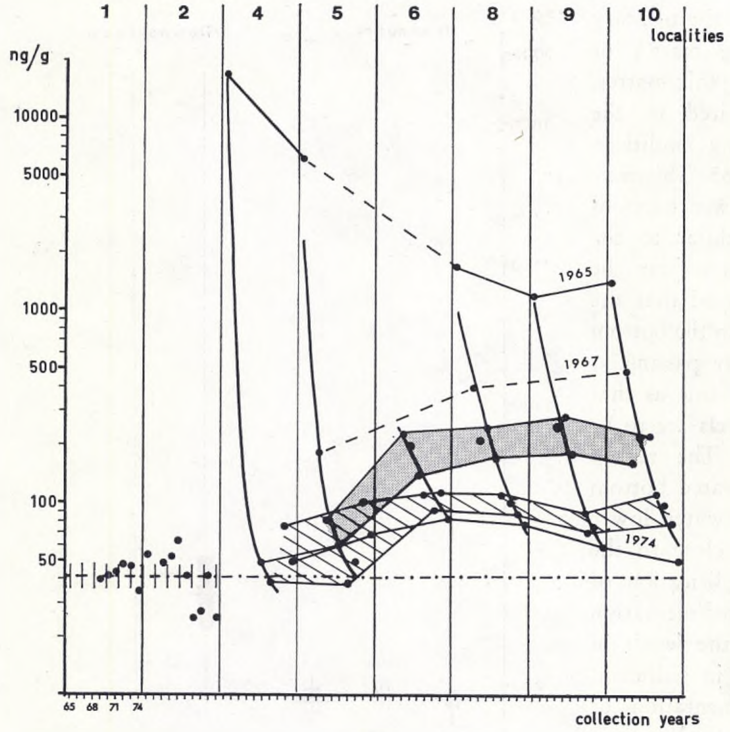

Fig 14. Levels of mercury (fresh tissue) in caddis fly larvae (*Hydropsyche*) during the period 1965—74. Mercury levels are given with a logarithmic scale. The localities have been arranged in the direction of the current. For each locality the curve of the calculated exponential decrease has been drawn. For Fridafors (4) and Hovmansbygd (5) the levels of 1973 and 1974 have not been taken into account when calculating the regression (see page 78). Lines have been drawn between the localities for the last year of discharge 1965, the first investigation year after the discharge had ceased 1967, and the last investigation year 1974. The intermediate period has been divided into two periods: the period 1968—70 by a shaded area and 1971—73 by a hatched area. Mean background levels and the 95 % confidence interval are given for localities upstream from the paper-mill.

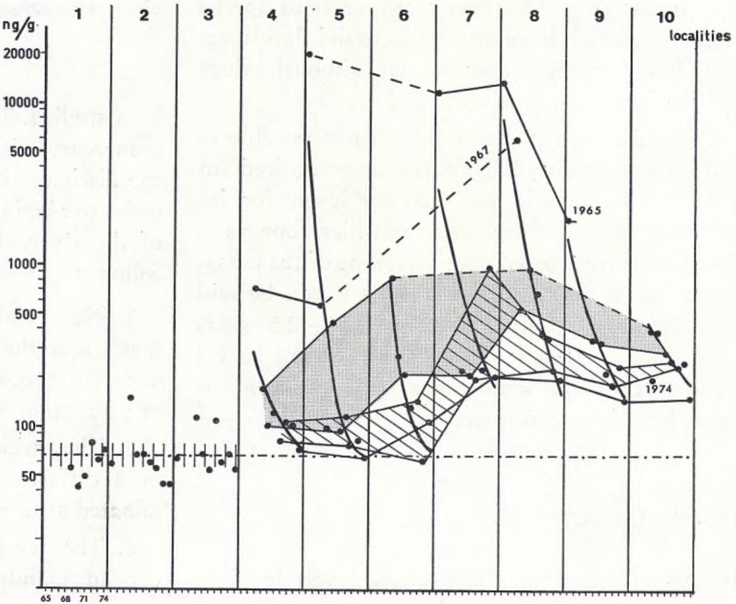

Fig 15. Levels of mercury (fresh tissue) in the isopod *Asellus aquaticus* during the period 1965—74. Mercury levels are given with a logarithmic scale. The localities have been arranged in the direction of the current. For each locality the curve of the calculated exponential decrease has been drawn. Lines have been drawn between the localities for the last year of discharge 1965, the first investigation year after the discharge had ceased 1967, and the last investigation year 1974. The intermediate period has been divided into two periods: the period 1968—70 by a shaded area and 1971—73 by a hatched area. Mean background levels and the 95 % confidence interval are given for localities upstream from the paper-mill.

4. For the main part of the material collected downstream from the paper-mill the decrease in the mercury concentration with time seems to be exponential.

5. The times required for a 50 % decrease in the mercury levels in the species studied vary from approximately 1 year to 2.5 years. That the periods are so short is probably due to the rapid water exchange in the river.

6. During the discharge period the highest levels occurred close to the paper-mill on the downstream side. After the discharge had ceased the highest levels were found lower down the river. The geographical change in the concentration maximum was probably due to the fact that the source of pollution became the sediments instead of the paper-mill and that water further down the river has passed over a larger area of the sediments.

7. The decrease in mercury levels has also been rapid in fish. In roach a 50 % decrease in the mercury levels takes about 2.5 years. The rapid water exchange in the river may explain the rapid mercury decrease. No effect on adult roach of the former mercury discharge was found since the 50 % decrease in mercury levels was approximately the same in adult fish as in fish fry.

8. In white wagtails — which birds have an insect diet — an increase of the mercury levels also occurred downstream from the paper-mill showing the influence on terrestrial organisms of aquatic insect imagines.

V. ACKNOWLEDGMENTS

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Ecological Effects of Heavy Metal Discharge in a Salmon River

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1 INTRODUCTION

Between 1960 and 1967 the Swedish Salmon Research Institute studied the Salmon population in the Rickleå river, a woodland river in northern Sweden (ÖSTERDAHL 1962—1969). A fish trap was built near the river mouth so that fish migrations could be controlled. Besides migrations the general biology of riverine fishes was also investigated. Because of its strategic position, the fitness of the river, and the fact that much biological information had already been collected here, the Section of Ecological Zoology at the University of Umeå in 1968 set up a biological field station on this site. The station was to serve as a base mainly for lotic biological studies.

In 1966 and 1967 a drastic reduction of the parr and smolt populations of salmon was noted; the population had not recovered in 1973. It became also evident that certain insects, important as salmon food, were strongly reduced in numbers. As no oxygen reduction could be suspected, the most plausible explanation was some kind of toxic pollution. For the biologists it became an urgent task to study and follow the symptoms and development of the surmised poisoning in order to reveal its causes.

2 THE RIVER RICKLEÅ

The Rickleå river is one of the smallest salmon rivers in northern Sweden. The total watershed, 1,673 km², lies entirely within the coniferous belt. The river orginates in Lake Bygdeträsket, 47.7 km from the mouth, and discharges into the Gulf of Bothnia at 64°05'N (Fig. 1).

In the river rapids alternate with fast and slow streams (Fig. 2). The water level of Lake Bygdeträsket is about 131 m above sea level. The community Robertsfors is situated 15.1 km from the river mouth. This point is 35 m above sea level. Below Robertsfors there are no tributaries of importance.

The bedrocks of the drainage area are mostly veined gneisses and the quarternary deposits are

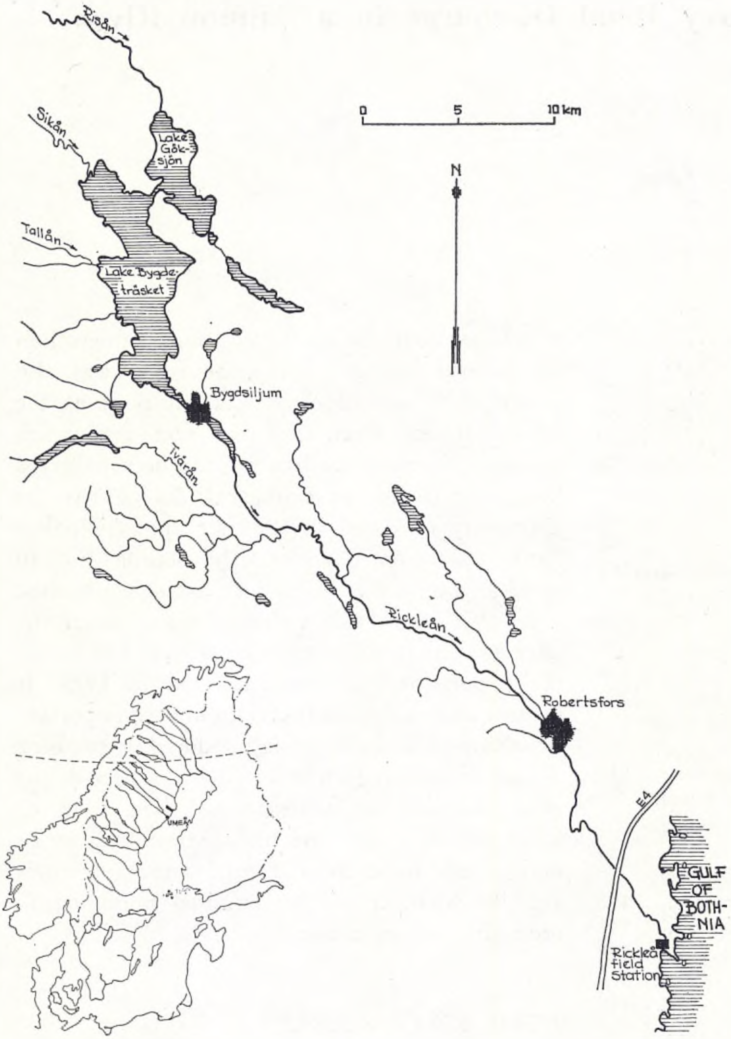

Fig. 1. The Rickleå river.

moraines. The vegetation of the area is dominated by coniferous forest. In the river valley, however, there are many farms. About 50 per cent of the river borders on agricultural land. Some of the cultivated areas have, however, become forest-cultures during the last decades.

Partly due to the stony bottom the higher vegetation in the river itself is rather scarce. Mosses dwell in the rapids, chiefly *Fontinalis dalecarlica* and *F. antipyretica*. In the slow streams it is possible to find *Ranunculus peltatus* on sandy or muddy bottom. In some places in the litoral zone there is a dense vegetation dominated by *Nuphar luteum, Potamogeton natans, Equisetum fluviatile* and *Comarum palustre*.

From the turn of the century the river has been exploited for hydro-electric power production. Dams have been built in Robertsfors (Hammarforsen, Sågforsen and Fredriksfors), at the outlet from Lake Bygdeträsket and in some tributaries to this lake. These impoundments have, however, a comparatively small influence on the natural flow of water in the river.

The mean water discharge is 16 m^3/s, but varies from about 3 m^3/s during low water conditions to

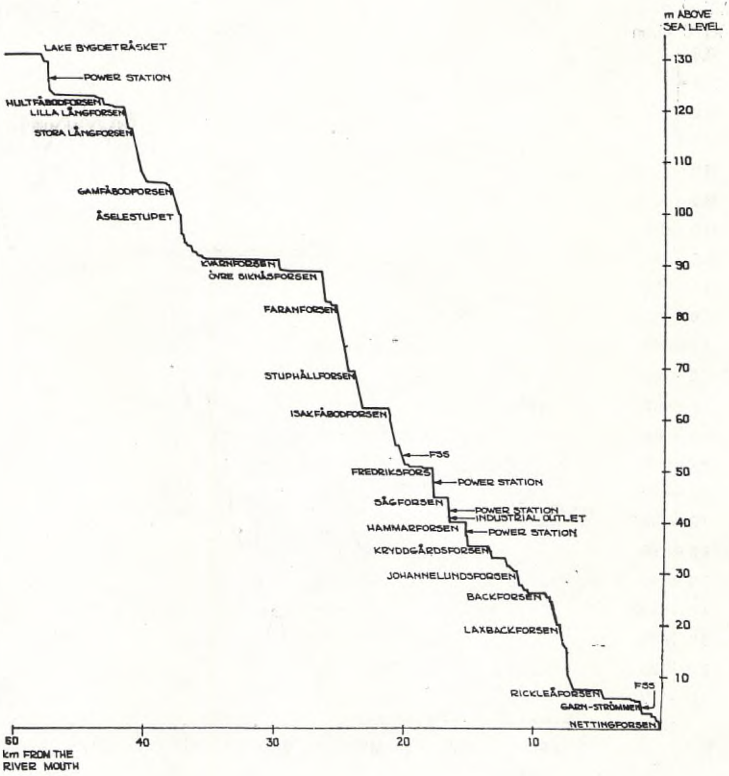

Fig. 2. Height of fall of different rapids in the Rickleå river. Fors = Rapid, Lax = Salmon, Netting = Lamprey. FSS = Fontinalis Sampling Station.

160—180 m^3/s during maximum spring flood (U KARLSTRÖM 1973).

Water level measurements at the Rickleå field station (situated at the rapids Netingforsen near the river mouth) show that spring flood normally peaks in the latter half of May or the beginning of June. Low water lasts from July to October (Fig. 3). The maximum waterlevel amplitude is about 1.5 m. Floods in summer and autumn caused by heavy rainfall rarely occur.

The river is covered by ice for five to six months. In the slow streams the ice cover can become thick, about 1.5 m. In the rapids, however, some midstream areas are always open. The break-up of the ice occurs during the end of April or the beginning of May. The water temperature rises rather slowly in May under high water conditions (Fig. 3). In June the water becomes warmer as the water level goes down. The highest water temperatures are reached in July. Beginning in August, the temperature falls in a rather uniform pattern until the ice starts to cover the river in October or November. Anchor ice often exists in large amounts in November.

The pH is about 6.5 and the brownish water is fairly rich in humic content and iron.

3. THE SALMON POPULATION

3.1 *Introduction*

The Rickleå River is, of course, not a pure salmon river. As is shown in Table 1 nineteen fish species are known from the river. The species of economic importance are: salmon, trout, grayling, whitefish, pike, burbot and river lampreys.

The most valuable fish, however, is the salmon, *Salmo salar* L. The Rickleå river was documented as a rich salmon river as early as the 15th century. The industrial development has narrowed the living space of the species considerably. In the period between 1899 and 1937, three hydro-electric power stations were built in Robertsfors. Since no fishways were built, the dams have ex-

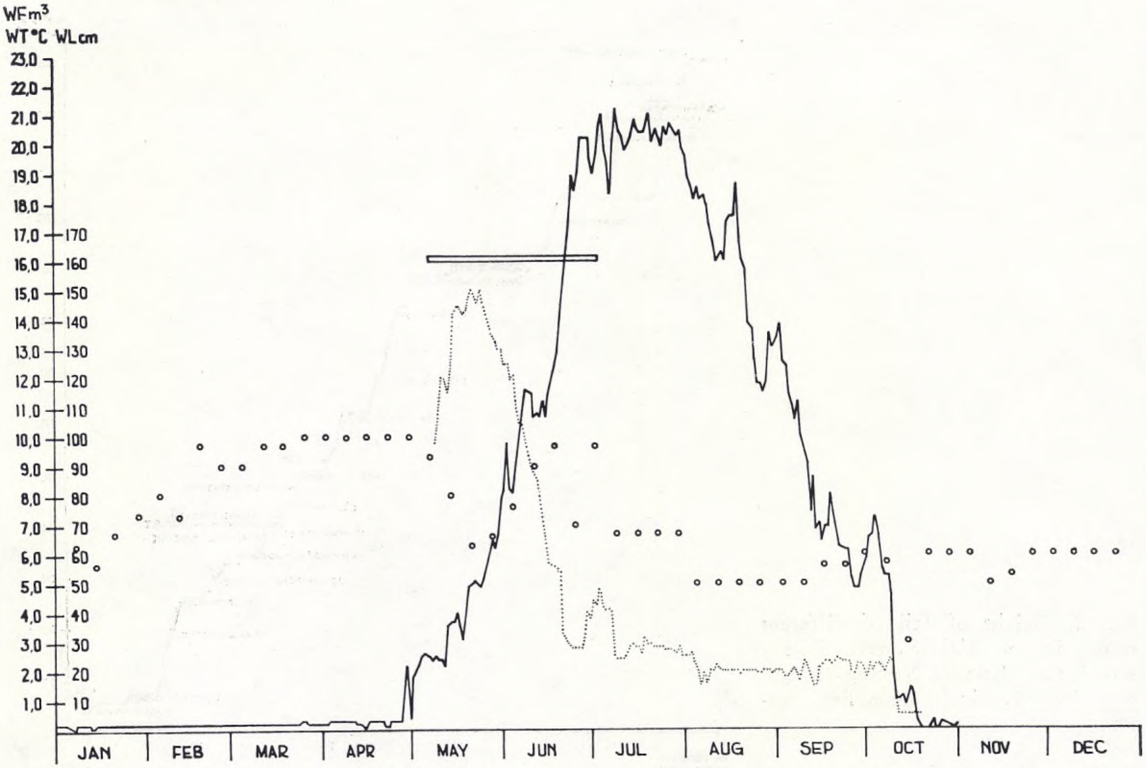

Fig. 3. Water temperature (solid line), water level at the Rickleå Field Station (dotted line) and estimated flow through the turbines in Robertsfors (open points) in 1973. The double line indicates the time for water going over the power dams.

Table 1. *List of fish species known from the Rickleå river.*

Salmon	*Salmo salar* L.
Brown trout	*Salmo trutta* L.
Whitefish	*Coregonus lavaretus* L.
Cisco	*Coregonus albula* L.
Grayling	*Thymallus thymallus* L.
Pike	*Esox lucius* L.
Roach	*Rutilus rutilus* L.
Dace	*Leuciscus leuciscus* L.
Ide	*Leusiscus idus* L.
Minnow	*Phoxinus phoxinus* L.
Bream	*Abramis brama* L.
Eel	*Anguilla anguilla* L.
Burbot	*Lota lota* L.
Perch	*Perca fluviatilis* L.
Sculpin	*Cottus gobio* L.
Three-spined stickleback	*Gasterosteus aculeatus* L.
Ten-spined stickelback	*Pungitius pungitius* L.
River lamprey	*Lampetra fluviatilis* L.
Brook lamprey	*Lampetra planeri* L.

cluded the salmon and other anadromous fishes from the larger part of their original spawning area. The part now accessible to the salmon is 15.1 km long and has an area of about 0.65 km².

Between 1904 and 1948, when a sulphite mill was working in Robertsfors, floating dead fish were often observed. Live fish caught often had a bad taste and smell. Since 1948 the salmon and other fish species have reestablished. The lower parts of the Rickleå river were again regarded as highly productive for salmon and trout.

3.2 *The salmon migration*

Between 1960 and 1967 the Swedish Salmon Research Institute performed investigations concerning the salmon population in the river. In 1960 a fish trap was built in Nettingforsen, a short distance from the mouth of the river. The smolt or "downstream" trap, Wolf-type (Wolf 1950), consisted of five 5×5 m horizontal grids capable of handling the whole volume of water except during maximum high water. The spacing of the grids was about 12 mm and permitted the smaller

Table 2. *Operation time and salmon catch in the Rickleå fish trap in the years 1961 to 1967. (Data from Österdahl 1962, 1963, 1964 b, 1965, 1966 and personal communication.)*

Year	Upstream trap		Dowstream trap		
	Operation time	Adults	Operation time	Smolts	Kelts
1961	10/6— 2/10	875	29/4— 6/ 5 31/5— 2/10	3,261	30
1962	16/6—26/ 9	188	22/5—26/ 9	3,100	9
1963	14/6—23/ 8 25/8— 2/10	78	16/5—23/ 5 26/5— 3/ 8 28/8—23/ 9 27/9— 2/10	3,200 [1] (2,910)	12 (4) [3]
1964	7/6— 4/10	48	18/5— 1/ 8	3,122	17(5) [3]
1965	14/6— 8/10	73	18/5— 8/10	3,560	10 (3) [3]
1966	14/6— 8/10	65	2/6— 8/10	585	0
1967	14/6—31/ 6 10/7— 1/ 9	27	14/6—30/ 6	200 [2] (97) [2]	0

[1] Estimated number. The actual catch was 2,910. The trap was not in operation in two days during the smolt run, justifying an addition of about 300 smolts.

[2] Estimated number. The actual catch was 97. The trap was not operating during the whole smolt run and in the first week of operation the trap did not work satisfactorily.

[3] Numbers between brackets stand for kelts tagged as upstream migrating spawners the previous year.

fishes to go through. Tests showed that 50 per cent of the salmon smolts in the length class 130—145 mm were caught; for smolts above that size the figure was 90 per cent.

The Rickleå fish trap was built primarily to catch wild salmon smolts for tagging in order to make comparisons with hatchery smolts. The tagged wild smolts were released together with 1,000 tagged hatchery smolts each year. The research plan also included general studies on the freshwater biology of salmon and trout. Data concerning other fish species were also collected (ÖSTERDAHL 1964 a).

Salmon, sea trout, and other fish species coming up the river were caught in a special "upstream trap" in connection with the smolt trap (ÖSTERDAHL 1964 a).

Most of the adult salmon were sold on the fish market, but tagged spawners were released to insure reproduction in the river. The upstream trap was removed in late autumn, making it possible for late migrants to go upstream to spawn. The fact that non-tagged kelts were caught in the "downstream trap" indicates that some salmon used that possibility.

The catch of salmon in the two traps is shown in Table 2. During the investigation period there was a considerable variation in the number of salmon caught in the "upstream trap". The catch was very big in 1961, but much smaller in the following years. The reasons for this are not known, but it is a well-known fact that the success in fishing for salmon in northern Swedish rivers varies from year to year. In 1961 the catch was also extremely high in other rivers. So, even if the numbers are astonishingly different, there is no reason to believe that the variation was unnatural.

According to ÖSTERDAHL (1969), the time for the salmon smolt migration was influenced by water temperature and water level in the river. The smolt run started in the latter half of May and lasted until the beginning of July. Most salmon smolts were caught in June.

About 75 per cent of the salmon smolts were 3 years old, 25 per cent 2 years, and very few 4 years (ÖSTERDAHL 1964 a).

Between 1961 and 1966 the smolt trap was used during almost the whole period of salmon smolt migration. The numbers given for salmon

Table 3. *Estimated number of fish per 100m² in two rapids in the Rickleå river in 1963—65. ——=Numbers not estimated. (From Karlström 1972.)*

Locality	*Salmo salar*	*Salmo trutta*	*Cottus gobio*	Other species
Nettingforsen	11.7	1.5	—	—
Laxbacksforsen, lower area, right side	7.7	0.3	79.2	3.4
,, , ,, ,, , left side	6.2	0.3	78.0	5.2
,, , upper area, right side	11.5	0.4	45.4	2.7
,, , ,, ,, , left side	11.1	0.8	25.5	9.0

smolts are, therefore, very accurate. The annual production of salmon smolts has been estimated to be between 4,000—5,000. The estimates are based on the catches from 1961 to 1965 and tests of the escape of small-sized smolts through the trap (Österdahl 1969). The smolt catches in those years were similar and indicate that the production of salmon smolts was nearly constant from year to year.

The number of sea trout smolts was more variable during the same years, ranging between 46 and 102. Based on taggings, the production of trout smolts has been calculated to be between 300 and 400. The escape of trout smolts was high, probably due to the fact that many trout smolts migrate before the smolt trap was set up in the spring.

Knowing the stability in numbers of salmon smolts from previous years, the very low catch in 1966 was astonishing. Only 585 specimens were caught, about one fifth of the expected number. There seemed to be no natural explanation for this.

The Swedish Salmon Research Institute finished its research program in the River Rickleå in 1966. To determine if the result from 1966 was a solitary event, the smolt trap was used during a shorter period in 1967. Beginning the 14th of June, the smolt trap was operated until the end of the smolt run. During that period only 97 salmon smolts were caught, showing that the total catch would not be much more than 200 if the trap had been used as long as it had in previous years. The 1966 finding was, evidently not a solitary event.

3.3 *Density of salmon and trout parr*

The fish populations in the rapids was first studied by Karlström (1966 and 1972) In 1963 he started electro-fishing in order to investigate the densities of salmon and trout parr. Some data from his investigations in 1963—65 are given in Table 3.

The dominant fish species numerically was the sculpin (*Cottus gobio* L.). The density of the species was high in comparison with other northern rivers in Sweden. Salmon parr were much more abundant than trout parr. Karlström claimed that the density of salmon and trout parr was 2—3 times greater here than in other northern rivers studied. The group, "other fish", was dominated by small graylings and minnows.

Table 3 also shows that fish density varied between different rapids and even within different parts of the same rapid. This is to be expected from the heterogeneity of the river bed.

The reduced catches of salmon smolts in the fish trap in 1966 and 1967 caused Karlström to repeat his electro-fishing in 1966 and 1969. In Table 4 density values over five years are given. The decrease in density during the period 1963—69 is drastic. In the rapids Laxbacksforsen, reduced densities were already recorded in 1965, which agrees with the fact that the number of smolts trapped in 1966 was small.

Unfortunately, there is no longer any monitoring of the smolt run. Karlström has not had the opportunity to closely follow the parr population since 1969. There is, however, information from other sources. Helped by colleagues at the field station, I have tried to estimate the parr population at two times. The first sampling was in October 1971 in the same areas of Laxbacksforsen previously investigated by Karlström. During two days of electro-fishing with a total of seven hours, effective time, over an area of 2,700 m², not a single salmon or trout parr was captured; sculpin, grayling, minnow, burbot, and pike, were how-

Table 4. *Estimated number of salmon and trout parr per 100 m^2 in three rapids in the Rickleå river in 1963—69. — =No fishings were made (From Karlström 1972.)*

Locality	1963 August	1964 August	1965 September	1966 July	1966 October	1969 October
Nettingforsen	15.9	10.3	13.4	—	—	7.8
Laxbacksforsen, lower area	8.6	7.4	5.4	1.9	1.5	0.7 [1]
„ , upper area	14.2	12.5	6.9	2.3	1.1	—
Kryddgårdsforsen	—	—	4.6	—	—	0.8 [2]

[1] Only trout parr.
[2] Only salmon parr.

ever, caught. The conclusion was that the population of salmon and trout parr had decreased to an extent that it was not possible any longer to work out reliable numbers of density.

The next sampling was made in October 1973 in Laxbacksforsen. After fishing an area of 1,960 m^2 one underyearling of salmon parr was caught. Electro-fishing was also conducted in Nettingforsen in October 1973. Some trout were caught here but no salmon parr.

The results from the investigations in 1971 and 1973 show that no recovery of the salmon parr population has occurred. On the contrary, the juvenile salmon population has continued to decline and seems to go to its complete extinction.

Several zoologists have performed electro-fishings in the lower part of the river in the years 1970—73. The purposes of their sampling have been different, but as a rule all fish caught have been noted even if the investigator has not been interested in all species caught. This gives an opportunity to illustrate the fishfauna in the rapids during these years. A summary of these data is given in Table 5.

The proportion of different species ($^0/_0$) during the period has been calculated, and the results can be compared with the corresponding values for 1963 (Table 6). Some reservations must be made, as the sampling conditions were not quite the same. In 1963 the investigations were conducted by the same man using one kind of fishing gear. In the later period several investigators were involved, and different machines have been used. It is, therefore, not possible to draw any definite conclusions based on small differences. Two features are, however, clear: the decreasing of the salmon and the relative increasing of sculpin.

Trout parr did not decrease in relative abundance in the way that did salmon parr. Besides a possible less sensitivity to the pollution, which will be discussed later, the comparison between the two species may be baised for the following reasons:

1. In the areas above Robertsfors there is a natural population of trout. Some trout may have been swept down or migrated downstream to colonize the polluted area.
2. In the later half of October 1971 about 2,500 reared 0+ sea trout parr were released in the area. The yearlings were not marked and some of the later catches may have been influenced by this stocking. In November 1971, for instance, one trout parr of the same age was caught in Laxbacksforsen in spite of the fact that no parr were caught in the rapids by the big fishing effort in the middle of October the same year.
3. In Nettingforsen reared sea trout smolts have been released in 1972 and 1973 in order to improve the fishing for sea trout. These smolts were marked by finclipping before the stocking and some have been recaptured by electro-fishing in the same area. So, in October 1972, two out of seven trout caught were marked and in October 1973, seven out of thirteen.

It is, of course, of interest to know if spawning of salmon is still a regular event in the river. In Table 7 the salmon parr caught during the last

Table 5. *Results of electro-fishing in rapids below Robertsfors in the years 1970—73.*

Locality	Date	Fishing area m²	Fishing time minutes	*Salmo salar*	*Salmo trutta*	*Thymallus thymallus*	*Coregonus lavaretus*	*Cottus gobio*	*Phoxinus phoxinus*	*Lota lota*	*Gasterosteus aculeatus*	*Pungitius pungitius*	*Esox lucius*	All species
Nettingforsen	16/ 7-71	150	45	1	1	19	0	29	0	30	33	0	0	
	23/ 7-71	320	60	0	1	12	0	45	12	1	38	1	0	
	17/10-72	?	?	1	7	0	0	54	0	0	0	0	0	
	26/ 6-73	?	?	0	5	0	0	69	0	0	0	0	0	
	12/10-73	400	60	0	13	0	4	36	0	0	0	0	0	
Garnströmmen	30/ 6-70	240	50	0	0	0	0	10	5	0	10	0	0	
	25/ 8-70	225	50	0	0	0	0	38	0	1	1	0	4	
	19/10-70	170	35	1[1]		1	0	28	0	1	0	0	0	
Laxbacksforsen	29/10-70	300	45	6	0	1	0	59	0	0	0	0	1	
	22/ 6-71	400	60	1	0	0	0	186	7	1	0	0	0	
	20/ 7-71	200	45	0	2	2	0	39	2	0	0	0	0	
	26/ 7-71	?	45	1	1	3	0	52	5	0	0	0	0	
	13/ 9-71	?	80	0	1	0	0	116	31	0	0	0	1	
	1/10-71	2160	350	0	0	6	0	814	14	2	0	0	1	
	14/10-71	650	93	0	0	0	0	183	3	0	0	0	1	
	5/11-71	275	60	0	1	1	0	57	0	0	0	0	0	
	17/10-72	?	?	3	1	0	0	209	52	0	0	0	0	
	18/10-72	?	?	0	10	0	0	80	20	0	0	0	0	
	12/10-73	1960	55	1	0	3	0	85	4	2	0	0	0	
Johannelunds-forsen	7/ 6-70	270	30	0	0	0	0	13	2	1	0	0	0	
	17/ 6-71	240	60	0	0	0	0	12	2	1	0	0	0	
	18/10-72	?	?	2	8	0	0	30	8	0	0	0	0	
Total				17	51	48	4	2244	167	10	82	1	6	2630
Per cent				0.65	1.94	1.83	0.15	85.32	6.35	0.38	3.12	0.04	0.23	100.00

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[1] Species not known, salmon or trout. In total counted as salmon.

Table 6. *The proportion (⁰/₀) of different fish species captured by electro-fishing in 1963 (Karlström 1966) and 1970—71 (Table 5).*

Species	1963	1970—73
Salmo salar	23	0.6
Salmo trutta	1	2.0
Thymallus thymallus	3	1.8
Phoxinus phoxinus	10	6.4
Cottus gobio	63	85.3
Other species	< 1	3.9
Total	100	100.0

years have been sorted into length classes. Judgying from the length, yearlings are known from 1970, 1971 and 1973. This proves that salmon must have spawned in 1969, 1970 and 1972. The spawning in 1971 is not documented because 0+ parr have not been found in 1972 and 1+ parr were not found in 1973. In investigations performed in September 1974 0+ and 1+ salmon parr have also been found in Laxbacksforsen, which confirms that spawning occured in 1972 and also in 1973. So, in four out of five years spawning of salmon is documented, and occurs more as a rule than an exception. The number of surviving offspring is, however, low in spite of the huge reproductive potential of the species.

3.4 *Food of salmon parr*

The feeding behaviour of salmon and trout parr is well known. The fact that parr are driftfeeders was recorded already by Norbäck (1884). Later investigators have confirmed this opinion (Müller 1954, Nilsson 1957 and Kalleberg 1958).

The seasonal feeding of salmon parr has been described by Carpenter (1940). In winter they feed only sparsely and intermittently. When spring comes they start to eat steadily and vigorously. In summer the feeding will cease on warm days. In autumn the feeding activity is also rather low. Carpenter claimed that this seasonal cycle was dependent upon the life histories of the various food organisms, which determine their availability to the fishes.

It is reasonable to belive that the population in the River Rickleå behaved in the same manner as some salmon smolts showed rapid growth in spring (Österdahl 1969).

Table 7. *Length and supposed age of salmon parr captured by electro-fishing in the years 1970—73.*

Length mm Supposed age	< 90 0+	91—150 1+	> 150 2+ or older	Unknown
1970	5	0	1	0
1971	1	0	0	2
1972	0	4	2	0
1973	1	0	0	0

In the literature there is much information given concerning the qualitative composition of the diet of salmon parr. Alm (1919) claimed that *Ephemeroptera* were the most important food of the parr. According to Maitland (1965) the most important groups are: Ephemeroptera (40 per cent by bulk), Diptera (20 ⁰/₀), *Plecoptera* (12 ⁰/₀) and *Crustacea* (10 ⁰/₀). For the present investigation it was important to gather information of the diet of salmon parr from the Rickleå especially during spring when they seam to eat most actively.

For that purpose Dr Östen Karlström has kindly provided material. He performed electrofishings in Laxbacksforsen on two occasions in April 1964. On the first occasion 17 April the ice in the rapids had just begun to break, giving the first chance for fishing. On the second occasion, 25 April much of the ice in the slow streams was gone.

In sum, 41 parr were collected and preserved in formaldehyde. When I recieved the specimens, the lengths and weights were determined. Fishes of 67 to 90 mm in length must be one year old parr, 104—129 mm two years old and 134—172 mm three years or possibly older.

In determining the stomach contents, all food above the pylorus was considered. There were no difficulties to determine the kinds of animals. Eight of the 41 fishes had eaten the worm *Eiseniella tetraedra*. The worms were not enough intact to calculate their number.

The number of food objects from parr caught on the earliest occasion was very low. The number of empty or almost empty stomachs was high. It was also noticed that many of those stomachs

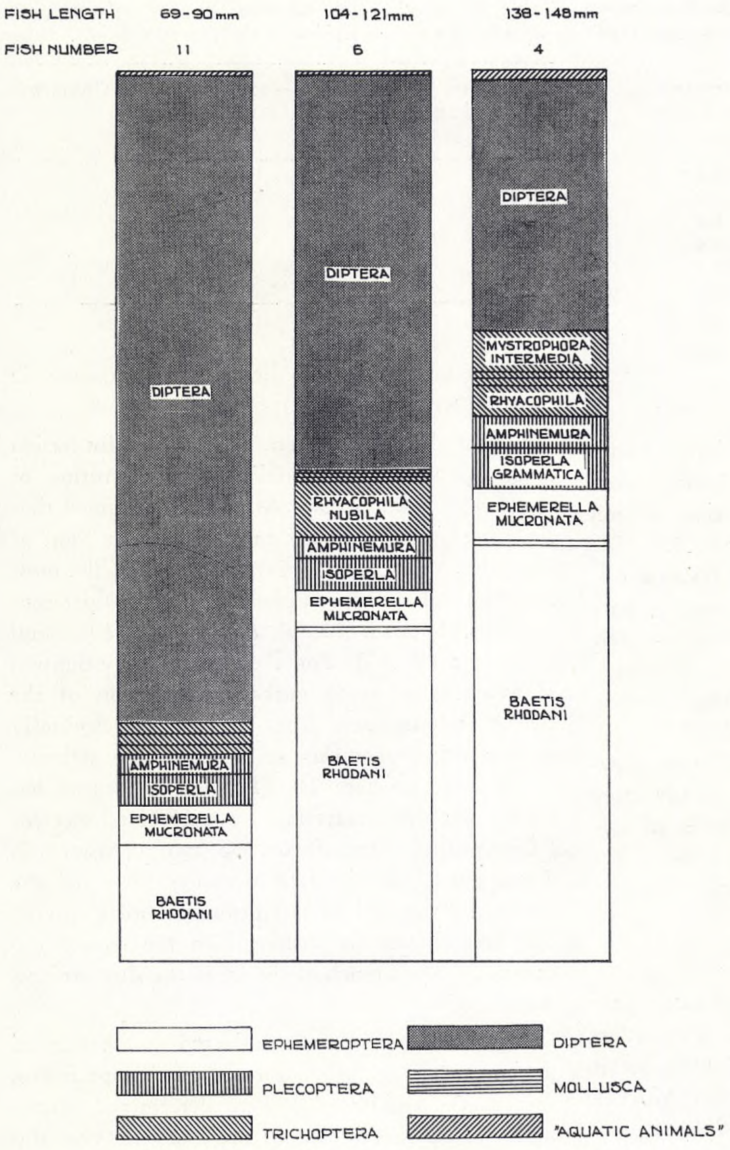

Fig. 4. The shares of different food items in per cent of total numbers in stomachs of salmon parr from Laxbacksforsen 25 April 1964.

appeared atrophied and had a narrow lumen. Fishes sampled one week later had eaten great numbers of insects and their stomach lumens were dilated. The increase in number of food objects was more than tenfold, and the number of empty stomachs was very low. This indicates that the feeding of salmon parr rapidly increases when the ice disappears.

The qualitative stomach content composition in fishes caught on 25 April, 1964, is shown in Fig. 4. Among small parr, chironomid larvae dominate numerically; in older parr, ephemeropteran nymphs dominate. During the evaluation of the data, it was noted that there was considerable variation in size among different kinds of food organisms. To get a better idea of the relative importance of different food species the following procedure was performed. Undamaged individuals of the different species were sorted out, dried in a desiccator over silica-gel for 48 hours, and their

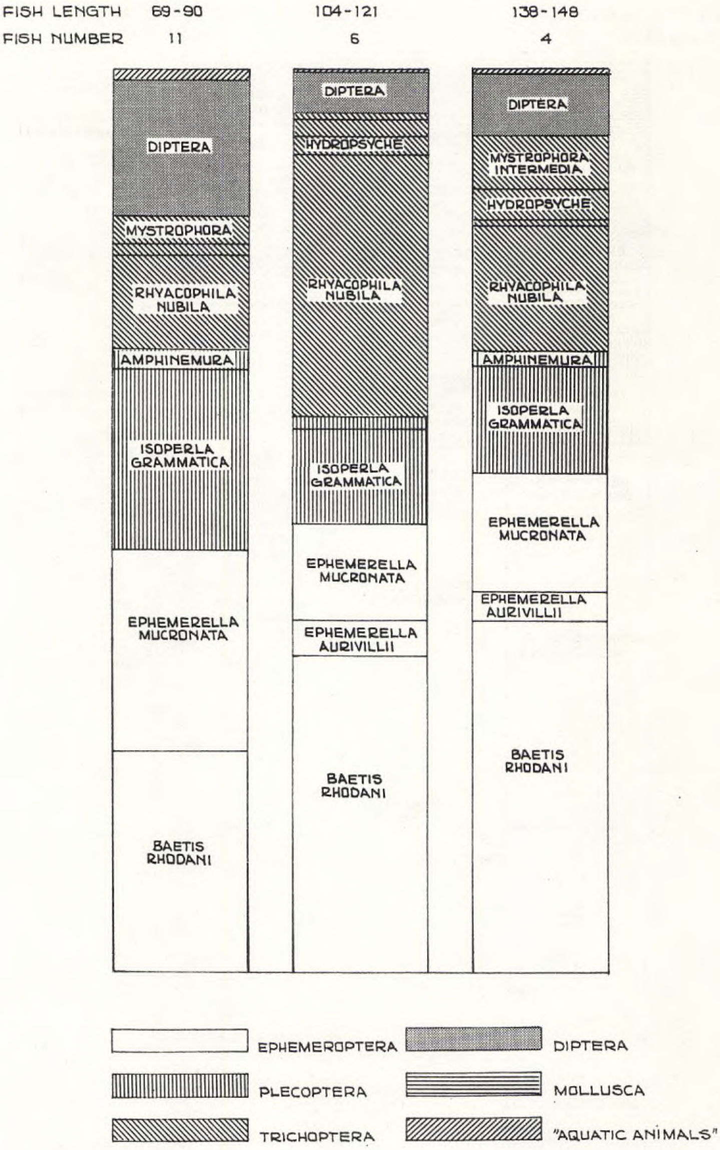

Fig. 5. The shares of different food items in per cent of total dry weight in stomachs of salmon parr from Laxbacksforsen 25 April 1964.

dry weights determined. Knowing the mean weight of undamaged individuals and the total number of individuals, it was possible to calculate the percentage of each food kind based on dry weight. The results are shown in Fig. 5.

Based on weight, the chief food organisms are *Ephemeroptera*, *Plecoptera* and *Trichoptera*. The Diptera are less important. At this time of the year *Ephemerella mucronata*, *E. aurivilli* and *Isoperla grammatica* are large nymphs. This explains their large share of the total weight, although there are few in the stomachs. *Baetis* nymphs, however, occur in all sizes in the river at the same time. When the body length of undamaged *Baetis* nymphs in the stomachs was measured it was shown that the most frequent length group was 6—7 mm and that nymphs less than 2 mm was not found. Apparently the parr selects the larger individuals.

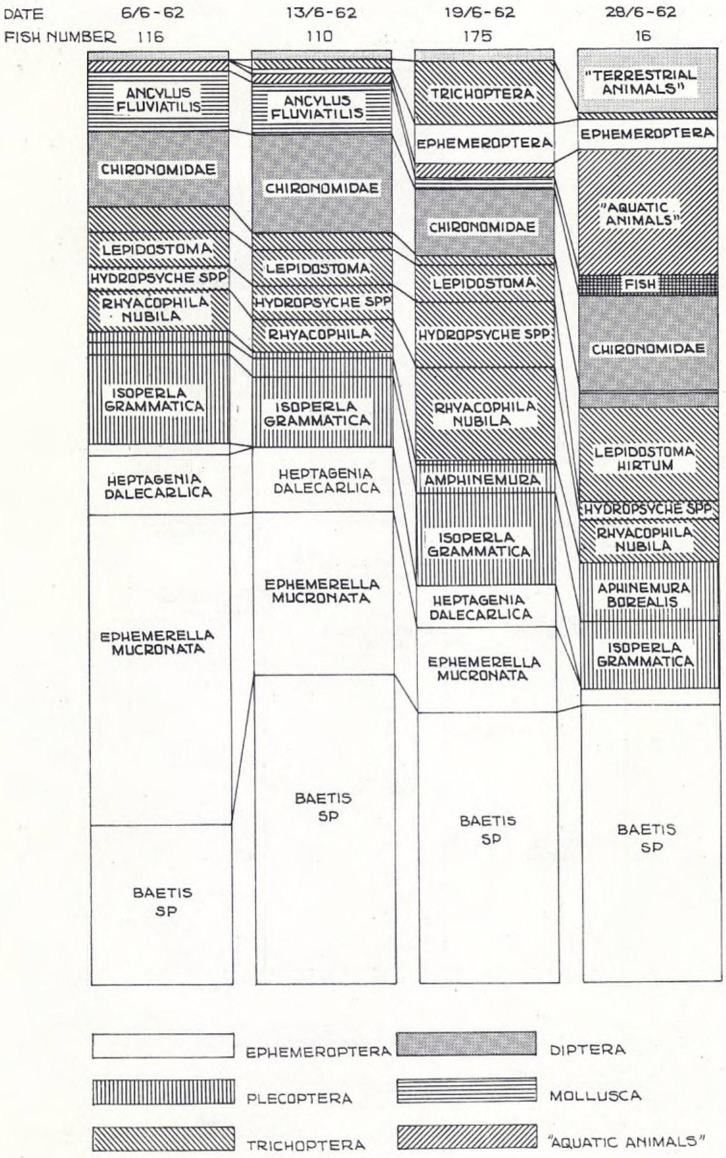

Fig. 6. The shares of different food items in per cent of total numbers in stomachs of salmon smolts from four samples during the smolt migration 1962.

3.5 *Food of salmon smolt*

According to Mills (1964), the food of salmon smolts does not differ much from the food of salmon parr. Therefore knowledge of the food of salmon smolt would give some information on the diet of salmon parr at the same time of the year. The stomach content of 417 salmon smolts from the Rickleå sampled at four occasions during the smolt run in June 1962 has previously been studied (Södergren and Österdahl 1965). From this study it is known that salmon smolts eat during the migration; only 2 % of the stomachs analysed were empty. During the migration period the volumes of the stomach content decreased, probably indicating that there was more food available during the beginning of the migration.

The qualitative composition of the food is given in Fig. 6. The similarity to the food of parr is great. Numerically *Ephemeroptera* nymphs are dominant. Calculations of the volume of the food items showed that mayfly nymphs formed about 64, 62, 40 and 39 per cent of the stomach content on the different sampling days. Two important species, *Ephemerella mucronata* and *Heptagenia dalecarlica*, decrease in numbers in the stomachs during the migration period. This is a reflection of the fact that the nymps become mature in the early summer and emerge as subimagines. On the other hand imagines of *Ephemeroptera* and *Trichoptera* and subimagines (top of figure) become more abundant in the food. Terrestial animals are only eaten to any extent towards the end of June. The relative stability in numbers of *Baetis* nymphs is probably due to the fact that the summer generation of nymphs in the river compensates for the emerging of the winter generation.

The most important food for salmon parr and smolt in the Rickleå river are mayfly nymphs. *Plecoptera* and *Trichoptera* are also important but not to the same extent. Therefore when later the ecological effects of the pollution will be considered the relations between pollution, mayflies and salmon will be stressed.

The food of salmon smolts caught in the fish trap in 1967 has also been studied. There were no significant differences in stomach content of those fishes and those trapped at the same time in 1962 (SÖDERGREN 1972).

4 THE INVERTEBRATE FAUNA

4.1 *Introduction*

The decrease of the juvenile salmon population indicated a pollution in the river. It became urgent to study if the food organisms of the parr had also decreased.

In the rapids Garnströmmen drift studies had been conducted in June 1963 (SÖDERGREN 1963) and 1964—64 (SÖDERGREN 1971). It was shown that mayfly nymphs constituted a major part of the drift, as in the food of the salmon parr. At the same occasions also qualitative *Fontinalis* samples were taken.

4.2 *The organic drift*

In order to make a detailed study of the diel drift of mayfly nymphs and subimagines a driftsampler was set up in Laxbacksforsen in spring 1969. The apparatus was of the kind described by MÜLLER (1965). The number of insects was low and the catch of mayflies was so small that it was not possible to carry the investigation out, although much time and money had already been invested. Additional information concerning the nature of the pollution was, however, gained.

Table 8. *Number of insects per 100 m^3 water caught in drift samplers in Isakfäbodforsen and Laxbacksforsen June 11—12, 1969.*

	Isakfäbod-forsen	Laxbacks-forsen
Ephemeroptera, nymphs	794	0
Plecoptera, nymphs	72	74
Trichoptera, larvae	72	55
Coleoptera, larvae	181	37
Simuliidae, larvae	542	9
Total	1,661	175

A clear decrease in the amount of drifting insects in 1969 was noted in comparison with 1963—65. To know if the conditions were different above the industries in Robertsfors, a similar, but not automatic driftsampler was set up in the rapids Isakfäbodforsen. At both places the water was taken through siphon tubes placed on similar locations in the rapids. The water leaving the lower end of the tubes had to pass sieves (meshsize 0.7 mm) where the animals were collected. The flow of water through the tubes was calculated on the time for filling a 15 l bucket. The sampling was started at 18.00 the 11th of June and ended at 06.00 the following day. The number of insects was later determined in the laboratory. Chironomid larvae were numerous at both places but not counted. The results are shown in Table 8.

This small investigation gave a clear picture of the differences between the two stations. The total catch was almost ten times higher at Isakfäbodforsen. The dominating group at Isakfäboda, mayfly nymphs, was totally lacking in the samples from Laxbacksforsen. The difference in amounts of blackfly larvae was tremendous. Concerning other insect groups the numbers were rather similar.

The first drift investigations in the Rickleå river

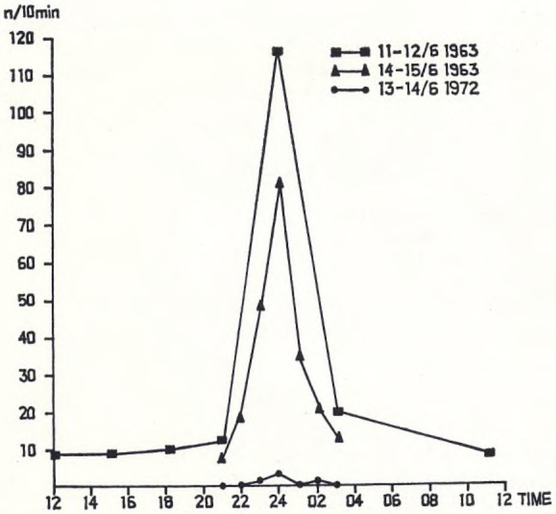

Fig. 7. Number of drifting *Ephemeroptera* nymphs per 10 minutes sampling with simple drift nets in Garnströmmen in the middle of June in 1963 and 1972.

were performed in Garnströmmen in the middle of June 1963 (Södergren 1963). At that time the drift was sampled in drift nets put out in the stream. The nets had a square aperture measuring 200×200 mm and were about 500 mm long. The mesh size was 0.7 mm. The sampling time was usually 10 minutes and the nets were set out just below the water surface. The method will here be referred to as method 1. As is shown in Fig. 7, there was a considerable diel variation in the drift of mayfly nymphs. In daytime the catch was about 10 nymphs, during the darkest period of the night, however, the drift increased about ten times.

In order to get information concerning the drift in Garnströmmen in later years, the sampling was repeated in the same way, on the same spot, and at the same time of the year in 1972. As shown in Fig. 7 the result was that no drift of nymphs could be detected during daytime and in the night the drift was about fifty times smaller than nine years before.

There are also values concerning the drift *in* Garnströmmen from the years 1964 and 1965. In these years, however, the sampling was made in a somewhat different way (Södergren 1971). The same kind of drift-nets as before were put in a steel cylinder with a device for measuring the water flow through the nets. The number of animals caught were related to the amount of water filtered. The method will be referred to as method 2. The sampling time with the apparatus was usually 55 minutes. The catches by using the apparatus can, of course, be related to the sampling time, and the catch per 10 minute samples can be calculated.

As has been shown earlier (Södergren 1971) there are big qualitative and quantitative differences in the drift of mayfly nymphs at different times of the year. In June, for instance, the winter generations of mayfly nymphs are dominant in the drift before their emergence. In the beginning of July and later, summer generations dominate. In comparing the drift of different years one must, therefore, be careful that the samples are taken at the same time. In Fig. 8 the results from sampling in the middle of June is given to the left and samples from the beginning of July is given to the right.

Regardless of the methods the drift of mayflies was much lower in 1971 and 1972 than before. This concerns both the drift in June and the drift in the beginning of July. A deterioration since 1965 is certain. Higher maximum values during the night have been obtained at the earlier sampling occasions than those later in June. This may be because the winter generation is emerging and that the nights are lighter on the later occasion. In June, as a whole, lower drift-values were achieved in 1965 than in 1963. It is probable that this is an indication that the pollution had already influenced the mayfly fauna in 1965. The drift of mayfly nymphs probably started to decrease at approximately the same time as the parr population was reduced.

Drift investigations were not made in the years 1966—68. The rate of the impairment of the drift is now not known. Since 1969, however, it is certain that low drift of mayfly nymphs is a very characteristic feature of the impairment of the river.

4.3 *The Fontinalis fauna 1964—73*

No quantitative bottom-fauna sampling was conducted in the years when salmon parr were still

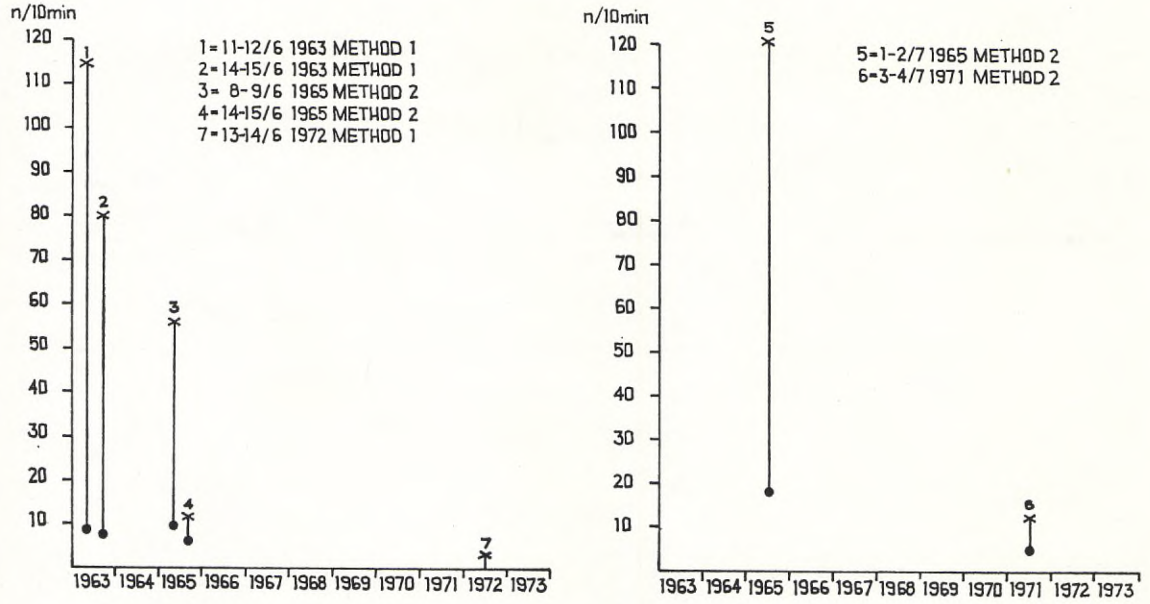

Fig. 8. Number of drifting *Ephemeroptera* nymphs per 10 min sampling with drift nets in Garnströmmen at seven occasions. Samples taken in June to the left and samples taken in the beginning of July to the right. Mean values during daytime . and maximum values during the nights ×.

abundant in the river. At the time of drift sampling in Garnströmmen in 1964 and 1965 *Fontinalis* tufts were often collected and analysed for dominant species. The tufts were studied in the field and some specimens of each species were sorted out and preserved. This material has now been re-evaluated to get information about the presence or non-presence of important salmon food insects. These samples were not quantitative in the way the moss samples taken in 1969 and later were. In the qualitative sampling the total number of the different species was not determined and the weight of the moss samples was not measured.

As the tufts collected were about the same size, there are some possibilities to perform a rough frequency analysis. The qualitative samples were sorted in the field, but the quantitative were treated in another way in the laboratory. Small individuals easily detected with the aid of a stereomicroscope in the quantitative samples could have been lost in sorting of qualitative samples in the field. If only samples taken at a time of the year when nymphs more than two millimetres long are taken into account a comparison is relevant.

For five insects the proper time of sampling has been determined. The times are given in the Figs 9, 10 and 11. The life-cycle of mayflies belonging to the genus *Baetis* is not completely known, but it is reasonable to believe that at least *Baetis rhodani*, the most common species, has two generations per year. Normally *Baetis* nymphs of different sizes occur at all times of the year, indicating that the generations to some extent are mixed. However, if only nymphs of the size class 2 mm are plotted in a frequency diagram it is probable that a "winter" and a "summer" generation will be seen graphically.

For both qualitative and quantitative samples the presence or absence of the different species has been noted. Only samples collected below Robertsfors have been taken into account and most of the samples were taken in Garnströmmen.

The mayfly, *Ephemerella mucronata*, was a frequent species in Garnströmmen in 1964 and 1965 (Fig. 9). In June 1969 it was not found any more. The population seems to have dropped down to zero in a few years. Moss samples were not taken in 1966, 1967 and 1968. The species was, however, found in stomachs of salmon smolts

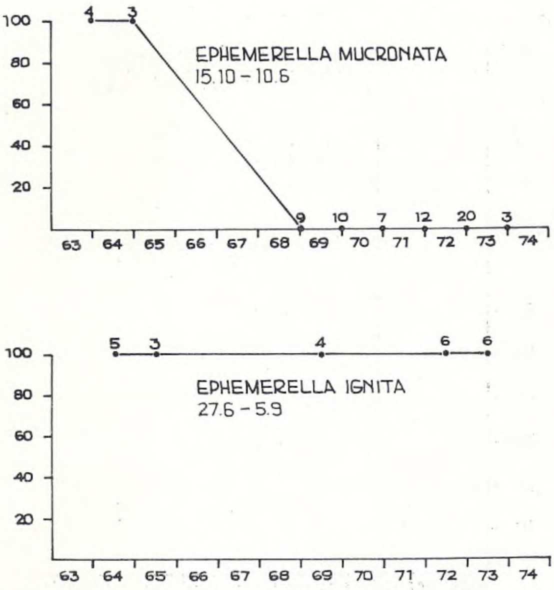

Fig. 9. The frequency, per cent, of *Fontinalis* samples containing big *Ephemerella* nymphs in 1964—73. Samples below Robertsfors.

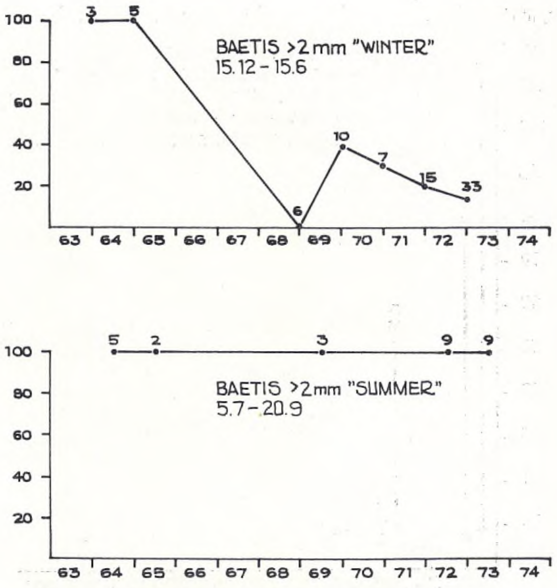

Fig. 10. The frequency, per cent, of *Fontinalis* samples containing big *Baetis* nymphs in 1964—73. Samples below Robertsfors.

in 1967 (SÖDERGREN 1972). For growth studies nymphs were sampled in the neighbourhood of the Rickleå Field Station in 1967 and 1968 (BENGTSSON 1968) but at that time the species was pretty hard to find.

In contrast to *E. mucronata* the "summer species" *E. ignita* seems to be as frequent as before. This species is very similar to the former and the only big ecological difference seems to be that it is growing in the summer.

The same phenomenon is shown by the *Baetis* nymphs. The 'winter generation' has become less frequent in later years in spite of the frequent occurrence of the 'summer generation' (Fig. 10).

In Fig. 11 the corresponding values for three common *Plecoptera* are given. A decrease in frequency is shown for *Isoperla grammatica* already in 1965. In later years the frequency is regularly so low that natural fluctuations can be excluded. *Protonemura meyeri*, which seems to be less important to the salmon, is still frequent even if some decline is recorded during the later years. The results concerning *Amphinemura borealis* are in contrast to the other species. This stonefly seems to have become more frequent with time. The number of relevant samples in 1963—64 was, however, small.

Frequency analyses of species important to the salmon in the *Fontinalis* samples show that drastic changes have occurred in the fauna. *Ephemeroptera* have been more harmed than *Plecoptera*, a phenomenon that was also illustrated by the drift investigations. Among the *Plecoptera*, *Isoperla grammatica* has been influenced more than the two nemurid species. Mayflies with a winter generation are much more influenced than the summer mayflies.

5 THE RIVER POLLUTION

5.1 *Introduction*

The biological investigations indicate that the river was polluted and that the pollution had started in the middle of the 1960's, probably in the community of Robertsfors. The symptoms suggest that toxic substances were released.

The community of Robertsfors, with about 1,800 inhabitants, had no purification plant before 1972. Small communities still released untreated sewage into the river. Due to the high turbulence, however, the water is always well oxygenated and the river does not show any symptoms of severe organic pollution.

Robertsfors is the chief industrial center of the area. A paper pulp factory was operating from 1904 until 1948 with a destructive influence on the fish population. When this activity ceased, other industrial activities took place in the same buildings: manufacture of bakelite, fiber glass and rubber insulation. The salmonid populations recovered quickly after 1948 and the mentioned activities could not have caused the noted impairments of the fauna that was started about 1965.

In 1963 a diamond factory began operation in Robertsfors and one year later an electroplating plant was started in the same place. In both factories heavy metals were used and discharged to the river. Heavy metals are known to be dangerous to salmon populations (SPRAGUE *et al.* 1965).

At "Factory A" synthetic diamonds are manufactured. The process can briefly be described as follows:

1) 'Reaction-elements' are made from graphite, aluminium silicate and metals. In the beginning (1963), nickel and iron were used; since 1967 cobalt and iron have been used.
2) These 'reaction-elements' are pressed in highpressure machines, whereby graphite is transformed into diamonds.
3) The diamonds are separated from the rest of the material in the elements. For this separation, sulphuric acid, nitric acid, hydrofluoric acid and sodium nitrate are used.
4) The diamonds are sifted and sorted.

The liquid wastes from "Factory A" were led to a tank where slaked lime was added to adjust the pH to about 8.5. Then the wastes were pumped out into the river at a point below the power station at Sågforsen (Fig. 2). Separation of the metals was not made before the discharge into the river.

In 1973 a purification plant was built at the factory, and the purification was started in November of the same year. Now the metal ions are precipitated with the aid of sodium hydroxide. Hydroxides, other precipitates and solid particles are now separated by a centrifugal process before the waste water is allowed to enter the river.

The other source of heavy metals was the electroplating plant "Factory B", which was operating between 1964 and 1969. In 1968 about 20,000 kg of brass was steeped and coated with zinc or nickel. Steel was also treated with cadmium. In the process cyanides were used, but it was declared that the cyanides were rendered innocous by oxidation to cyamate before discharge into the river. The wastes from this plant were treated in the same place and in the same way as the wastes from "Factory A".

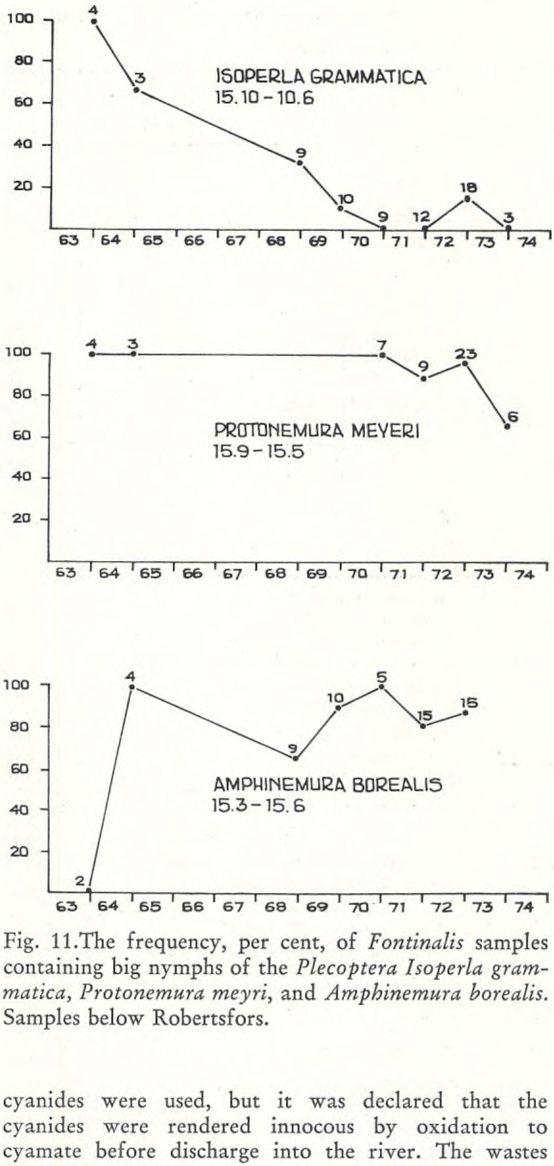

Fig. 11.The frequency, per cent, of *Fontinalis* samples containing big nymphs of the *Plecoptera Isoperla grammatica*, *Protonemura meyri*, and *Amphinemura borealis*. Samples below Robertsfors.

5.2 *Kinds and amounts of metals discharged*

Known values of consumption at the factories are given in Table 9. From the table it is evident that "Factory A" was a greater consumer than was "Factory B". The activity of "Factory A" was also of a longer duration, from 1963 on. The chemical activities at "Factory B" were terminated in April, 1969. The diamond factory's consump-

Table 9. *Known consumption of elements and chemicals at "Factory A" and "Factory B" in Robertsfors, kg/year.*

Year	1966[1]	1968[2]	1969[3]	1972[4]	Prognosis 1982[1]
"Factory A":					
Cobalt	—	2,400		5,000	10,000
Nickel	1,200	—	3,600	—	—
Iron	?	?		1,000	2,000
Graphite	?	2,400	2,080	3,000	7,500
Aluminium silicate	?	?	52	?	?
Sulphuric acid	?	119,000	104,000	150,000	300,000
Nitric acid	?	22,000	31,200	50,000	60,000
Hydrofluoric acid	?	1,500	1,150	1,000	1,000
Hydrochloric acid	?	1,200	1,040	1,000	1,000
Sodium nitrate	?	6,000	5,200	3,000	10,000
Sodium hydroxide	—	—	—	—	10,000
Calcium hydroxide	?	60,000	?	180,000	—
"Factory B":					
Zinc cyanide	200	150	—	—	—
Potassium tadmium cyanide	250	200	—	—	—
Cadmium candorite	150	—	—	—	—
Chromium oxide	20	—	—	—	—
Nickel sulphate	—	180	—	—	—
Potassium hypochlorite	?	2,500	—	—	—
Potassium pyrosulphite	?	200	—	—	—
Potassium hydroxide	?	30	—	—	—
Sulphuric acid	?	500	—	—	—
Nitric acid	?	1,500	—	—	—
Calcium hydroxide	?	8,000	—	—	—

[1] Data from notes made by Prof. A. LINDROTH visiting the factories in November 28, 1966.

[2] Data from a letter from "Factory A" to the National Swedish Environment Protection Board, October 10, 1968.

[3] Data from a letter from "Factory A" to the National Swedish Environment Protection Board, August 22, 1969.

[4] Data from an announcement from "Factory A", October 26, 1972.

tion has been increasing during the ten year period at about ten per cent per year.

It is probable that in "Factory B" most of the metals from the salts were kept as coatings on the metal elements treated. It is impossible to say how much actually leaked out into the river.

At "Factory A", on the other hand, most of the chemicals used have been transmitted to the river. There must have been some losses of elementary cobalt, nickel and iron, probably about 20 per cent, in preparing the reaction elements. So about 80 per cent of the metals must have gone out into the river.

Large amounts of sulphuric acid, nitric acid, calcium hydroxide and sodium nitrate were used at the diamond factory. These chemicals must have been transmitted to the river mostly as sulphates, nitrates and calcium and sodium ions. To find out, whether the discharge increased the content of these ions in the river water, data from the Limnological Survey have been used in an upstream-downstream comparison. The values are given in Table 10. The P-values show that there are no statistically significant differences between the samples taken above and below the factory. The best P-value is recorded for magnesium, an element that is not used at the diamond factory.

The problems of fluorine and fluorine-compounds have not been considered in this study.

Among the chemicals discharged from the factories, nickel and cobalt must be regarded to be dangerous to the ecosystem as:

Table 10. *Upstream—downstream values of calcium, sodium, magnesium, sulphate and nitrate in the Rickleå river for 1971. The water samples were collected at Fredriksfors (above the discharge) and at Rickleå Field station (16 km below the industrial discharge, Fig. 2.) in the middle of each month and analysed at the Limnological Survey of the National Environment Protection Board.*

Month	Calcium meqv/l		Sodium meqv/l		Magnesium meqv/l		Sulphate meqv/l		Nitrate mg/l	
	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream
January	0.186	0.205	0.073	0.081	0.080	0.090	0.210	0.204	0.104	0.066
February	0.172	0.178	0.069	0.072	0.084	0.079	0.179	0.177	0.069	0.084
March	0.167	0.183	0.076	0.080	0.073	0.075	0.178	0.186	0.114	0.138
April	0.177	0.200	0.077	0.077	0.092	0.104	0.194	0.256	0.216	0.227
May	0.145	0.161	0.062	0.064	0.074	0.079	0.171	0.175	0.100	0.100
June	0.165	0.174	0.062	0.067	0.074	0.078	0.171	0.193	0.000	0.000
July	0.160	0.154	0.058	0.062	0.079	0.081	0.173	0.164	0.003	0.002
August	0.181	0.157	0.062	0.070	0.078	0.083	0.178	0.173	0.007	0.003
September	0.158	0.163	0.069	0.073	0.081	0.083	0.169	0.176	0.002	0.001
October	0.154	0.179	0.074	0.080	0.082	0.095	0.182	0.211	0.074	0.089
November	0.156	0.166	0.067	0.077	0.083	0.088	0.189	0.220	0.085	0.086
December	0.168	0.185	0.075	0.080	0.082	0.089	0.191	0.202	0.102	0.136
Mean	0.166	0.175	0.069	0.074	0.080	0.085	0.182	0.195	0.073	0.064
Standard deviation	0.012	0.016	0.006	0.007	0.005	0.008	0.012	0.026	0.064	0.070
t-value	1.66		0.16		1.82		1.54		0.17	
P	n.s. $0.20 > P > 0.10$		n.s. $0.90 > P > 0.80$		n.s. $0.10 > P > 0.05$		n.s. $0.20 > P > 0.10$		n.s. $0.90 > P > 0.80$	

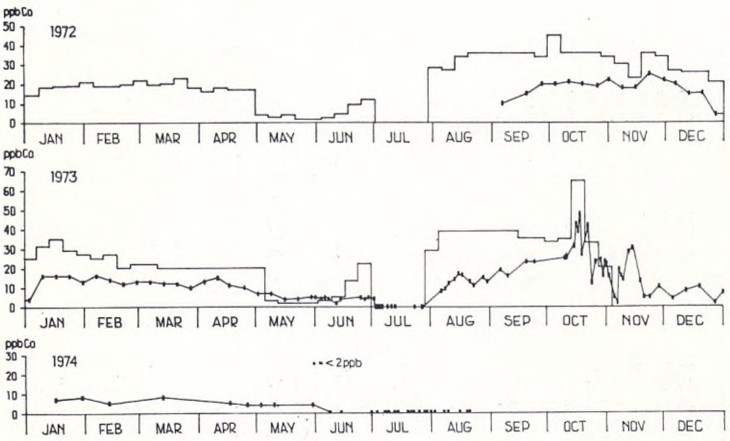

Fig. 12. Cobalt concentrations in water below Robertsfors in 1972, 1973 and 1974. Bars represent calculated concentrations and the curve represents measured concentrations.

1. Nickel and cobalt have been pumped out from the diamond factory continuously, in comparatively large amounts and over several years.
2. The content of nickel and cobalt is very low in natural waters. Iron on the other hand occurs in comparatively high natural concentrations in the Rickleå water.
3. Nickel and cobalt are known to be very toxic to some aquatic organisms.

In the diamond factory the acids containing the metal ions were treated with slaked lime, adjusting the pH of the wastes to about 8.5 before discharge. It is to be supposed that the metals in this process precipitated as hydroxides or oxides. As has been demonstrated in biotests, however, cobalt hydroxide, but not cobalt oxide, are toxic to cultures of *Chlorella* (SÖDERGREN and SANDSTRÖM 1972), when cultured in slightly acid media. A natural explanation of this might be that cobalt hydroxides are not stable.

In titration experiments it can easily be shown (SÖDERGREN 1974 b) that if acid nickel and cobalt solutions are precipitated as hydroxides, the precipitates dissociate again when the pH is brought down to 7. As the water in the Rickleå is acid, free nickel and cobalt ions must have been liberated, when the discharge was mixed with the river water.

5.3 *Concentrations of cobalt in the river water*

The fact, that nickel and cobalt must have dissolved in the river water, implies that the ions should be easy to detect by water analysis. No nickel analyses have been conducted during the time nickel was being used in "Factory A". Cobalt values exist since September, 1972.

The discharge of wastes from the factory was continuous; this permits calculations of theoretical concentrations of cobalt in the water. This has been performed for the years 1972 and 1973. In the calculations it has been assumed that all cobalt consumed, 5,000 kg and 5,500 kg in the respective years, was discharged into the river. The chemical treatment of the reaction elements occurs from Monday to Friday. It was assumed that the discharge was the same all 232 working days in the two years, except in November and December, 1973, when the new purification plant was running. Under these assumptions, the discharge was calculated to be 21.55 in 1972 and 23.71 in 1973, expressed as kg cobalt per working day.

To calculate the theoretical concentrations in the river water, the discharge values from the hydroelectrical power plants in Robertsfors have been used (compare Fig. 3). The water flow here is estimated only once a week. The concentrations have been calculated as if the water flow was the same every day of the week, which is certainly not correct. During floods all the water is not measured at the power stations and, therefore, the water flow during spring flood had to be estimated with the aid of water level readings from the Rickleå field station.

The weekly calculated cobalt concentrations are shown as bars in Fig. 12. The highest values occurred in autumn when the water flow was low both years. In winter the theoretical cobalt content was also high but during the spring flow, the concentrations fall. A small peak is shown when the water went down in the end of June before zero values were achieved during summer holidays.

Since September, 1972, water samples for cobalt analysis have been collected at the Rickleå Field Station almost every working day. Some of the samples, 134, have been analysed for cobalt by the Research Laboratory of the National Environment Protection Board. The method used was atomic absorption, permitting determinations down to 1ppb. The accuracy of the method is ±1 ppb. In concentrations more than 35 ppb, the accuracy is ±2 ppb. The analytical data have been plotted in Fig. 12.

The general pattern of the yearly fluctuations in cobalt concentrations is in agreement with the calculations. During summer holidays the concentrations soon sink to less than 1 ppb. Low values are also present during spring flood. The highest values are noted in the middle of October, 1973, when the water flow was extremely low. The rapid respond must depend upon the short turnover time of the river water.

In May and the beginning of June, 1973, the measured values are higher than the calculated values. Possibly this is due to overrating of the water flow at a time when no good flow values were given. Mostly, however, the measured concentrations were lower than the calculated.

Two water samples taken above the factory showed that the cobalt concentration here was less than 1 ppb (November, 1973).

The years 1972 and 1973 can be regarded as typical as far as water flow is concerned. It is probable that the heavy metal concentration has followed the kind of curve shown in most of the later years, even if the total discharge has increased.

The result of a literature survey (MITCHELL 1951, BENOIT 1957, HUTCHINSON 1957, GOLDMAN 1964, WETZEL 1966, KÖLLE *et al.* 1967, MERLINI *et al.* 1967, GROTH 1971) was that natural concentrations of cobalt in inland waters are very low and that rather advanced analytical methods must be used to get accurate values. It appeared that 0.2 ppb would be a maximum value for lakes. It is possible that brooks and rivers may have slightly higher concentrations than lakes. The difference is, however, slight. For lakes and rivers in the USSR, MALIUGA (1946) has given values from 0.74—19.0 ppb. The polarographic method used by MALIUGA has however been criticized by BENOIT (1957).

The purification plant at the diamond factory was started in November, 1973. If the plant worked properly the concentration of cobalt would soon have dropped down below the detection limit. This was not the case, cobalt was present in rather high concentrations till June 1974. From then on cobalt has not been detected in the river water. It has later been admitted that the purification was not complete in the first half year of 1974.

5.4 *Heavy metals in the sediments*

Sediment sampling was performed from the ice with a sediment core sampler February 23, 1973. Samples were taken at 9 localities, numbers 1—3 above and numbers 4—9 below the factories. The distances from the factories are given in Fig. 13. Sampling station 2 was at the dam above the power station at Fredriksfors, 3 at the middle hydroelectrical dam, 4 and 5 at the lower dam. The samples were sent to the Research Laboratory of the National Swedish Environment Protection Board at Drottningholm for analysis.

Cobalt, nickel, mercury, zinc, copper and iron have been found in all samples analysed. Only cobalt occurred in constantly higher concentrations below the factories. The results concerning cobalt and nickel are shown in Fig. 13. Above the "Factory A" the cobalt concentrations varied between 2.5 and 7.4 mg/kg dry weight, below between 2.7 and 24. Characteristic of the downstream samples was the high cobalt content in the uppermost 3 cm. The difference between the samples was not due to varying organic content in the cores. According to Fig. 13 the nickel discharge has not given any lasting high concentrations in the sediments.

As is shown in Table 11 it is not probable that the activity at "Factory B" has caused lasting accumulations of zinc and copper.

Cobalt was shown to have been accumulated

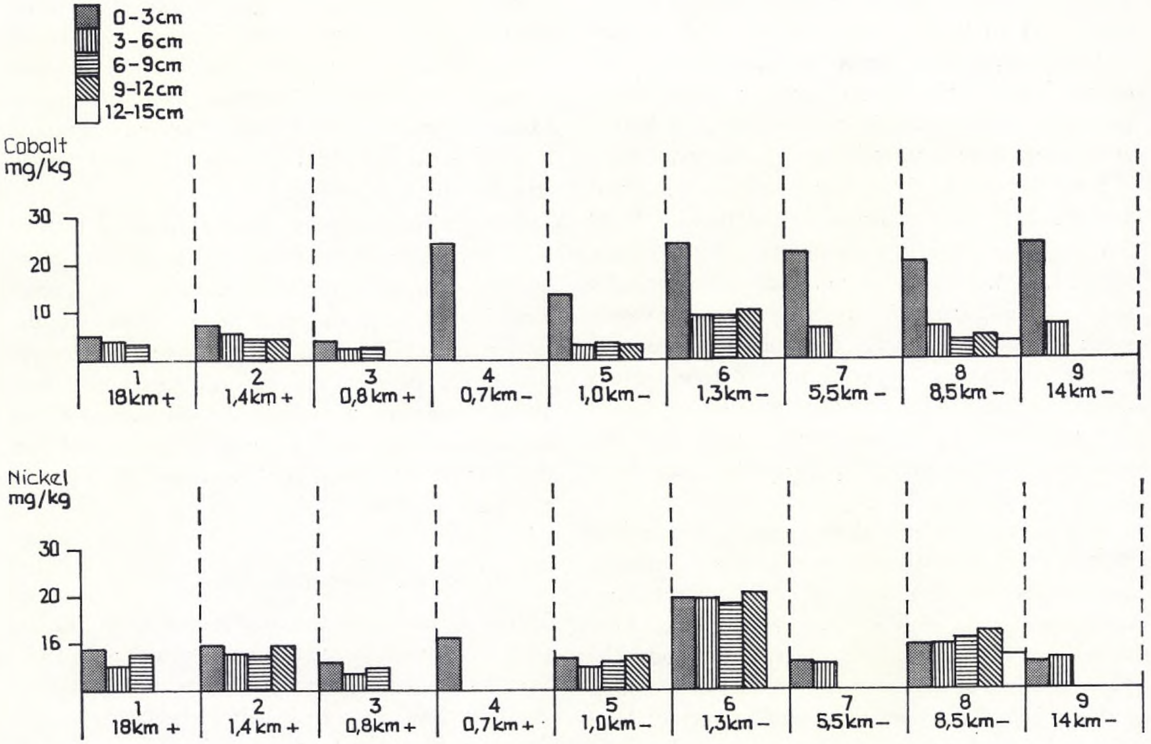

Fig. 13. Cobalt and nickel content in different layers of sediments from 9 localities at different distances upstream (+) and downstream the industrial outlet. Metal in mg/kg dry weight. Samples from February 23, 1973.

in the superficial layers at all downstream stations. In comparison with other waters (Table 12) the concentrations were not very high even here. Cobalt may have a low affinity to the sediments or the sediments do not grow old in the river as they to some extent are washed out in each flood.

5.5 *Heavy metals in the Fontinalis community*

Plants have the ability to accumulate heavy metals. Terrestrial leaf mosses are good indicators of air transported metals (Rühling and Tyler 1971). For that reason tufts of *Fontinalis* sp. were sampled at five places in the Rickleå river. The mosses were collected and excess water was permitted to run off through a sieve. After drying in the laboratory, samples from Isakfäbodforsen and Laxbacksforsen were sent to the Research Laboratory for analysis.

The results are shown in Table 13. Concerning zinc and copper, there are no differences in concentrations between samples from the two stations. The concentration of cobalt, however, was about 19 times higher below the factory.

For comparison, the concentrations of these

Table 11. *The concentration of zinc, copper and iron in the uppermost 3 cm of sediments from localities at various distances upstream (+) and downstream (–) from the pollution source. Samples from February 23, 1973. mg metal/kg dry weight.*

Locality no	Distance from pollution source km	Zinc	Copper	Iron
2	1.4+	66	—	—
3	0.8+	35	5.6	9,900
4	0.7–	84	—	—
7	5.5–	29	9.4	9,200
8	8.5–	56	—	—
9	14.0–	27	5.5	9,100

Table 12. *Cobalt concentration in sediments from different waters.*

Locality	Co mg/kg (dry weight)	Reference
Atlantic red clay	21—39	Smales *et al.* 1957
Atlantic Globigerina	2.3—33	„ —
Smith Lake, Alaska	13—19	Barsdate 1966
Castle Lake, California	30	Goldman 1966
Rhine	24	de Grooth *et al.* 1970
Ems	22	„ —
Chao Phya	12	„ —
Amazonas	13	„ —
Schöhnsee	9.5—12.2	Groth 1971
Ekoln, Lake Mälaren, Sweden	21—31	Lann 1972
Västerås' harbour, Sweden	8—30	„ —
Lake Vänern, Sweden	35—74	„ —
Noncontaminated lakes in Hälsingland, Sweden	9—85	„ —
Acid laken in western Sweden	7—44	Hörnström *et al.* 1973

metals in macrophytes from Lake Maggiore are given (Merlni *et al.* 1971). For these plants the concentrations were given in mg/kg ash weight. To make the comparison relevant, the values in Table 13 for *Fontinalis* (mg/kg dry weight) have been multiplied by a factor 5.99, which is the ratio between dry weight and ash weight.

The submerged plants *Elodea* and *Myriophyllum*, having a similar way of growth to *Fontinalis*, show the highest concentrations of the metals. Zinc and copper in the *Fontinalis* occurred in concentrations not very different from the recorded concentrations in the plants from Lake Maggiore. The cobalt concentrations, on the other hand, were much higher in all *Fontinalis* samples.

The *Fontinalis* tufts were not cleaned of periphyton before drying and analysis. So it is not known how much of the cobalt accumulated belongs to the *Fontinalis* itself. To be cautious, the metal concentrations must refer to the whole *Fontinalis* community. It is probable, however, that most of the cobalt has been accumulated by the *Fontinalis*.

Table 13. *The concentration of cobalt, zinc and copper in Fontinalis from the Rickelå river. Samples from April 16, 1973. mg metal/kg dry weight.*

Locality	Cobalt	Zinc	Copper
Isakfäbodforsen	43	190	14
(Above outlet)	41	87	16
Laxbacksforsen	770	83	13
(Below outlet)	820	230	14

When compared with the sediments, the tendency to accumulate cobalt is much higher in *Fontinalis*.

5.6 *The synchronization between heavy metal pollution and the impairment of the juvenile salmonid population*

The change of the salmon population and the pollution situation have already been described. An attempt will be made here to determine whether the impairment of the salmonid fauna is correlated to the heavy metal pollution.

Since the knowledge of the amount of metals discharged is scarce, some assumptions must be made in order to proceed further. In Fig. 14 the known values of yearly consumption of cobalt and nickel at "Factory A" are plotted as crosses. The crosses are distributed as if they were lying on a straight line. The first assumption is that the consumption of metals at the factory has increased approximately as is indicated by the line. The second is that the discharges increased in the same way. Nickel was used in the first years and from autumn 1967 cobalt was used.

The working time of the electroplating plant at

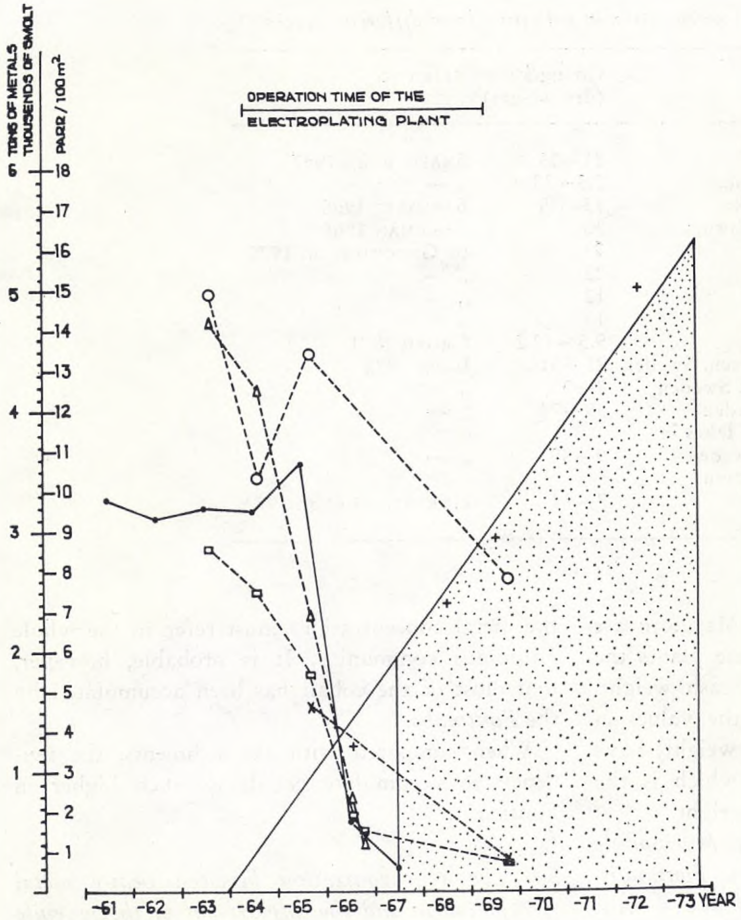

Fig. 14. The activity in the industries using heavy metals in relation to the development of the juvenile salmon and trout population. Operation time of the electroplating plant is given in the top of the figure. The consumption of nickel and cobalt in tons per year at the diamond factory is indicated by the white and dotted area respectively.

• ------ • = Number of salmon smolts caught in the fish trap.
○---○ = Density of salmon and trout parr in Nettingforsen.
□---□ = Density of salmon and trout parr in the lower part of Laxbacksforsen.
△---△ = Density of salmon and trout parr in the upper part of Laxbacksforsen.
×---× = Density of salmon and trout parr in Kryddgårdsforsen.
+———+ = Known consumption of metal at the diamond factory.

"Factory B" is given at the top of the figure. As described earlier, it is impossible to give quantitative data concerning the discharge from this factory.

In the figure the catches of salmon smolts in the fish trap is indicated by dots. The big drop in catches occurred in 1966. At that time the consumption of nickel in the diamond factory exceeded 1,000 kg/year and the electroplating plant was in operation. In 1967 the cath of smolts was still smaller. Since 1967 the smolt migration has not been controlled.

The densities of salmon and trout parr in different rapids is also given in Fig. 14 (data from Karlström 1972). In Laxbacksforsen, a decrease in numbers appears in 1965 and this result is confirmed by the reduced catch of smolts in 1966. It is interesting to note that the density values here are lower in 1964 in comparison with the previous year. This might be an indication that the impairment had started in 1964. In 1965 the smallest densities are recorded in Kryddgårdsforsen, the rapids nearest to the factories, and the largest densities in Nettingforsen the rapids most far away from the outlet. In 1969, however, the number of parr in Nettingforsen had become small even here.

The deterioration of the juvenile salmon and trout population is well synchronized with the onset of the heavy metal pollution. The insufficiency of data, however, makes it impossible to prove the connection and to discriminate between the effects of the different discharges from the two factories.

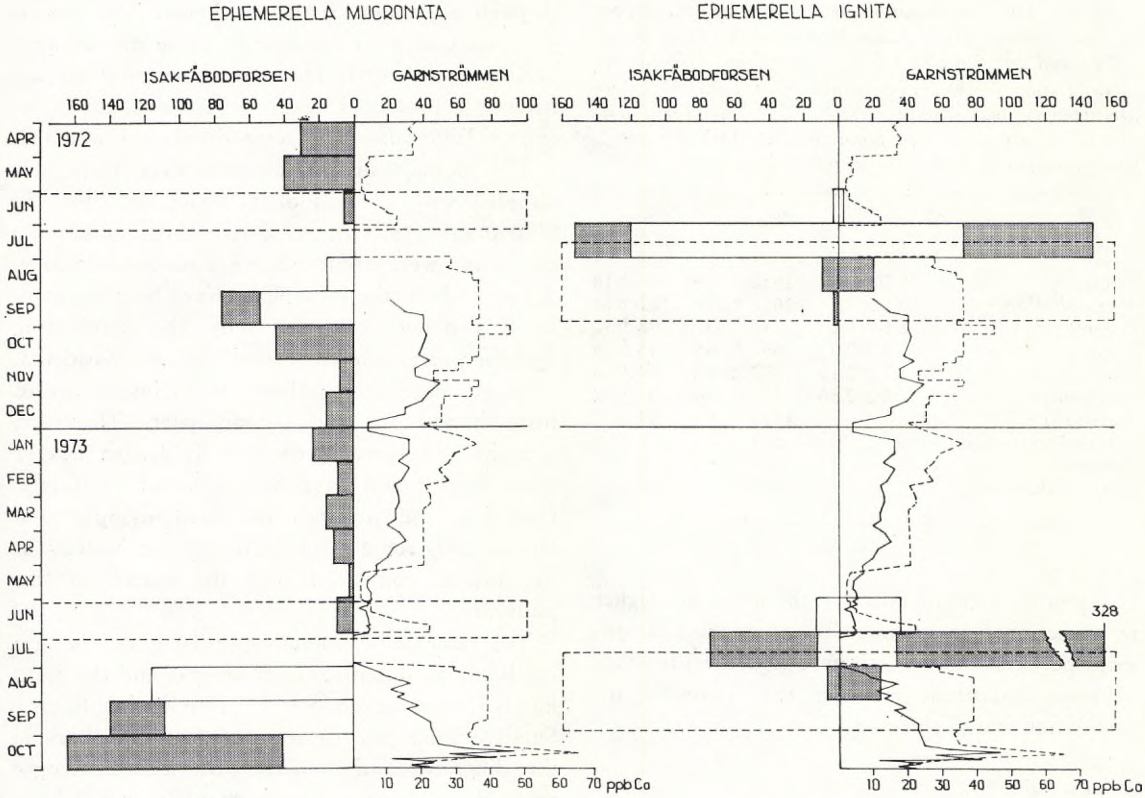

Fig. 15. The development of *Ephemerella mucronata* and *E. ignita* at Isakfäbodforsen (above the outlet) and Garnströmmen (below the outlet) in relation to the annual cobalt curve in 1972 and 1973. Mean number of nymphs/10 g dry *Fontinalis*. Black bars represent nymphs longer than 2 mm and white bars shorter individuals. Flight periods limited by broken lines. Solid curve represents measured concentrations of cobalt, broken curve calculated cobalt concentrations.

In 1969 the density of parr was less than in 1966. The switch from nickel to cobalt in the diamond factory had apparently not changed the situation. In spring 1969 the electroplating plant was stopped, and if this heavy metal source was the only or the chief cause of the impairment, some improvements should be expected in the years to come.

The fact that the salmon population has been more harmed since 1969 is an indication that the cobalt discharge is the cause of the present situation. The deterioration of the parr population is well correlated to the heavy metal discharge from the diamond factory, no matter if nickel or cobalt was released.

5.7 *The annual cycle of some Fontinalis species in relation to the annual cobalt curve*

Introduction

The impairment of the invertebrate fauna was well correlated with the decrease in density of juvenile salmon and trout. This implies that there should also be a negative correlation between the heavy metal discharge and the drift and frequency of mayflies in the mosses. This connection is evident if the Figs. 9—12 are compared with Fig. 15.

The winter generation of mayfly nymphs was completely or almost lacking in the mosses during later years which correlates with the fact that the

Table 14. *The concentration of cobalt, zinc and copper in macrophytes from Lake Maggiore (*Merlini *et al. 1971) and in Fontinalis from the Rickelå. mg metal/g ash weight. (The values from Lake Maggiore are mean values ± standard error. The values for Fontinalis are calculated from the data in Table 16 A, using a factor of 5.99 = dry weight/ash weight).*

	Cobalt	Zinc	Copper
Elodea	18.0 ± 2.7	1950 ± 419	189 ± 18
Myriophyllum	19.9 ± 2.8	1600 ± 211	181 ± 11
Potamogeton	8.0 ± 1.0	740 ± 157	98 ± 30
Najas	3.8 ± 0.3	560 ± 65	45 ± 5
Nuphar	1.7 ± 0.15	570 ± 42	64 ± 3
Phragmites	2.5 ± 0.56	350 ± 56	52 ± 12
Fontinalis	258	1138	84
Isakfäbodforsen	245	521	96
Fontinalis	4612	497	78
Laxbacksforsen	4912	1378	84

heavy metal concentrations in the water are higher in winter than in summer. To study the relationships between the cobalt curve and the life cycle of some important mayflies the following investigation was performed.

Methods

Moss samples were taken in the middle of each month in Garnströmmen and Isakfäbodforsen (station 5 and 2 in Fig. 2) in the period April 1972 to October 1973.

At each station three samples were taken. The first sample was collected near the bank, the second in deeper and faster water, and the third in fast and deep water. In the sampling process a drift net (mesh size 0.7 mm) was put behind a *Fontinalis* tuft and drawn forward so that the tuft was enclosed in the net. Most of the water was allowed to run off through the net before preserving in 80 % ethanol. At high water, in spring and at the time of bottom ice formation, in autumn, it was, however, impossible to bring the samples up enclosed in a drift net. On these occasions a rake was used to grab the tufts and to pull them to the surface of the water. It may be that this sampling procedure was less effective.

In the laboratory the *Fontinalis* tufts were put in a big jar with water and shaken vigorously so that the animals became free. Then the tufts were put aside and the water with animals filtered through a gasoline funnel with net. The process was repeated until no animals came out or were visible in the tufts. The animal material on the filter was preserved again in 70 % ethanol. The empty *Fontinalis* tufts were dried and weighed.

The animals in the samples were then subsampled with the aid of a device described by Södergren (1974 a). As a rule three subsamples out of ten were counted using a stereomicroscope. All animals in the subsamples have been counted. In this paper, however, only the dominating *Ephemeroptera* and the *Simuliidae* are considered.

As has been shown above, small insects are of little importance for salmon parr. Therefore, nymphs and larvae with a body length less or more than 2 mm have been counted separately. However, the presence of small nymphs and larvae gives some information on the biology of the insects concerned and the extent of the pollution.

The number of animals per 10 g dry weight has been calculated for each sample, and the mean number in three samples is given in the figures. Small animals are represented by white bars in the diagrams and animals with a body length more than 2 mm are represented by black bars.

Results and discussion

The mean number of animals per 10 g moss is given for each month in Figs 15—16. In the diagrams the upstream and downstream samples can be compared and the sampling facilities were the same on the same occasions. In the figures the approximate flight periods of the insects concerned are indicated. The solid curve illustrates the concentration of cobalt in the river water according to the analyses and the broken line the calculated cobalt concentrations.

In the Rickleå river three species belonging to the genus *Ephemerella* are present. Two of these are normally very abundant in the *Fontinalis*: *Ephemerella mucronata* and *E. ignita.* As shown in Fig. 15 the development of the nymphs is well separated in time. The flight period of *E. mucronata* lies in June and beginning of July. After oviposition the eggs seem to develop directly with the first small nymphs appearing in August.

The nymphs of *E. mucronata* then grow through the winter and will be fullgrown in June. The

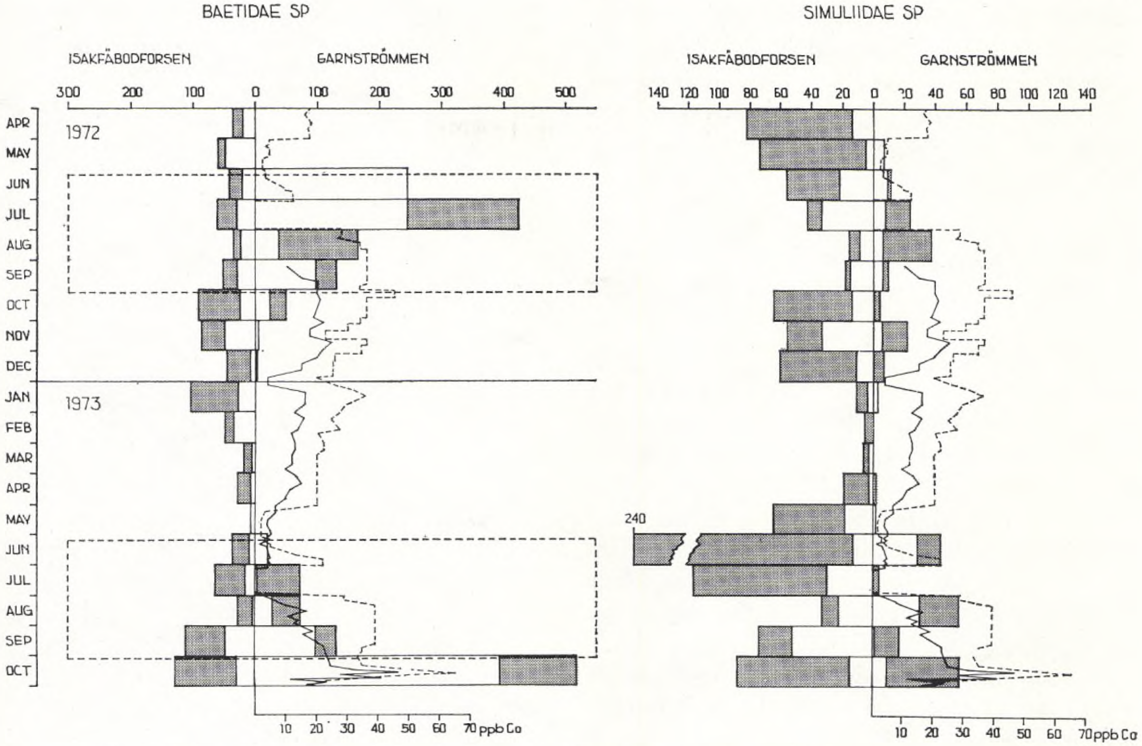

Fig. 16. The development of *Baetidae* nymphs and Simuliidae larvae at Isakfäbodforsen (above the outlet) and Garnströmmen (below the outlet) in relation to the annual cobalt curve in 1972 and 1973. Explanations see Fig. 15.

species was lacking in Garnströmmen in 1972 and 1973. (A single specimen was found here in August 1973.)

Ephemerella ignita is in contrast to the former species, a typical summer form. This species is known to overwinter as diapausing eggs (MACAN 1961). Small nymphs become apparent in June and the density of nymphs increases rapidly to reach a maximum in July. The growth is rapid with the flight period starting in the later part of July. Due to emergence the nymphs are rare in September. The species is still found in Garnströmmen in abundance.

The two *Ephemerella* species dwell in the same habitat and it is difficult to believe that their habits are much different. The summer species, *E. ignita* has its development during a time when the cobalt concentration is low, whereas the development of the winter species occurs at a time when the cobalt concentration is very high. The occurrence of *Ephemerellidae* and the cobalt concentrations seem to be negatively correlated. It is reasonable to believe that the winter concentrations of cobalt are high enough and the time long enough to kill the specimens of *E. mucronata* which hatched in or have drifted into the polluted area.

The occurrence of *Baetidae* nymphs and *Simuliidae* larvae are rather similar. In summer these animals may be very abundant in Garnströmmen. During autumn their numbers, however, decrease and the populations are more or less eliminated during the winter. New populations are built up again in the next summer (Fig. 16). The elimination of the *Baetis* and simuliid populations is, however, not a rapid process and does not follow the cobalt curve very closely. Some delay is incorporated, which may indicate that dying might be a slow process or that new individuals are generated in the system as long as there is hatching of eggs.

The elimination of sensitive winter species and restoration of species regarded as sensitive in the summer cannot be explained in any other way than a poison is striking the fauna in autumn and winter year after year. It is possible that the effects noted here are the result of several years of pollution.

6 THE SENSITIVITY OF EPHEMERELLIDAE TO COBALT

6.1 *Introduction*

The *Fontinalis* studies have clearly shown that there was a close correlation between the disturbance of mayfly nymphs and blackfly larval development and the annual cobalt curve. The best illustration of this was offered by the mayflies *Ephemerella mucronata* and *E. ignita.* This correlation, does not prove that the cobalt discharge was capable of causing the elimination of winter growing mayflies and blackflies.

In static tests[1] it has been shown by WARNICK and BELL (1969) that a mayfly, *Ephemerella subvaria,* was more sensitive to several heavy metals, including cobalt and nickel, than a stonefly and a trichopteran. Earlier, SCHWEIGER (1957) showed that trichopterans and chironomids are less sensitive to cobalt and this is another indication that poisoning by heavy metals was the cause of the conditions in the river.

The effect of long term exposures to sublethal does of cobalt has not been studied for riverine invertebrates. In order to get more information about the sensitivity of mayflies to cobalt it was decided to conduct two kinds of tests. For practical reasons a static test was made with *Ephemerella mucronata* and a running water test with *E. ignita.*

6.2 *Sensitivity in static water test*

Methods

The tests were made in 1 l glass beakers containing 0.5 l liquid. The liquid consisted of water from the Rickleå river with metal salts added. The water was taken at the upper dam in Robertsfors. Two salts were used, cobalt nitrate and nickel nitrate. The prepared concentrations were:

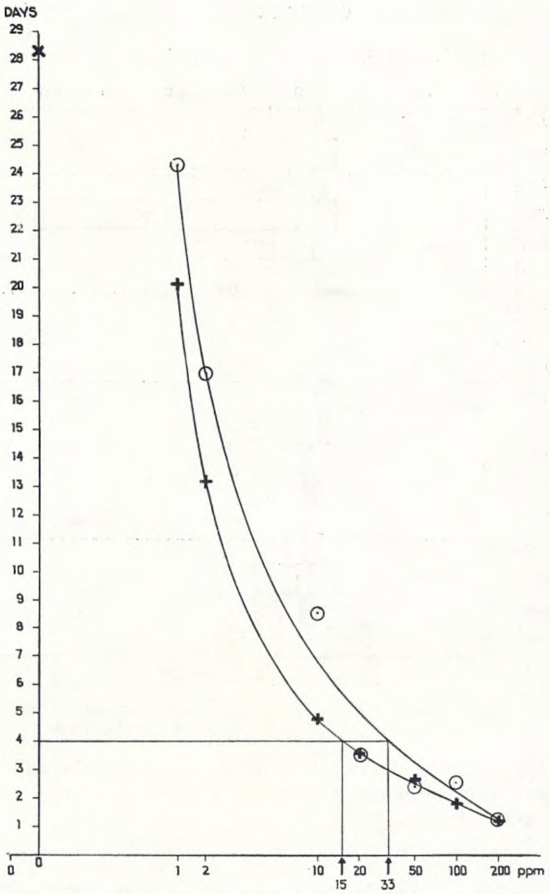

Fig. 17. Median survival time of *Ephemerella mucronata* in nickel (crosses) and cobalt (circles) solutions of different concentrations in the static water test. The cross on the Y-axis indicates the median survival time in the controls. The extrapolated 96 hour LC 50 values for nickel and cobalt are indicated below the X-axis.

Ni^{2+} ppm ...	0	1	2	10	20	50	100	200
Co^{2+} ppm ...	0	1	2	10	20	50	100	200

In each beaker a piece of nylon net allowed the nymphs to hold fast in the current created by the air bubbles from an aerator.

The nymphs of *Ephemerella mucronata* were collected at Isakfäbodforsen 23 May 1974 and 10 mature or almost mature nymphs were transfered to each beaker. The experiment was started at 19.00 the same day in a room in the basement

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[1] Static test = a test where the experimental water is not changed and the toxic agent is administered only in the beginning of the experiment.

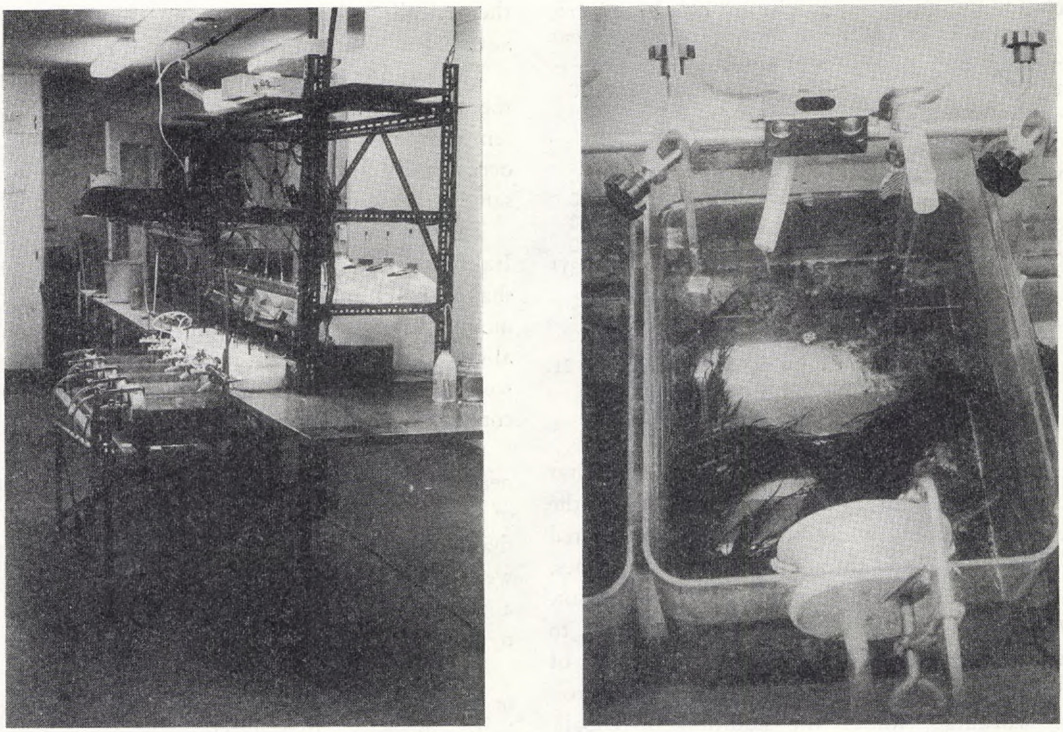

Fig. 18. The equipment used in the running water test with *Ephemerella ignita.* Explanations see text.

of the institute in Umeå. The temperature was kept between 12.5 and 14.0°C.

The beakers were inspected several times a day, dead animals were removed and the time was noted. No food was added but some cannibalism was observed. Very few individuals emerged as subimagines.

Results

The median survival time has been calculated for each concentration and the values are plotted in Fig. 17. Using the method of "fitting by eye" two curves have been drawn, one for cobalt and one for nickel.

By intrapolation it is shown that the 96-hour LC50 [2] is about 15 ppm nickel and 33 ppm cobalt for *Ephemerella mucronata* under the given circumstances. The numbers are a little higher than those given by WARNICK and BELL (1969). The results will be discussed later.

6.3 *Sensitivity in running water test*

Methods

The tests were conducted at Rickleå Field Station in July 1974. The apparatus was set up in the laboratory as is shown in Fig. 18. Five 10 l acryl-plastic aquaria were placed on a low bench. Each aquarium was equipped with an outlet, maintaining a water volume of seven litres. The outlets were covered with nettings to prevent the nymphs from escaping. Over the aquaria there was a light fixture with two 40 W fluorescent lights giving a light of 1,600 lux at the water surface. The lights were turned off at night with the aid of a timer.

A stand for the dosing of river water and cobalt was set up behind the aquaria. Water was taken from the station's river water system and pumped into a 15 l bucket located on top of the stand for stabilizing the water pressure. In the bucket

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[2] 96-hour LC50. During an experimental time of 96 hours the LC50 for the organism is determined. LC50 (Median Lethal Concentration) = the concentration needed to kill fifty percent of the experimental population.

Table 15. *Measured concentrations of cobalt (±2 ppb) in five aquaria with different intended concentrations.*

Intended concentrations	0	5	50	500	5000
June 30	<2	5	33	410	3600
July 7	<2	5	28	440	4900
July 14	<2	5	33	500	3800
July 21	<2	6	33	500	3500
July 28	<2	5	36	500	(<2)[1]
Mean	<2	5.2	32.6	470	3950

[1] The addition of cobalt was terminated July 21.

there was a 0.2 mm nylon net filter. The filter was rinsed at least two times a day. From the bucket the filtered water was equally distributed to five dosimeters through polyethylene tubes. The dosimeters are described by BENGTSSON (1972). Four of the dosimeters were connected to Mariotte-bottles containing $Co(No_3)_2$-solutions of different strengths. One dosimeter, the control, was working without the addition of cobalt. After passing through the dosimeters the river water and cobalt solutions were mixed in jars before reaching the aquaria.

The aquaria were filled through the dosing system on the afternoon of the 29th of June. The intention was to give the following concentrations of cobalt: 0, 5, 50, 500 and 5,000 ppb, all concentrations should be well below the approximate 96 hour LC50-v of 33,000 ppb for *Ephemerella mucronata*. During the experiment water samples were collected in the aquaria. The samples have been analysed for cobalt by the Research Laboratory. The results are shown in Table 15.

The experimental water was taken from the river. It is, however, not probable that the experiment was influenced by river water pollution as the experiment was conducted in July when the factory was closed. Before that the cobalt concentration had dropped below detectable limits in the first half of June due to the purification plant (Fig. 12).

The water flow was maintained constant with the aid of tube clips. The flow was measured; it ranged from 0.21 to 0.29 litre/minute, which means that the water in the aquaria changed theoretically about two times per hour. The aquaria were aereated during the experiment.

The mean water temperature in the river during the period was 16.5°C (range 14.3—18.3). The temperatur in the aquaria was about 1°C higher, occasionally 2°C. The pH values were almost the same as in the river, 5.6 to 6.5.

Tufts of *Fontinalis dalecarlica* were collected at Isakfäbodforsen the 29th of June. The moss was shaken in clean water and all animals were removed. The moss was laid on blotting paper and allowed to dry for half an hour. Bundles of moss weighing about 36 g were knit together with cotton strings and put into the aquaria at 21.00.

Nymphs of *Ephemerella ignita* were collected near the laboratory on the afternoon of the 30th of June. *Fontinalis* tufts from the river were shaken carefully in jars with water. Free nymphs were transferred to the aquaria with the aid of a pipette. Each aquarium was stocked with 75 nymphs.

There was some variation in size of animals in the river. Only individuals more than 2 mm in length were collected. The animals were sorted in such a way that the populations in the aquaria had the same size distribution. The stocking of *E. ignita* was finished at 17.00.

During the following four weeks the aquaria were inspected every day. The bundles of *Fontinalis* were lifted up two of three times to allow dead nymphs to fall off. Dead nymphs were collected and preserved in 70 % ethanol and the time and aquarium noted. On July 13 the aquaria were covered with mosquito netting to prevent emerging subimagines from escaping. The subimagines could be collected from the underside of the netting and preserved. Upon finishing the experiment in the afternoon, July 28, the *Fontinalis* bundles were removed and carefully examined for remaining nymphs.

For practical reasons it was impossible to check the growth of the nymphs during the experiment. Later the wet weight of preserved subimagines and surviving nymphs has been determined with the aid of an analytical balance.

Results

The fate of the nymphs in the different aquaria is shown graphically in Fig. 19.

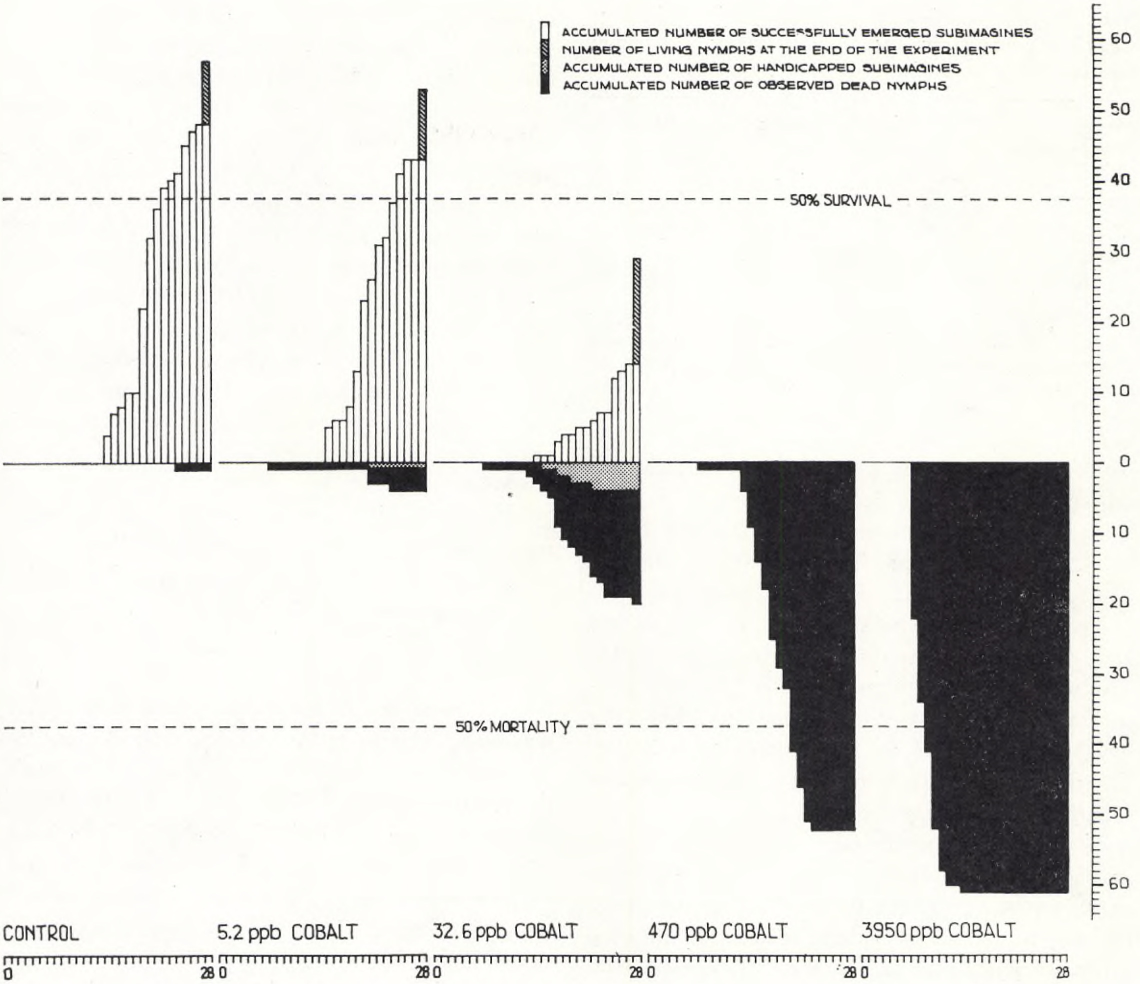

Fig. 19. The sensitivity of *Ephemerella ignita* to cobalt in the running water test. Success in emerging and mortality of nymphs at different concentrations of added cobalt at nitrate.

In the control no cobalt added, the observed mortality was very low. Only one dead nymph was collected in the last week of the experiment. It was observed that the nymphs were growing rapidly and emergence of subimagines started the 14th of July. Emerging specimens were then collected almost every day until the end of the experiment. Fifty per cent of the stocked population emerged within 22 days. After 28 days 64 per cent had emerged, and 9 large nymphs were found alive in the aquarium.

In sum 58 specimens were found again after four weeks which corresponds to a recapture of 77 ⁰/₀. The number of lost individuals was 17 (23 ⁰/₀). As the animals could not escape this loss must be regarded as non-observed mortality. It is known that nymphs of the genus *Ephemerella* exhibit cannibalism which may explain the non-observed mortality.

In all aquaria with addition of cobalt the mortality was greater than in the control (in 470 and 3,950 ppb all nymphs died). In 32.6 ppb and 5.2 ppb some subimagines not capable of flying emerged. They never left the water surface and were floating around for more than one hour before they were picked up. As such specimens

Table 16. *Weight of surviving nymphs of Ephemerella ignita in the running water test. (Wet weight after preservation in 70 % ethanol, mg.)*

Mean concentration ppb	Number of survivors	Mean weight	Variance s^2
< 2	9	7.49	1.19
5.2	9[1]	7.00	1.26
32.6	15	3.95	2.28

[1] The number of survivors was 10. One nymph was damaged before preservation and the true weight could not be determined.

never will reproduce in nature the handicapped subimagines were classified as dead.

The number of emerged individuals was lower in 32.6 and 5.2 ppb in comparison with the control. The emergence was also retarded.

The wet weights of surviving nymphs at the end of the experiment are summarized in Table 16. The weights of the nymphs in the 32.6 ppb concentration was statistically smaller than the weights of nymphs in the control ($P \leqslant 0.001$). The difference between nymphs in the control and 5.2 ppb of cobalt was not significant.

The weight of preserved subimagines is shown in Table 17. Analysis of variance showed that there was a significant difference between sexes, females being heavier than males. As the sex ratios were not the same in the different aquaria, the sexes had to be separated in the further calculations. When Student's t-test was used it was seen that the males in the control were heavier than the males in both the 32.6 and 5.2 ppb concentrations ($P < 0.02$). The females in the control were heavier than the females in the 32.6 ppb aquarium ($P < 0.001$). Between the females in the control and in the 5.2 ppb concentration there was no statistical difference ($0.70 > P > 0.50$) when the whole material was considered. As shown in Fig. 20 one of the females in the 5.2 ppb aquarium was extremely heavy, 9.2 mg, that is out of the range of all other subimagines. The subimaginal material was weighed once more because of this individual, but the same result was obtained again. The reason for this one to be so heavy is not known.

Table 17. *Weight of emerged subimagines of Ephemerella ignita in the running water test. (Wet weight after preservation in 70 % ethanol, mg.)*

Mean concentration ppb	Sex	Number	Mean weight	Variance s^2
< 2	Males	15	4.68	0.29
< 2	Females	31	5.14	0.43
5.2	Males	17	4.08	0.54
5.2	Females	21	4.91	1.57
5.2	Females	(20)[1]	(4.70)[1]	(0.64)[1]
32.6	Males	8	3.39	0.37
32.6	Females	12	3.58	0.51

[1] One aberrant specimen excluded.

When this aberrant individual was excluded from the calculations a significant difference in weight between females in the control and in the 5.2 concentration was obtained ($0.05 > P > 0.02$).

6.4 *Discussion*

In the static water test it was seen that nickel was more toxic to nymphs of *Ephemerella mucronata* than was cobalt. This was in agreement with the results obtained by WARNICK and BELL (1969) when testing *E. subvaria*. They reported 96 hour LC50 values for nickel and cobalt to be 4 and 16 ppm respectively. The values of the author are somewhat higher. There can be several explanations for this difference.

These differences are, however, small in comparison with the differences in sensitivity for cobalt obtained in the static water test and in the running water test. In the four week test with *E. ignita* increased mortality and reduced capability of growth occurred in very small concentrations. In this experiment the animals lived under conditions similar to those in nature: the water was constantly changing, the nymphs lived on natural substrate, they had sufficient food etc. It is apparent that a running water test would be more powerful to test the sensitivity of running water animals.

BIESINGER and CHRISTENSEN (1972) have studied the effects of various metals on experimental populations of *Daphnia magna*. In acute tests they showed that the 48 hour LC50 in Lake Superior water was 1,110 ppb cobalt without food and

1,620 ppb when a food suspension was added to the water. During a three week long experiment it was possible to study long term effects. The 3 week LC50 for cobalt was shown to be 21 ppb. This shows that cobalt in very low concentrations may have much more severe effects on sensitive animals than can be expected from acute tests. Reproductive impairment was noted even at 10 to 12 ppb. Knowing the results of BIESINGER and CHRISTENSEN the events recorded in the running water test with *Ephemerella ignita* are no longer astonishing.

When animal toxicologists determine LC50 values and similar "critical limits" in acute and chronic tests they usually use clean aquaria for rearing the animals, and food is administerated from outside the system. Plants should not be used in the aquaria. In the case of the running water test with *E. ignita* the animals were living on their natural substrate, *Fontinalis* and they have been eating *Fontinalis* and periphyton. As the experiment was performed in an inorthodox way it is not possible to serve the results in established terms of toxicity like LC50 and others. The test must be taken for what it was: an attempt to evaluate the possibilities of cobalt in noted concentrations being the cause of the faunistical changes.

In the running water test the control population was more successful in survival and growth than the others. The differences between the control and the 5.2 ppb population was small but it is probable that the differences may have been more pronounced in an experiment of still longer duration. According to BIESINGER and CHRISTENSEN (1972) reproduction was the most sensive parameter in studying the effects of cobalt and other metals. It has for practical reasons not been possible to study the effect of cobalt addition on the reproduction of *E. ignita* but the lower weights of subimagines from the 5.2 ppb population might indicate that the reproductive capacity was decreased by the addition of the metal.

As has been shown above, the *Fontinalis* accumulates cobalt very easily. In experiments with laboratory cultures it has also been shown that microalgae do so. The concentration factors of the algae increased with increasing concentrations of cobalt in the medium (COLEMAN *et al.* 1971). It is possible that the concentration factors of *Fontinalis* and other macrophytes varies in the same way. Probably the sensitivity of *E. ignita* is due mostly to the fact that the nymphs were eating accumulated cobalt. As was shown in the static water test they can withstand rather high cobalt concentrations in the medium when they were prevented from eating.

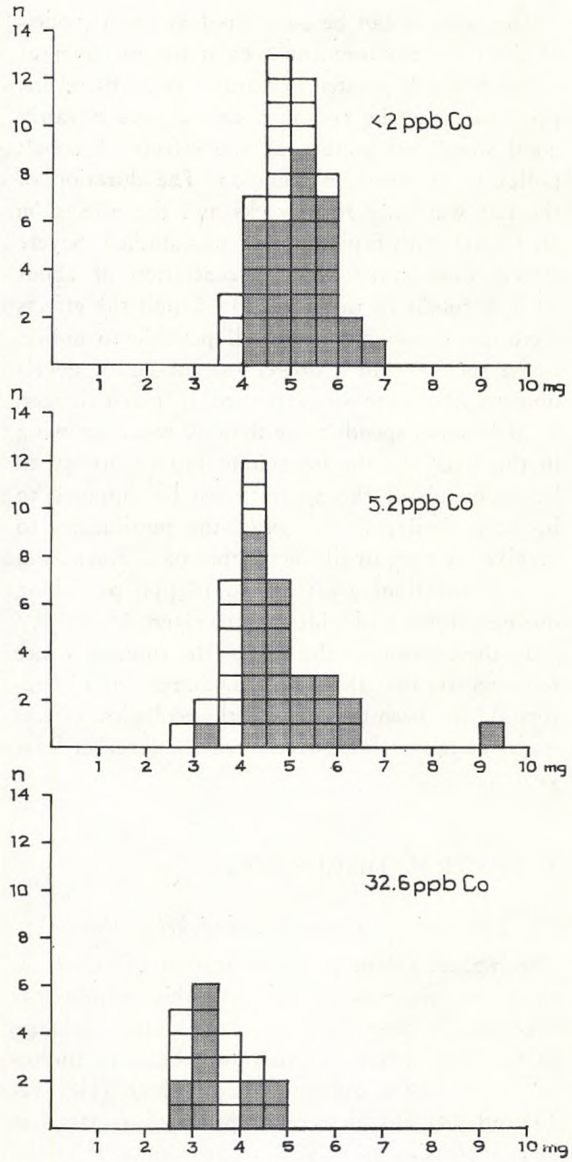

Fig. 20. Weight distribution of subimagines from the running water test. Black bars = females, white bars = males.

The aquaria can be considered as small models of the river environment even if the turnover of water is much greater in nature. It is, therefore, probable that the results obtained give a fairly good simplified picture of the effects of cobalt pollution in rivers in common. The duration of the test was only four weeks and the effects on an animal with rapid growth was studied. Severe effects were noted at a concentration of about 33 ppb cobalt in the water. In 5 ppb the effects were less pronounced but still possible to notice. For a species with a slower rate of larval development the time of exposure is much longer. *E. Mucronata* spends more than 40 weeks growing in the river. As the behaviour and sensitivity to heavy metals of this species must be supposed to be very similar to *E. ignita* the possibilities to survive are very small for nymphs of *E. mucronata* at concentrations greater than 10 ppb prevailing during autumn and winter in the river.

In the opinion of the author the running water test suggests that the cobalt discharge from "Factory A" has been the cause of the ecological effects noted in the polluted section of the river in later years.

7 GENERAL DISCUSSION

7.1 *The toxicity of cobalt and nickel to fish*

The highest measured concentration of cobalt in the river water is 47 ppb and this sample was taken in October 1973 when the water discharge in the river was very small and the consumption of cobalt in the diamond factory high (Figs 12, 13 and 14). As the consumption of metals has been increasing from year to year since 1963 the heavy metal concentrations must have been lower in earlier years even at low water. In 1966 and 1967 when the impairment of the juvenile salmon population became evident it is not probable, that the nickel concentrations due to the discharge from the diamond factory was higher than 15 ppb for any lasting periods.

Acute toxicity levels of cobalt and nickel to fish are much higher, the lowest values recorded are 800 ppb for nickel and 10,000 ppb for cobalt (Murdoch 1953, Shaw and Lowrance 1956, Schweiger 1957, Pickering and Hendersen 1966, Jones 1969, Pickering 1974). So the concentrations of heavy metals in the river have been of a magnitude permitting only sub-acute effects to be suspected.

According to Sprague (1971) and Bengtsson (1974) reproduction is one of the most sensitive responses to chronic or sublethal heavy metal pollution in fish. Mount and Stephan (1969) have proposed a "laboratory fish production index" (LFPI) as a measure of the acceptability of a specific environment to fish. They recommended that data should be gathered over at least one generation and the study should include effects on growth, reproduction, spawning behaviour and the viability of eggs. A "Maximum acceptable toxicant concentration" (MATC) could then be established on the basis of chronic exposure using the LFPI as a measure of toxic effect.

Pickering (1974) has determined the experimental MATC-value for nickel to fathead minnow (*Pimephales promelas* Rafinesque) in hard water to be between 68 and 132 ppm. Even if the salmon in soft water might be more sensitive it is not safe that the nickel discharge in the first years was toxic to the fish, as far as poisoning via the water is concerned.

From 1964 to 1969 there was also an electroplating plant. In spring 1967 a dead female salmon was found in Garnströmmen on the ice. There were no signs of injury on the fish. Analysis showed that the concentration of zinc in the gills was 220 mg/kg fresh weight. Unfortunately the concentrations of, for instance, cadmium and nickel was not determined. The facts are too few to permit an evaluation of the condition during those years.

Since 1969 only cobalt has to be considered in the Rickleå case. In literature no MATC-values are given for this metal. It is, however, not probable that the concentrations was toxic to fish, as other fish like sculpins and burbut were still present in the polluted part. Trout, grayling and sculpins have been kept at the Rickleå Field Station in river water for several months without detectable effects. Shabalina (1964) has shown that the growth of under-yearlings, yearlings and two year old rainbow trout (*Salmo irideus* Gibbon) is stimulated if cobalt salts are given with the food. Fishes apparently have some mechanism which removes surplus cobalt that has entered via the water or food (Frolova 1960, Larsson 1969 and Kimura and Ichikawa 1972).

Shabalina (1964) studied also the influence of cobalt chloride on the development of hard trout (*Salmo irideus* Gibbon) eggs. The eggs were incubated in aquaria with circulating water. Highest mortality occurred on the 14th day of experiment in all concentrations of cobalt and in the control. All the concentrations of cobalt favoured the development of *Saprolegniales*. The mortality during the experiment was as follows:

5	ppm Co	15.8 %
0.5	,,	38.4 %
0.05	,,	26.1 %
Control		8.4 %

All concentrations of cobalt caused an increased mortality. It was observed that the blastomeres of the exposed eggs were much larger than those of the control, indicating that cleavage was proceeding faster in the control than in the experimental eggs. Thus cobalt retarded the rate of cell divisions. There were no pronounced differences in the subsequent stages of development, the experimental and the control eggs developing at the same rate. When hatching occurred, however, it was observed that the experimental larvae were smaller than in the control.

In the work of Shabalina, harmful effects have been documented on salmonidae eggs by addition of cobalt ions in concentrations down to 50 ppb in a circulating system. In the polluted parts of the Rickleå, 50 ppb of cobalt has not been documented, but the actual values are not far below (Fig. 12). Some influence on the development of salmon eggs can, therefore, not be excluded, even if the mortality may not have been very high. According to the electro-fishing in later years spawning has occurred and at least some eggs developed normally.

At the present state of knowledge, there is no proof that cobalt or nickel are harmful to fish in concentrations below 50 ppb. Even if direct effects can not be excluded it seems more probable that the production of salmon and trout was damaged indirectly via the deterioration of the invertebrate fauna.

7.2 *The toxicity of cobalt to invertebrates*

As has been shown by Schweiger (1957) and Warnick and Bell (1969) different taxonomic groups differ in their acute sensitivity to heavy metals. A poor development of the mayfly fauna might be a symptom of heavy metal pollution (Sprague *et al.* 1965). Populations of *Daphnia magna* have been shown to be negatively influenced in concentrations of 10—21 ppb of cobalt (Biesinger and Christensen 1972). This implies that the prevailing concentrations in the Rickleå river water should be harmful also to other cladocerans.

By this study it has been shown that also *Ephemeroptera* and *Simuliidae* are very sensitive in the actual concentrations of this metal. The mayfly nymphs in the mosses live in exposed places and eat food in which heavy metals are easily accumulated.

All invertebrates have not been investigated in this study, but mayflies, important to the salmon parr, seem to be among the most sensitive to the poison.

7.3 *The toxicity of cobalt to plants*

In literature there was no indication of cobalt in the measured concentrations being toxic to macrophytic vegetation. This is in agreement with the fact that the vegetation in the polluted areas looked quite normal.

In the laboratory the toxicity of cobalt to algal cultures has been studied (Coleman *et al.* 1971, Södergren and Sandström 1972). Harmful effects below 1 ppm was not noted.

When the rearing conditions were developed somewhat to be more similar to conditions in running waters, it was possible to note deleterious effects of cobalt ions in lower concentrations (Sandström and Södergren 1974). The *Chlorella* cultures were here reared in dialysis tubes and put into jars where the medium and cobalt ions were continuously renewed by a dosing apparatus. It was shown that the respiration of the cultures was considerably lower at 0.35 and 0.20 ppm than at 0.01 ppm.

In culture tests the conditions are unfortunately not similar to the true conditions in nature. In studying the effects of copper on the photosynthesis and growth of algae, STEEMAN-NIELSEN and WIUM-ANDERSEN (1970) have also shown that EDTA, citric acid and colloidal $Fe(OH)_2$ present in most culture media reduce the toxic effects of the metal. When for instance, high concentrations of colloidal $(Fe(OH)_2$ was present about 50 g Cu/l was necessary to depress growth to the same degree as 1 g Cu/l in a growth medium which contained very little iron. Addition of EDTA and citric acid was further sufficient to prevent any influence of Cu at concentrations found in nature. The examples given indicate that it must be hard to predict from culture experiments what concentrations of heavy metals might be dangerous in nature.

Experiments performed *in situ* must be of a much higher predictive value. Cobalt is an essential element for life and is suspected to be a micro-nutrient limiting factor for production in lakes in areas where the cobalt content in rocks and soils is very low. In such lakes addition of small amounts of cobalt to the water may stimulate the primary production (GOLDMAN 1964). In a lake with a higher natural concentration of cobalt GOLDMAN has found that the addition of 5 ppb cobalt as $CoSo_4$ was inhibiting. (GOLDMAN 1966.)

It is not possible "to translate" the results from *in situ* experiments in lakes to the conditions in running water. In the Rickleå river the concentrations of cobalt in the water has been much higher than the lowest values known for inhibition of photosynthesis. The metal was also administerated more or less continuously. So it is possible that the primary production of the ecosystem might have been influenced by the cobalt discharge.

7.4 *The sensitivity of the ecosystem*

In the case of the Rickleå river the possible direct toxic effects of cobalt to the fishes in all riverine stages may have been of smaller importance than the indirect effects via shortage of food. SPRAGUE *et al.* (1965) found that sublethal copper-zinc pollution in a salmon river affected both the migrations of salmon and the abundance of mayfly nymphs. It is, therefore, possible that a poor development of the mayfly fauna is typical for rivers polluted by heavy metals.

As has been shown above, the juvenile salmon is a drift feeder with a high demand for mayfly nymphs and other drifters. In natural waters there is a heavy drift of large nymphs in spring and early summer and the parr utilizes that resource. This is reflected in a high growth rate at that time of the year. As the pollution has harmed some of the most important winter growing food species the early spring and early summer has become a period of starving instead. Parr, normally living for about three years in the river, now should have had to pass three starving periods.

According to the electro-fishings the population of trout parr seems to have been less harmed than the juvenile salmon population. As has been shown earlier this might partly be the effects of the stockings of juvenile trout and colonisation from upstream areas. There are also some other possible explanations. Even if both species are drift feeders, it has been shown, that trout parr are less dependent upon mayflies (MAITLAND 1965) and eat terrestrial insects to a higher extent than juvenile salmon (ALM 1919, FROST and WENT 1940). This may be due to the fact that trout parr in contrast to salmon parr usually occupy the shallower areas of the rapids near the banks where air borne terrestrial insect are more likely to be common in the drift (LINDROTH 1955, KARLSTRÖM 1972). According to LINDROTH (1955) and KALLEBERG (1958) the trout parr are more aggressive and successful in defending territories than salmon parr. In the competition for remaining suitable feeding habitats the trout might have been stronger than the salmon.

That secondary production was disturbed by the cobalt discharge was clearly shown in the drift and *Fontinalis* investigations. The results obtained in the running water test may also be expressed in terms of production:

Cobalt ppb	mg subimago/aquarium and 28 days
< 2	229.5
5.2	172.4
32.6	70.0
470	0
3950	0

All aquaria with added cobalt gave lower values of production than the control. Production is a function of two main processes: survival and growth. In the running water test both were influenced, but growth seemed to be the most sensitive. The harmful effect of cobalt ions on secondary production of sensitive species seems to be a well documented fact.

At first it was not realized that the decreased production of salmon smolt could be a manifestation of a lessened production capacity of the whole ecosystem. The reading of a paper written by Dimond (1967) made connections more evident. Dimond studied the abundance of bottom fauna and drifting fauna in streams treated with DDT at various times in the past. Recovery of the bottom fauna was rapid, but that of drift was delayed. The relationship of quantity of drift to the increasing bottom standing crop during recovery from spray effects was found to be curvilinear and Dimond proposed that drift is a density related process.

In order to make the discussion easier the results of Dimond are shown in Fig. 21. In the recovery after the DDT spraying, the drift densities increased considerably in the second and later years after the spraying although the bottom fauna abundance was not changed. A similar development is to be expected in the Rickleå river in the years to come if the cobalt purification plant will function properly. In the past, however, the effects of a pollution that was slight from the beginning, but increasing year after year has been studied, *i.e.* a process opposite the situation shown in Fig. 21 and possible to predict by reading the numbers in the opposite order. In such a situation a decrease in number of drifting insects would occur much earlier than could be documented from a decrease in number of bottom insects. Among riverine fishes salmon parr are the fishes most dependent upon drift so it is quite natural that the salmon population has been affected much more than typical bottom feeders like sculpins and burbot.

The idea that drift is dependent upon production has been proposed by Müller (1954) and Waters (1961, 1962, 1965, and 1966). It appears that drift is a mechanism of removing excess production, operating to control population density as do other density dependent processes such as predation of disease. Drift seems to some part be a function of production rate. The ideas of Waters are in accordance with Dimond (1967).

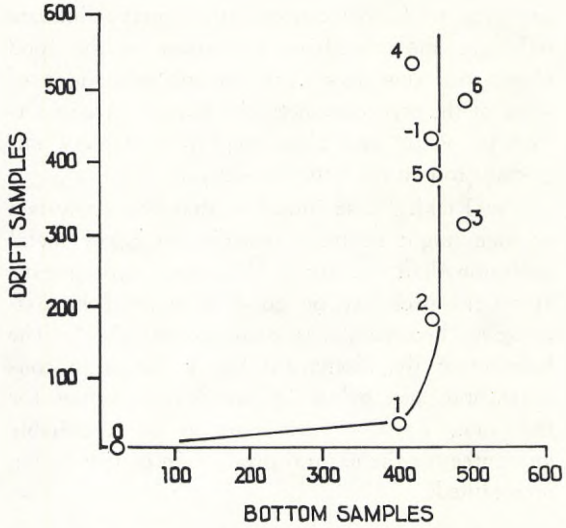

Fig. 21. Relationship between number of total insects in drift to number of insects in the bottom standing crop in streams of varying DDT-treatment history. Number accompanying the plotted points indicate elapsed since treatment of the streams. Redrawn from Fig. 2 in Dimond (1967).

In the example of the DDT sprayed streams, high production expressed as drift could not be reached before the time when optimal abundance of animals in the bottom was surpassed. The fact that the drift has decreased in the Rickleå river not only indicates that it is impossible for salmon parr to get enough food, it can also be regarded as a manifestation of a deterioration of the secondary production of the ecosystem.

When dealing with heavy metal pollution problems in rivers it must be considered that the metals are discharged into an ecosystem and not solely on fish populations. If it is reasonable to believe that fish are the most sensitive to the poison in question, the fish sensitivity must be investigated. In the opinion of the author there are often other organisms in the river that are more sensitive than fish, for instance mayflies.

From the study it is evident that the effects of released heavy metals in nature are difficult to overestimate. Observed mortality in nature occurs only when relatively high concentrations are present. Lower concentrations may eliminate only the most sensitive organisms in the food chains but this may cause drastic reductions of some of the top consumers like salmon. Accumulation in plants and algae may play a very important role in the lethal processes.

The Rickleå case indicates that the ecosystem as such might be more sensitive to heavy metal pollution than are fish in laboratory experiments. It would probably be good if many fish toxicologists became "ecosystem toxicologists". The keeping of the discharged heavy metals in concentrations just below known MATC-values for fish does anyhow not seem to be a reliable guarantee for the natural production of fish beeing maintained.

8 SUMMARY

In the Rickleå river in northern Sweden, salmon (*Salmo salar* L.) are present in the lowermost 15 km. The salmon population has been studied since 1961. In 1965 the density of salmon and trout parr decreased in some of the rapids and a drastic reduction of the numbers of sea-migration salmon smolts was recorded in 1966. In recent years the juvenile salmon population has decreased still more, and it is now very hard to find salmon parr by electro-fishing. It was not reasonable to believe that the decrease was caused by organic pollution or failure of spawning. Trout (*Salmo trutta* L.) has decreased to a lesser extent than salmon, and sculpin (*Cottus gobio* L.) is still very abundant in the rapids.

Simultaneously there has been a drastic impairment of the invertebrate fauna. Some of the insect species important as food for salmon parr are now absent or reduced in number. This has been shown by drift sampling and investigations on the *Fontinalis* community in the rapids. Although nymphs of the mayflies, *Baetis rhodani* and *Ephemerella ignita*, and backfly larvae are present in the mosses during summer, the winter-growing nymphs of *Ephemerella mucronata* and *Baetis rhodani* and winter-growing backfly larvae are absent or reduced in number in the area of salmon habitat. Most of the *Plecoptera* species are still present. The reduction of the invertebrate fauna explains the decreased population of salmon parr in recent years.

In 1963 a diamond factory began operation in the upper end of the area accessible to the salmon. Here nickel was used from 1963 to 1967, and since 1967 cobalt was used instead. In the process the metals have been dissolved in acids and the wastes were discharged into the river after neutralization with slaked lime. A laboratory investigation has shown that the treatment with lime did not prevent the metals from dissociating in the acidic river water. The consumption and the discharge of heavy metals has increased from year to year since 1963. A purification plant was not installed and in operation before November 1973. The decrease of the salmon population and the impairment of the invertebrate fauna are well synchronized with the activities at the diamond factory. An electroplating plant was also in operation in the same place in the years 1964—69.

Due to varying discharge, and water flow in the river the concentration of cobalt in the water, fluctuated in the years 1972—73. When the factory was closed in summer the concentration was below the detection limit of the analytical method (Atomic absorbtion = 1 ppb). In May and June the content of cobalt was low, 2—5 ppb, due to the spring flood. The highest concentrations prevailed during autumn and winter, 10—43 ppb, when the water discharge of the river was low. The yearly fluctuation was in accordance with the elimination of mayfly nymphs and blackfly larvae in the mosses in winter.

In the superficial layer of the sediments the concentrations of cobalt were higher below the discharge (14—24 ppm) than above (4—8 ppm). These values are not very high in comparison with other watercourses. In *Fontinalis,* however, the accumulation of cobalt was much more pronounced; 41—43 above and 770—820 mg/kg dry weight below the discharge (April 1973).

The sensitivity of the mayfly, *Ephemerella ignita,* to cobalt was investigated in a four week running water test. The nymphs were living on their natural substrate, *Fontinalis.* Cobalt nitrate was administered constantly. Drastic effects were recorded in sub-acute concentrations. In concentrations of 3,950 and 470 ppb added to the water,

all nymphs died within three weeks. With 32.6 ppb the mortality was higher and the emergence of subimagines was retarded in comparison with the control. The growth of the nymphs was slow and the appearance of handicapped subimagines was frequent at this concentration. The differences in development in 5.2 ppb and in the control were small but always in favour of the control. The weight of subimagines was decreased by 5.2 ppb of cobalt.

The experimental running water investigation suggests that heavy metal discharge from the diamond factory is the cause of the ecological damage noted in the river.

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Liming: An Overestimated Method for Preventing the Spread of the Crayfish Plague

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I. INTRODUCTION

In attempts to limit the local spread of the crayfish plague in upstream creeks and small rivers caused by the fungus *Aphanomyces astaci* SCHIKORA, treatment of the water with slaked lime has been the method most frequently used in Sweden (VALLIN 1936, UNESTAM *et al.* 1972, UNESTAM *et al.* 1974). By killing all the animals in part of an infected stream, the intention has been to prevent contact between healthy animals and live, diseased animals from the down-stream water. For reasons hitherto unknown, the method has in many cases been unsuccessful (VALLIN 1936). The present study was conducted to determine, under natural conditions, as well as under controlled conditions in laboratory experiments, the efficiency of $Ca(OH)_2$ in killing crayfish.

II. MATERIAL AND METHODS

Experiments were undertaken in a portion of River Svartån at Hörnsjöfors (Fig. 1). The crayfish, *Astacus astacus* L., (70—90 mm body length) were captured in Hörendesjön. In order to investigate the effect of liming on crayfish hiding in their burrows, standard draining tiles were used as artificial burrows. The inner diameter of the tiles was 5 cm and the length 25 cm. The tiles were enclosed in galvanized wire netting (mesh size 13 mm) to prevent crayfish from escaping. One end of the tile was sealed with a thick plastic foil, and at the other, open end, the netting formed a bag into which the animals could walk when leaving the tube (Fig. 2). Slaked lime $Ca(OH)_2$, was obtained from Cementa Ltd. In the field experiments, the tiles with animals were placed at a control station, 2 m upstream from the site of liming, and at stations 5 m and 25 m downstream from the site of liming. The tubes were placed in the direction of the current with the open end facing downstream.

One crayfish was placed in each tube and was replaced by a new one before each experiment. At all these stations and at the 40 m site (Fig. 1) (without crayfish), the pH was measured at regular intervals during the experiments. The water temperature was about 20°C.

Laboratory experiments were also undertaken to test, under controlled conditions, the tolerance of the crayfish to high pH values. In an aquarium, with 6 litres of tap water, the pH was adjusted and maintained by slaked lime. Continuous air-bubbling was maintained during the experiments. The aquaria were kept at a constant temperature of about 14°C. The crayfish were exposed to the limed water for various lengths of time. After exposure, the crayfish were placed in aquaria with fresh tap water.

All pH measurements were made with a field pH meter (E 488, Metrohm Herisau).

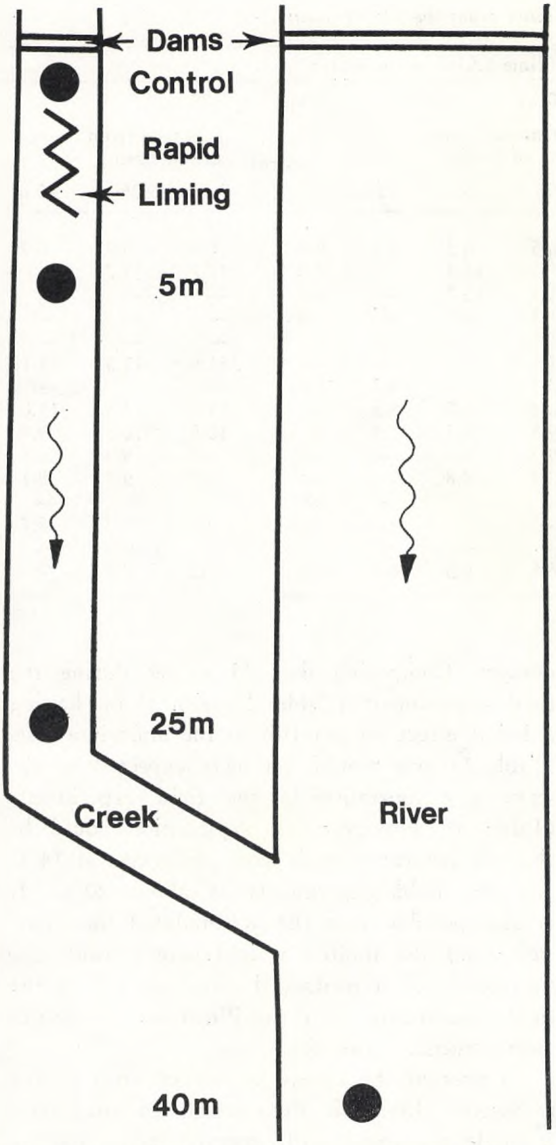

Fig. 1. Schematic picture of the area used for the field experiments. The average width and depth of the creek was between 1—2 m and 0.3 m. The water flow was approximately 0.05 m^3/s in the creek and 0.5 m^3/s in the river (●) sites for pH measurements and encaged crayfish at different distances from the site of liming. No crayfish were at the 40 m station.

III. RESULTS

Table 1 shows the effect of slaked lime on crayfish in aquaria. It was apparently necessary to raise the pH to about 11.7 for more than 5 hours at 14°C in order to kill all the crayfish; pH 10.7 during 16 hours had no effect on their survival.

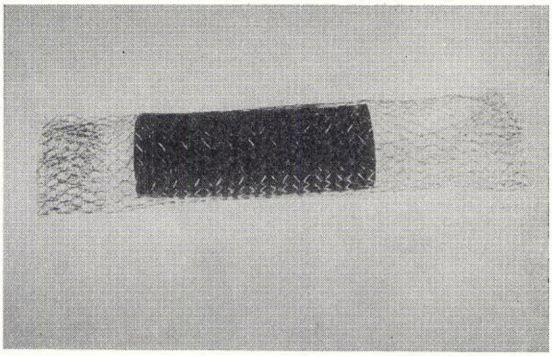

Fig. 2. An artificial burrow for crayfish. Standard draining tiles (inner diameter 5 cm, length 25 cm) were enclosed in galvanized wire netting (mesh size 13 mm). One end was sealed with thick plastic foil, and at the other end the netting formed a bag into which the animals could walk when leaving the tube.

In the field experiments, pH values above 11.5 could not be maintained for more than approximately 1 hour at 5 m and 25 m downstream from the site of liming, despite the fact that 300 kg of $Ca(OH)_2$ was used (Table 2). At the 25 m site only the 300 kg dosage, but at the 5 m site also the 50 kg dosage gave substantial lethal effect on

Table 1. *Survival of crayfish in aquarium water at different pH values. The pH was continually adjusted with lime, $Ca(OH)_2$, and 3—8 crayfish were exposed to different pH values for varying periods of time. After exposure, they were maintained in fresh tap water. Temperature 14°C.*

Exposure time, hours	Killed crayfish/total crayfish pH 10.7	pH 11.7[1]
0	0/3	0/4
1	1/3[2]	0/4
2	0/3	0/4
3	0/3	1/4[3]
4	0/3	0/4
5	0/3	5/8[4]
16	0/6	6/6[5]

[1] Maximal pH, saturated solution of $Ca(OH)_2$.

[2] Dead after 7 days in fresh tap water.

[3] Dead after 5 days in fresh tap water.

[4] Three individuals dead after 4 days and two after 7 days, in fresh tap water.

[5] Dead after 1 day in fresh tap water.

Table 2. *pH variation versus time in a creek at different distance from the site of liming.*

Time after liming, huors	Dosage of slaked lime added in the water											
	0 kg	25 kg			0 kg	50 kg			0 kg	300 kg		
	Control	Distance from site of liming			Control	Distance from site of liming			Control	Distance from site of liming		
		5 m	25 m	40 m		5 m	25 m	40 m		5 m	25 m	40 m
0	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.9	6.9	6.9	6.9
0.05	6.8	11.8	10.8	—	—	11.1	11.3	—	7.0	11.7	11.7	—
0.1	—	11.3	11.0	—	—	11.5	11.7	—	—	—	—	—
0.15	6.6	10.9	10.7	—	6.6	11.3	11.5	—	6.9	—	—	—
0.25	—	10.7	10.4	—	—	11.1	11.2	—	—	—	—	—
0.5	—	9.9	9.8	—	—	11.0	11.0	—	—	11.6	11.5	11.1
0.75	—	9.7	9.5	8.6	6.5	10.5	10.4	9.3	6.9	—	—	—
1	—	9.5	9.1	7.7	—	10.2	10.0	8.5	—	11.5	11.5	11.0
2	6.5	8.9	8.5	6.7	—	9.5	9.3	7.4	—	10.5	10.5	9.7
3	—	8.3	7.2	—	—	9.3	9.3	—	—	9.8	9.9	8.8
4	—	7.7	7.0	6.6	—	8.9	8.8	—	—	9.7	9.7	8.1
5	—	7.2	6.8	—	6.5	—	—	—	6.9	—	—	—
6	—	—	—	—	—	—	—	—	—	9.3	9.2	7.7
7	6.5	—	—	—	—	—	—	—	—	—	—	—
20	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	7.1	7.2	7.2	7.1

the animals. However, no complete killing of crayfish was obtained at any station (Table 3). Also, the time for death of affected animals, after exposure to the 50 kg dosage, was much longer than that after exposure to the highest dosage.

IV. DISCUSSION

The smallest dosage of $Ca(OH)_2$ used (25 kg) gave the maximum pH at a distance of 5 m from the site of liming (Table 2), but this pH lasted for only a very short time. The higher dosages, of course, affected the pH at a longer distance downstream from the site of liming, and also had a prolonged effect compared with the lower dosages. Comparing the pH values during the field experiments (Table 2) with those having a lethal effect on crayfish in the aquarium tests (Table 1), one would not have expected to observe any mortality in the field experiments (Table 3). However, an explanation could be that the laboratory tests were performed at 14°C and the field experiments at about 20°C. It is also possible that the accumulated lime particles and the limited water current inside the tiles produced a prolonged effect on pH in the field experiments that is not illustrated by the pH measurements (Table 2).

Table 3. *Effect of slaked lime on crayfish in natural environment. All 5 test animals survived at the control site, 2 m upstream of the site of liming.*

Distance from site of liming m	Killed crayfish/total crayfish Dosage of slaked lime, kg		
	25	50	300
5	0/5	3/5[1]	4/5[2]
25	0/5	0/5	3/5[2]

[1] Mean time for death 3 days.
[2] Mean time for death 1 day.

To prevent the spread of the crayfish plague in Sweden, liming is often conducted using only a single treatment with approximately 100 kg $Ca(OH)_2$ in creeks of the size used in our experiments. Such treatments are probably quite ineffective in giving rise to a crayfish free zone. It is therefore evident that liming is a very unreliable method against the plague. If, however, liming has to be used, the following considerations should be born in mind in order to obtain optimal conditions for local killing of crayfish in a water system:

1. The place chosen should be one where the water is completely stationary or can be made stationary during the treatment.

2. The pH must exceed 11.5 for at least one day.
3. Repeated liming during two or more consecutive days is recommended.
4. The effect of the treatment on caged crayfish after the liming should always be checked.

To obtain full protection against the spread of the plague it is strongly recommended that liming shall be combined with the installation of an electrical barrier (UNESTAM *et al.* 1972, UNESTAM *et al.* 1974), which today is the only effective method of preventing migration of crayfish. Liming can, for instance, be used in ditches and other small tributaries joining the creek below the site of an electrical barrier in order to eliminate any possibility of prolonged survival of the parasite. This would also reduce the risk that people or animals will transport diseased crayfish to the water above the electrical migration barrier, or even to other crayfish waters.

V. SUMMARY

The lethal effect of liming with slaked lime, $Ca(OH)_2$, on the crayfish, *Astacus astacus* L., was studied. It was obvious from both laboratory and field experiments that this method had little or no effect on the animals unless saturated solutions were used. A long exposure in an aquarium for about 16 hours at pH values above 11.5 was required to kill the total crayfish population. In a natural environment, a small crayfish stream, such conditions do not occur unless the water flow is extremely slow. Recommendations are given on how to apply liming in order to limit the spread of the crayfish plague.

VI. ACKNOWLEDGMENTS

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The Decline of the Baltic Eel Population

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I. INTRODUCTION

The Baltic basin, with its brackish water and tens of thousands of freshwater lakes on numerous rivers, is an important growth area for the European eel (*Anguilla anguilla* L.). The elvers reach the Danish Straits, Øresund and the southernmost coast of the Baltic in late spring. From northwestern Skåne (Scania) and from Lithuania in the east the young eels proceed northwards more slowly. They require 5—6 years to spread to the mid-Baltic, say the Åland archipelago. Very little is known, however, about this gradual dispersal northwards along the coast.

Most of the Baltic basin is populated by female eels only. These have an almost incredibly efficient dispersal mechanism. In a sample of 1,670 Swedish lakes in southern and central Sweden, eels were recorded in 73 %. Eel inhabited 92 % of the lakes below 50 metres altitude. Above 300 metres, eel were still recorded in 49 % of the lakes (SVÄRDSON 1972).

In northern Sweden and in Finland, eels are rarer. They still inhabit most of the lower lakes around the northern part of the Gulf of Bothnia. Eels may grow to a considerable size in the northern parts of the Baltic basin. JÄRVI (1909) found 580 eels from the Kymmene river, Finland, to weigh an average of 1.36 kg. NORDQVIST and ALM (1920) noted an average of 0.78 kg for 1,400 silver eels in the River Ljusnan, Sweden. Eels of 4—5 kg are now and then recorded, the biggest known specimen weighing 7.6 kg (SVÄRDSON 1972, p. 175).

The Swedish exploitation of the eel is traditionally based on the silver eel, which is caught during its emigration from the lakes or on route along the coast. The commercial fishery takes advantage of the concentration of migratory silver eel along the south-east coast of Sweden. The crowding of eel here results from their heading south-west during the emigration from the Baltic (Fig. 1).

II. TRENDS OF THE FISHERY

Big pound nets were introduced, from Denmark, to the coast of Skåne in 1909. They proved rather efficient and their use gradually spread, especially in the 1920s. In 1948 there were some 1,100 commercial eel fishermen, operating 1.500 pound nets. Most of these were on the south-east coasts of Sweden. The yield of the pound nets is best with the wind from the SE sector and a new moon. The season for the commercial fishery is August—November.

Fyke nets of varying size are also used. Other forms of fishing, some surviving from medieval times, are less significant from an economic point of view. In recent years, small fyke nets, called "pair nets" have become popular with noncommercial fishermen in the Øresund area. Nowadays there is also a demand for yellow (growing) eels, as the price for eels has risen considerably.

The best fishery, that on the south-east coast, had its peak already in the late 1930s (Fig. 2). During the 1960s, however, the yield dropped at an alarming rate. The catch is now about 500 tons, *e. g.* half of the best yield 30 years ago.

In the second best fishery, in the province of Skåne, the peak was not attained until the late 1950s, when the fishermen produced a thousand

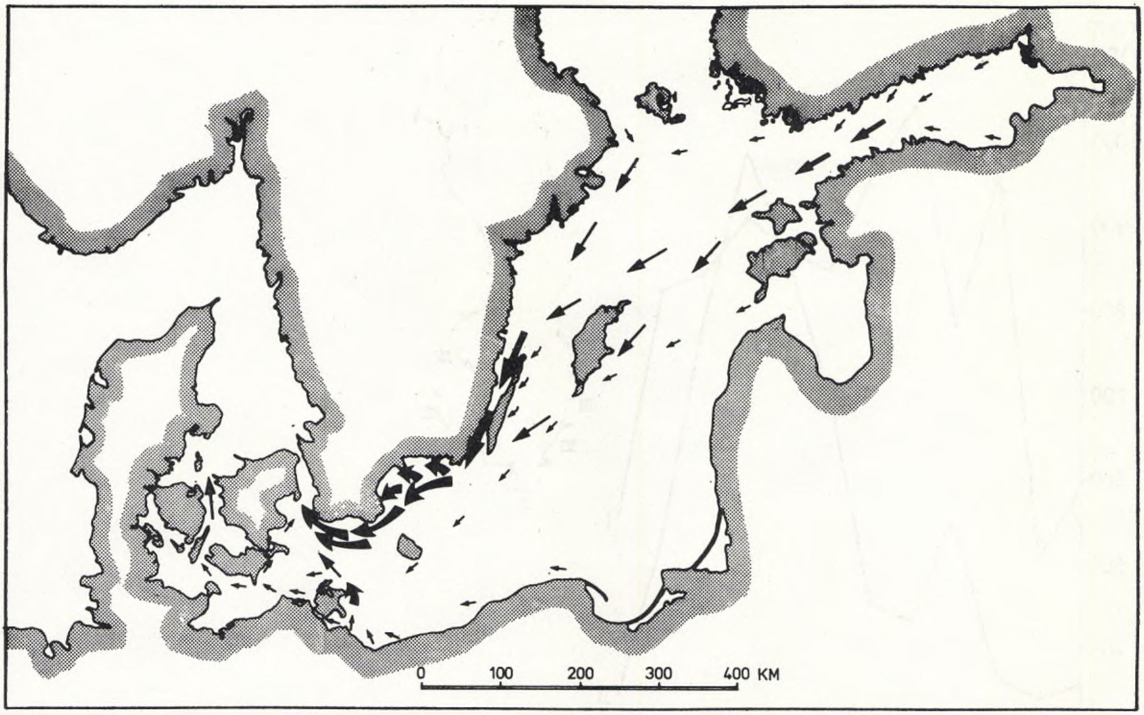

Fig. 1. Silver eel migration in the Baltic, as revealed by several tagging experiments.

tons. In the early seventies this stretch of the coast reported only 300—400 tons.

On the northernmost part of the Swedish west coast, yellow eel were, until quite recently, being trapped in increasing numbers, figures of 200—300 tons being reached in the 1960s. During the last few years, however, this fishery too has suffered a downward trend. The small eel fishery on the east coast, off Stockholm, has also declined recently (Fig. 2).

The general picture emerging from the official statistics is consistent with the interpretation that the various fisheries produced higher yields with increasing effort up to a certain turning point. The new, downward trend was first experienced by the most advanced fishery and subsequently spread to all the other coast regions. This indicates a gradual decline of the eel population, presumably since around 1940.

From international statistics it appears that the Swedish eel fishery in the Baltic is fairly representative of the eel fishery in the whole basin.

III. ELVER AND YOUNG EEL RECORDS

The eel has always been esteemed in Sweden. There are records of introductions of young eel into new lakes from the 18th century (GYLLENBORG 1770). It was early recognized that climbing young eels accumulated below waterfalls. They could be trapped and used elsewhere for management purposes.

TRYBOM (1893), who later became head of Sweden's national fishery administration, strongly recommended the activities of a profitable private enterprise to trap and sell young eels below the huge waterfalls at Trollhättan on the Göta river, just downstream of the great Lake Vänern. To this day, Trollhättan eels have a wide reputation as stocking material. They vary in size (8—45 cm), with an average of 20—30 cm (Fig. 3). Most of them are 3—5 years old (ASK *et al.* 1971) and the age distribution is 1—10 years.

When rivers were blocked by dams for hydroelectric plants, the damage done to the eel fisheries upstream was dealt with by special water courts.

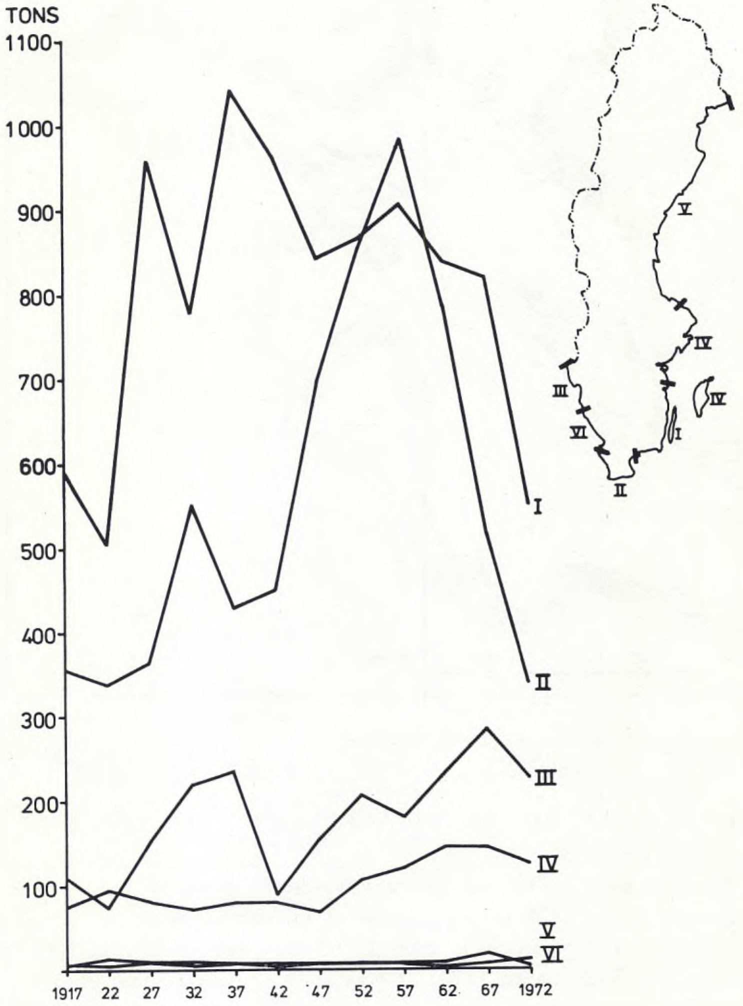

Fig. 2. The eel catch on the Swedish coast. Freshwater yields are not included.

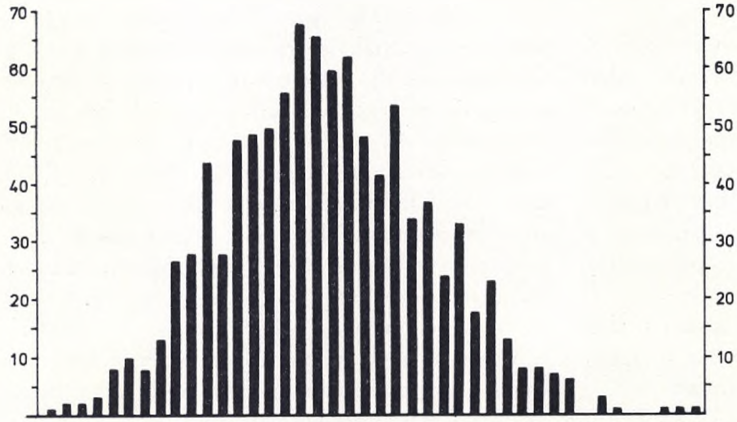

Fig. 3. Size distribution of ascending eels at the Trollhättan water falls.

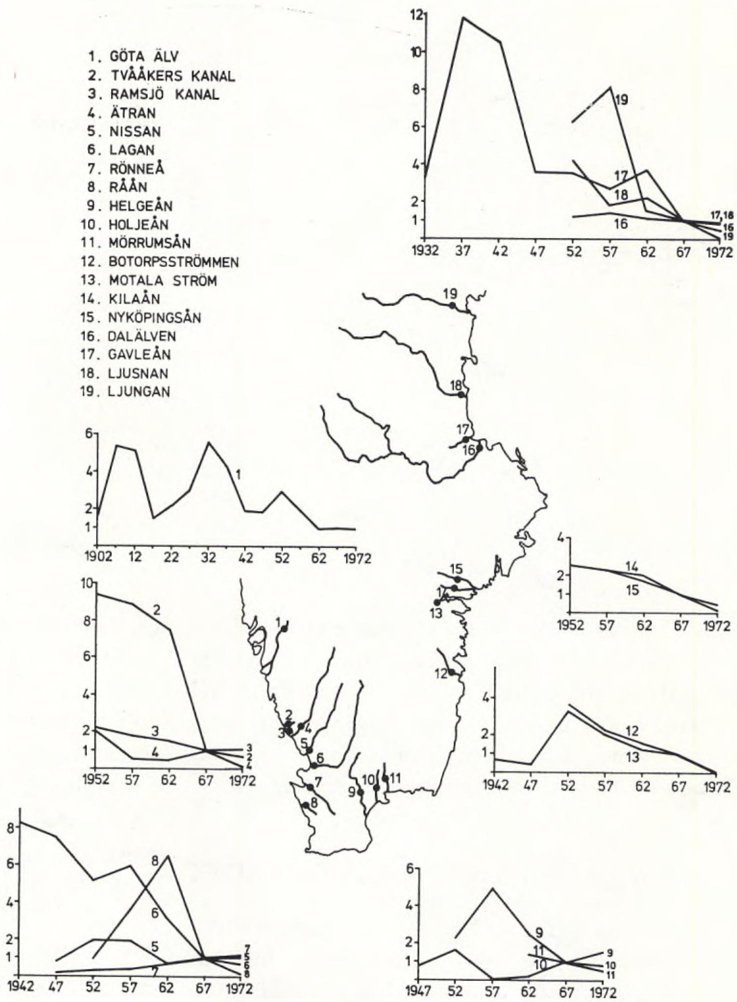

Fig. 4. Trends in numbers of elvers or young eels, collected near the coast.

In many cases the verdict was that the hydroelectric company should provide the fishery-right owners with young eels as compensation. This gradually led to the construction of "stations" where elvers or young eel were trapped annually and redistributed elsewhere. This activity has created a series of official records of the eels handled.

This information is summarized in Fig. 4. At every station the annual variation in elvers or young eel varies greatly, according to the summer temperature and other, less known, environmental factors. Stations 2—8 mainly register true elvers. The other stations trap eels of varying age; on the east coast, on the River Dalälven, the climbing young eels are 6—7 years of age, *e.g.* the post-elver age (Ask *et al.* 1971).

The records relate to numbers (thousands or hundreds) or kilogrammes. In order to construct Fig 4 the records were smoothed to five-year means and a relative scale was constructed where the average of 1965—69 was used as unit (1). In this way the overall trend of declining numbers, on both coasts, became evident. The reduction of numbers is considerable, and the longest series indicate that the trend has been steady since the late 1930s.

The conclusion is that, for some reason, the annual number of elvers entering the Skagerrack

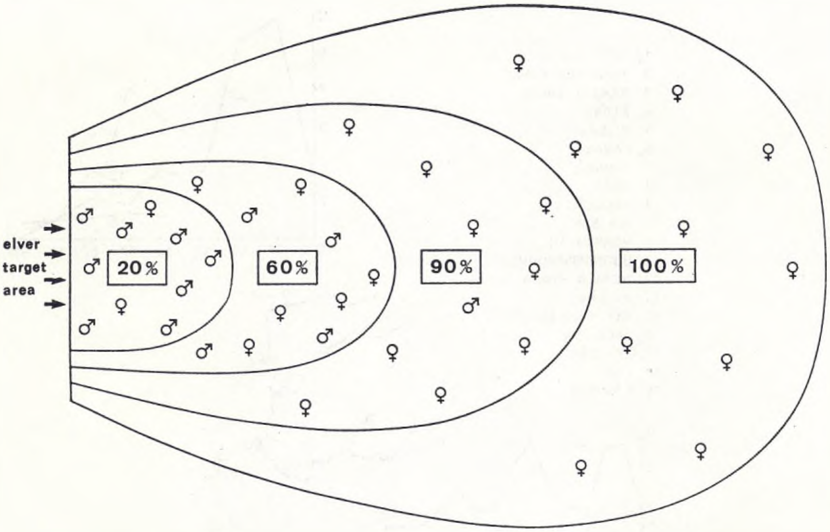

Fig. 5. Differential spread of male and female eels.

after passing through the North Sea has been declining over a long period. This must be the ultimate factor behind the fate of the Baltic eel fishery. Local environmental problems, *e.g.* pollution, which have been blamed in the general discussion, seem to be of lesser significance.

IV. SEX RATIO AS A POPULATION INDEX

The sex ratio of the eel has confused many writers. The discussion has been rather sterile and has tended to focus on genetic *versus* environmental sex determination.

A more fruitful point of view is the evolutionary strategy of the two sexes in the freshwater eel *Anguilla*. The male sex takes advantage of the growth area in order to acquire a size and an energy potential large enough to take the individual back to the spawning grounds in the far-away Sargasso Sea. Excess size is not selected for, since the males, as well as the females, all die after spawning. It is illuminating that in Europe as a whole there is only a small variation in the average size of the male, *viz.* 38—50 cm.

The female, however, is under a quite different selection pressure. The more it can grow, the higher is the number of eggs produced (a rough estimate runs into millions). The genes of the biggest females have the best chances of being carried over to the next generation. The pressure selects for a female eel, utilizing the growth potential of the freshwater (or brackish) area to its maximum. This calls for a more advanced dispersal mechanism than the male needs to have.

Territorial behaviour is the normal way by which individuals are evenly dispersed over a suitable area. Eels in aquaria are aggressive, in the same way as trout or other well-known territorial species (NYMAN 1972). Field observations, however, indicate that eel fan out and disperse within a water system rather secretly, and apparently fights or threat display have not been recorded.

The olfactory capacity of the eel is remarkably well developed (TESCH 1973) and the lateral location of the nostrils may indicate a potential for recognizing spatial odour gradients. This may enable the eel to locate other eels in the vicinity. In this way territorial behaviour could be enforced from a distance. It is a fact that yellow eels, at the age of 10 years or more, may still be caught in traps climbing upstream, *e.g.* they are heading for growth and fattening habitats still more distant from the spawning grounds.

Elvers are attracted by the odour of older eels (MILES 1968). This reaction must be selected for, as it leads them to suitable rivers. When they start growing into the yellow stage, however, the reaction to the stimulus should switch to the

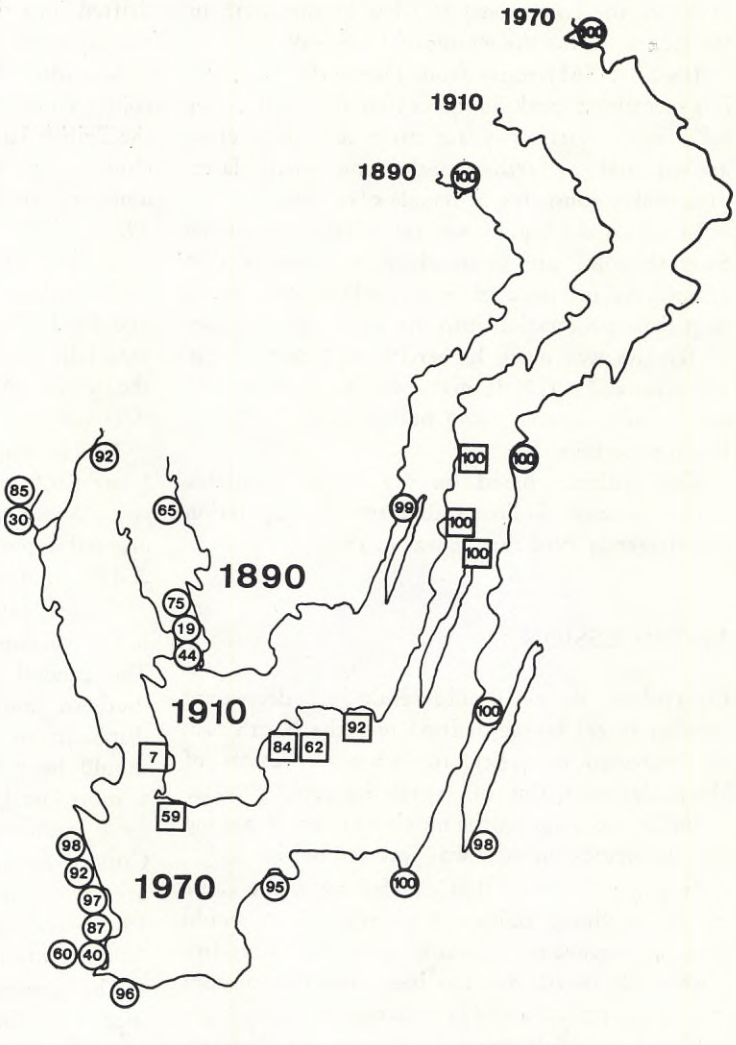

Fig. 6. Percentage of female eels along the Swedish coast in different periods.

opposite; otherwise they would crowd in the river mouths and become stunted. The males actually do this — and thus present next year's elvers with the proper stimulus. The females, on the other hand, behave in a way indicating they are repelled by the odour of their own species.

The consequences of this evolutionary scenario are depicted in Fig. 5. The higher the number of elvers striking a target area of the coast, the lower will be the future percentage of female eels within the target area, since the higher the population pressure, the more the females are stimulated to get away.

If this be true, the sex ratio at the coast could be used to give some additional evidence of population fluctuations. If the same area is found to display an increasing number of females in two time periods, the population trend should be downward.

There was an unusual influx of elvers in 1957 on the German coast of the western Baltic. In several streams elvers appeared as early as April and continued to climb until July (Hermann 1957). In 1963, the catch of silver eels in the area was 400 tons above the average and the number of males was "besonders gross" (Tesch, 1973, p. 187).

The elver station on the River Rönne, Sweden, registered a peak in 1961. Ask *et al.* (1971) found a temporary peak in the frequency of yellow eel males at the coast some 100 km to the south of the Rönne during the winter of 1968—69.

Jensen (1961) states from Denmark that there is generally a peak in the catch of small silver eel (males) some 7 years after a record elver arrival and a further peak some years later, presumably consisting of female silver eels.

In Fig. 6 the known sex ratio figures from the Swedish coast are summarized. It appears that around the province of Skåne, where most males stop their penetration into the Baltic, the number of females was much higher in 1970 than in the years around 1910. It may even be that females were also somewhat more numerous in 1890, but this is uncertain.

The evidence based on sex ratios, available from the coast, indicates that the eel population was bigger in 1910 than it was in 1970.

V. DISCUSSION

Overfishing the eel should result in a decreasing number of eel larvae drifting into the North Sea. An increased mortality, for whatever reason, of the eel larvae within the North Sea could produce a similar reduction of the number of larvae passing the Skagerrack on their way into the Baltic.

In order to prove that overfishing is the cause of the declining Baltic eel population, it would first be necessary to show that the mortality within the North Sea has been roughly constant during the period under consideration.

This is certainly not possible. On the contrary, there is strong evidence that conditions have changed. Most probably the conditions have become more adverse for the eel larvae, which are believed to drift into the North Sea from the north of Scotland.

In the first place, the frequency of westerlies, *e.g.* winds from the W or NW, is lower than earlier. Lamb (1969, 1972) summarized the weather changes over the British Isles during the period 1861—1971. He found the westerlies to be most frequent during the months December—January (when the eel larvae are around) and to have increased from 1880s to the 1920s, followed by a lower frequency and a new minimum (so far) in the 1960s. Thus, already the chance of being drifted into the North Sea has been reduced for the eel larvae.

Secondly, the temperature has changed, giving a colder climate. Since 1940 the growing season on the British Isles has been shortened by two weeks, eliminating two thirds of the gain during the amelioration of the climate in the period 1900—39.

In the north-western part of the North Sea, the abundance of diatoms decreased between 1958 and 1972 (Reid 1975). The zooplankton biomass, especially the copepods, has become smaller and the season of its occurrence has become shorter (Glover *et al.* 1973).

The cooling of the North Sea (Dickson and Lamb 1972) seems to have favoured the cod, which is an Arctic species (Dickson *et al.* 1974). There are old reports from the Öresund area that the cod may gorge on elvers (Willumsen 1892).

Coombs (1975) reported reductions in the number of various fish larvae around the British Isles. The general change was a lower frequency of southern fauna elements as well as a southward displacement of the larvae of some species. It should be remembered that the eel larvae have a subtropical origin and should be looked upon as a southern element of the North Sea fauna. Coombs found that "many, perhaps most, pelagic organisms underwent a marked change in about 1965—67, in the waters of the north-western Atlantic and the North Sea".

The general overfishing of commercial fish species in the North Sea has caused a turmoil of changes in the relative abundance of various species. The competition for planktonic food as well as the predatory pressure must have changed profoundly for the eel larvae in this region of the Atlantic.

VI. MANAGEMENT

For the Baltic fishermen there lies little hope in waiting for a climatic change or for the overfishing of the North Sea to be remedied. There is no elver penetration into the Baltic north of Skåne and Lithuania on the east coast. Experiments should be performed, as previously suggested by the present writer (Svärdson 1966), to release elvers from the Atlantic into areas of the southern Baltic, *e.g.* between the islands of Bornholm and Öland. They could grow in the Baltic proper or climb rivers of their own choice.

The Swedish authorities have been hesitant in their attitude towards this proposal. They have referred to the risk of contamination by the salmon disease UDN. However, in 1975 this disease had an outbreak in some Swedish Baltic rivers. Therefore, no additional risk seems to be connected with experimental plantings of large numbers of elvers. A first planting was made in 1976.

VII. SUMMARY

Catch records indicate a declining eel population along the Baltic coast of Sweden. The trend, which may have started around 1940, has in recent years accelerated at an alarming rate.

Records from 19 stations along the Swedish west and east coasts, where elvers or climbing young eels are caught, show a decline in numbers over several decades. This proves that the eel larvae drifting into the Skagerrack from the North Sea must have become fewer.

The sex ratio of eels along the coast of Skåne has changed during the period 1910—70. Females have become relatively more numerous, a development which is interpreted as further evidence of a decreasing eel population pressure.

The mortality of eel larvae within the North Sea has in all probability increased in recent years as a result of the trend towards a cooler climate and the consequences of overfishing various fish species.

Large-scale introductions of elvers into the southern Baltic are suggested as experiments for future management of the eel stock.

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Interspecific Population Dominance in Fish Communities of Scandinavian Lakes

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I. INTRODUCTION

In animal societies individuals are often ranked in hierarchies with or without dominance (see WILSON 1975 for a general discussion).

In freshwater fish communities the different species build up populations of varying density. Often a few species dominate the standing crop of fish in a lake. As an analogy to individuals in societies, it may be fruitful to think of specific dominance hierarchies in lake or river communities.

The essential point of such an analogy is that the elimination of the top-ranking individual in an animal society or the reduction of the top-ranked population in a community brings about more or less drastic changes in the lower-ranked categories.

For a better understanding of the dynamics of a lake or river ecosystem, some knowledge of the dominance order of the various fish populations is a prerequisite. For management purposes it is very important to know whether the upper population limits of a valuable fish species are set by abiotic factors or, conversely, by the presence of another fish species that may have little or no economic value and consequently has been but poorly studied.

A small change in water chemistry or shore topography may have great consequences from the multiplier effect brought about by the dominance order of the various specific populations. If the "key" species, starting the multiplier effect, has for historical reasons a patchy regional distribution, the strikingly divergent population development in two lakes or rivers under similar environmental stress may seem confusing.

It is the purpose of this paper to review the Scandinavian evidence on dominance phenomena among some freshwater fish species.

II. METHODS

All kinds of interaction between species may be operative in a freshwater fish community. Obviously, it is of great interest to know, whether competition for food, predation or aggressive behaviour is the main mechanism by which one species interferes with the population size of another species. First, however, it is necessary to document the general trend of population influence, *i.e.* to find out which one of a species pair is normally numerically dominant, and to discover in what marginal environment this rank order can be weakened or, possibly, reversed.

The simplest way to study the rank order of a species pair is to survey the greatest possible number of lakes in similar environments and to record the relative sympatric abundance. Then there come into focus the extreme cases, where one of the pair is exceptionally rare or possibly does not exist at all. In such cases the population of a subordinate species tends to flourish.

Population fluctuations may also give some hints. Rich year classes in one species may tend to give poor year classes in the subordinate species and, since fishing pressure is seldom the same for both species, the reactions of each to exploitation may give some further evidence.

Particularly instructive are cases where one species has been introduced by man into ecosystems formerly inhabited by the other species under study. An introduced dominant may ruin the population of the subordinate species in a short time. Conversely, the introduction of the subordinate species may result in a total failure.

Normally there are more species in a lake than the two specifically under study. The majority of species produce a "background noise" that should not be dealt with until the relation between the first two species is revealed. If the rank order, in all its complexity, is examined in only one or a few lakes with many species, the interspecific web of interaction will almost certainly be too complicated for analysis.

Scandinavia is inhabited by few freshwater fish species. Only half a dozen had postglacial possibilities of invading western Scandinavia from the Atlantic. The Baltic basin was twice filled by fresh water, first during a cold early postglacial period when hardy arctic species could spread, secondly during the warm Ancylus period when even warm-water fish like the European catfish (*Silurus glanis)* could reach Sweden from the south-east. The total fauna comprises some 40 "Linnaean" species (sibling species excluded). The largest lakes of southern Scandinavia have some 20—30 species, while the high-altitude mountain lakes have only one, two or up to half a dozen species of fish.

Introduction of fish into new lakes has been very popular among Scandinavian fishery-right owners since time immemorial. The oldest record (telling of the introduction of brown trout into a barren lake) comes from Norway, where it is inscribed on an 800-year-old runestone from the Viking era (Dahl 1913). The discovery of artificial fertilization of fish eggs in the 19th century took this introduction activity to new peaks.

III. RESULTS. REVIEW OF CASE HISTORIES

Brown trout (Salmo trutta) versus Arctic char (Salvelinus alpinus)[1]

The relation between brown trout and char is the most intensively studied interaction phenomenon in Scandinavia. It was mentioned by Løberg (1864) in a book on Norway's fish fauna that the currently numerous introductions of char into trout lakes had become detrimental to the trout. The overall experience, verified again and again up to the 1970s, was explicitly expressed by Huitfeldt-Kaas (1918): "where char is introduced and thrives, the trout regularly becomes sparser, and in lakes without spawning streams I know of cases where the char has completely exterminated a formerly dense trout population" (author's translation from the Norwegian).

Sometimes the introduction of char into lakes was no doubt a deliberately planned management operation in order to raise the total production of fish. As illustrated in Fig. 1, the combined catch of both species is normally higher than when trout is the only fish species in the lake. The Lapps, roaming about with their tame reindeer in the Scandinavian mountain area, credit the char with having more delicious flesh, being more durable when fished and, above all, giving better yields from a certain lake area. Consequently they spread the char to barren or brown trout lakes.

As used in this paper, the term dominant is given to a species which builds up a more numerous population, *i.e.* a larger standing crop, than a second species, which is then dominated. Clearly the char dominates the trout in mountain

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[1] The Arctic char complex comprises three species in Scandinavia (Svärdson 1961 a, Nilsson and Filipsson 1971, Nyman 1972). Dominance of the most pelagic sympatric char species seems to occur. In order to keep the discussion as short as possible, however, the char complex is treated in this paper as a single species.

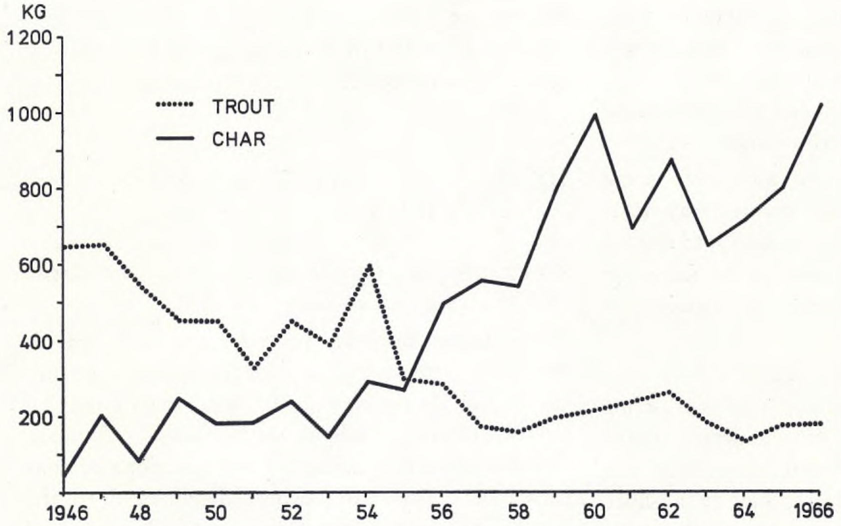

Fig. 1. In Lake Loutaure, Vindelälven river, introduced char has reduced the brown-trout population. Total yield, however, has increased.

lakes. Since the ecology of both species is fairly well known, the dominance of char can be traced to its being more planktivorous and flexible in diet, less aggressive (sometimes even schooling) and having a broader range of potential spawning grounds.

The diet of the two species has been studied by a number of authors (DAHL 1916, 1920, SCHMIDT-NIELSEN 1939, DAHL and SØMME 1947, AASS 1957, 1971, NILSSON 1955, 1964, 1965, 1967). Generally the two species have rather similar diets, but the char is a more adept plankton predator and the trout starts a predatory fish diet earlier in life. Both can feed on *Gammarus* to the extent that the amphipod becomes rare. When trout and char live sympatrically, their diet is different from it is when they live allopatrically; it is also more specialized. This phenomenon was termed interactive segregation by NILSSON (1967).

Fig. 2 demonstrates that the stabilized balance

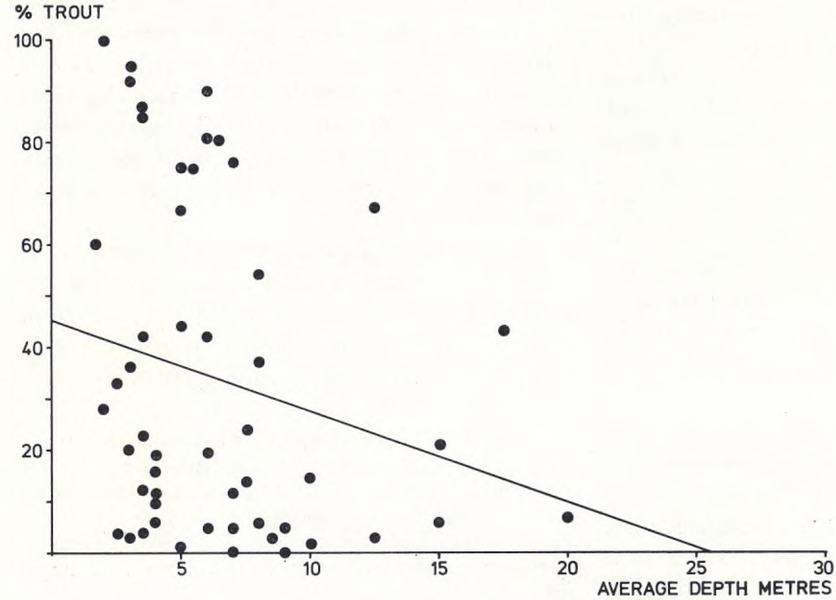

Fig. 2. Percentage of brown trout in 53 mountain lakes, northernmost Sweden. The sympatric char is more abundant in deeper lakes.

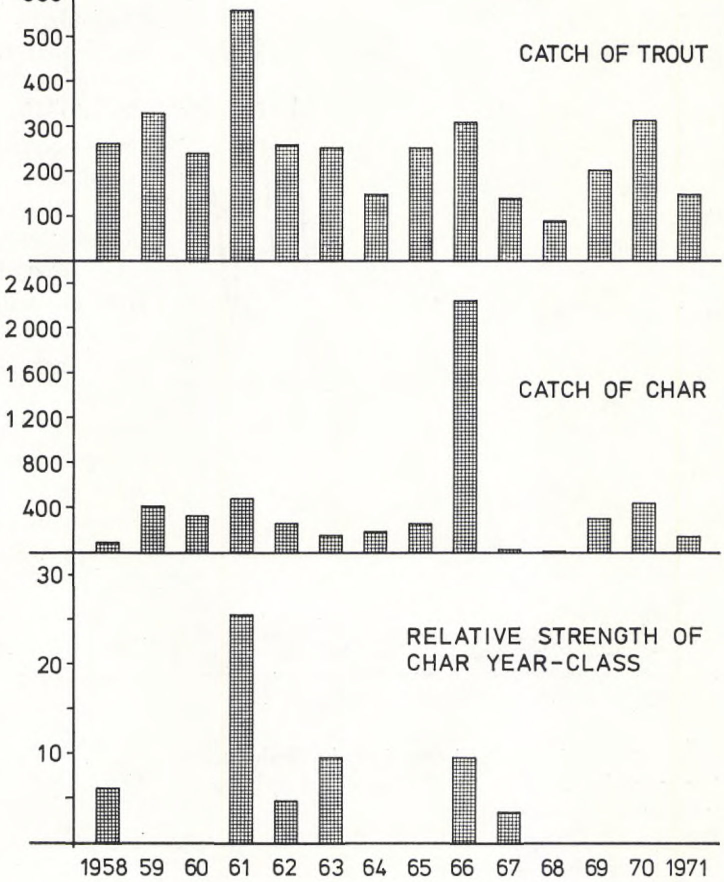

Fig. 3. Population-reduction experiment in Lake Långbjörsjön (*cf.* Fagerström 1972). Note the rich year-class of char in 1961 when many (predatory) trout were removed.

between trout and char may swing widely. The lake sample comes from the northernmost part of the Swedish mountains. Of the 15 lakes where trout was recorded as comprising at least 50 per cent of the catch, all but two had an average depth of 7 metres or less. This confirms the opinion of Huitfeldt-Kaas as to the importance of littoral habitats (including the streams). If the stream area of the lakes had been recorded in the sample, the stronghold of the trout in streams would certainly have appeared. Curry-Lindahl (1957) noted that char lived in streams only in the very highest mountains and he found a small creek where char lived above a small waterfall whereas trout lived below it.

Fig. 3 is based on material published by Fagerström (1972). Management experiments in Lake Långbjörsjön included removal of exceptional numbers of trout or char in different years in order to push the balance in favour of larger brown trout, which is the fish preferred by anglers. When, in 1966, four times the average number of char were removed, the effect on the char year-class hatching the next spring was small. When, however, twice the average number of trout was eliminated from the lake in 1961, the survival of first-summer char trebled. This indicates the pressure by trout on char; this probably took the form of predation by larger trout on small char, mainly fingerlings of the year.

In spite of the considerable effort made by Norwegian and Swedish biologists over the years to reveal the diets of both species, no period of concentrated predation on char fingerlings has been found so far. It may be that there is one in the late autumn, when trout move back from the

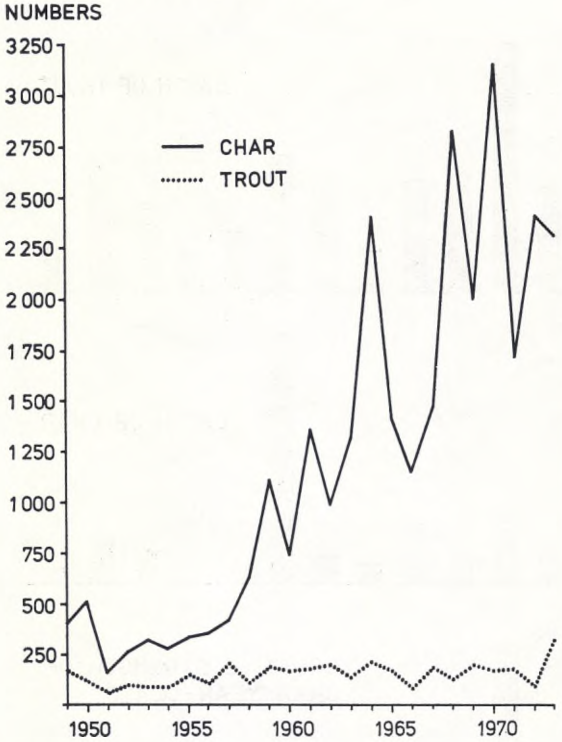

Fig. 4. Catch of trout and char in Lake Skalsvattnet. The expansion in numbers of char is found in many Scandinavian mountain lakes.

streams to the lakes and prefer the warmest water available in fairly deep layers. DAHL (1917) first noted that trout were found in deep waters at that time. The predatory habits of larger trout are, of course, well known, as is also the relatively low frequency of cannibalism. AASS (1957, 1971) found that 70 % of 638 trout from the large Lake Tunnhovdfjord were fish predators in the period 1949—51, when the lake abounded in small-sized char, while 400 trout from 1927—31 were all non-fish predators at a time when char had not yet invaded the lake from an introduction made far upstreams in 1910 (DAHL 1916, 1920).

Figs. 4 and 5 demonstrate what Swedish fishery managers have called "the char problem". In many mountain lakes, principally inhabited by trout and char, the population of char started to increase in the late 1950s. At the same time, the average weight went down, the quality of the flesh deteriorated (the colour changing red-yellow-white) and the frequency of parasites increased. The char simply became more stunted than before, in spite of high fishing pressure.

FILIPSSON and SVÄRDSON (1976) reviewed the problem at some length and concluded that the principal change was a shift in the trout-char balance. The nylon gill nets, generally introduced

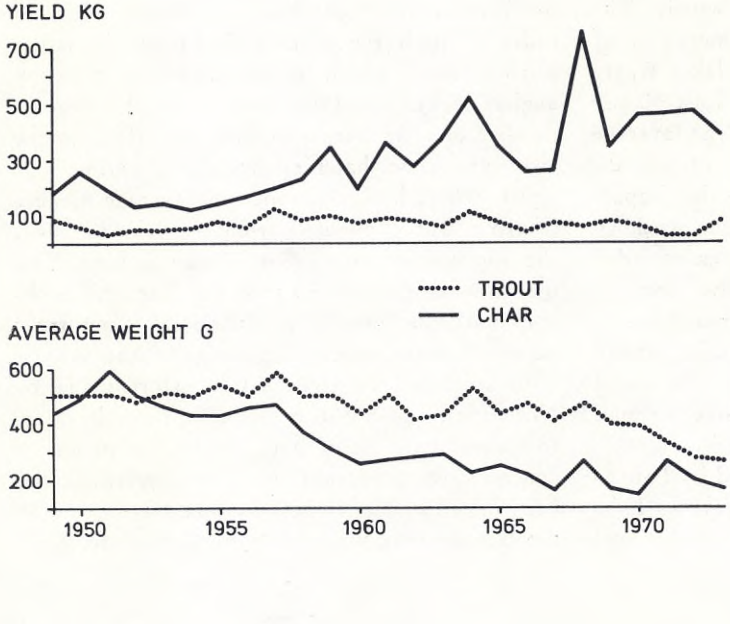

Fig. 5. The average weight of char and trout has deteriorated in Lake Skalsvattnet.

in the midfifties, are mostly used in the littoral region, less often in the pelagic water layers. The nylon nets can be used throughout the summer and are more effective than older nets. Mr. Filipsson, fishing Lake Blåsjön 1967—72 in the open-water season, confirmed the general opinion that trout tend to be more often fished in summer. In Lake Blåsjön the average percentage of char in experimental nettings was 83 in June and early July, 84 in October, and only 71 in late July and August.

By looking through old notebooks of fishery officers and surveying other local evidence, Filipsson and Svärdson also found that the mesh size used has progressively become smaller. In the 19th century the fish were larger and, when fishing effort was low, they had big heads and were thin. When fishing became more intense, the first effect was a better condition of the fish. The older methods, including the seine used on spawning beds, took proportionately more char than did the recently introduced nylon nets.

Since the second world war sport fishing has increased greatly. In summer this mostly consists of trout fishing in streams. In winter, however, char is taken on hook and line through the ice.

The shift of balance is illustrated by Fig. 6. It was suggested by Filipsson and Svärdson that a reduction of the larger predatory trout increased the survival of char fingerlings, thereby intensifying the food competition between the individuals of char as well as between char and trout. Both species are eager to feed on *Gammarus*. The growth of trout, just starting their lake life, should deteriorate and their winter survival may be lower. The number of trout predators (predominantly fish over 20 cm of total length) should progressively decrease, hence the survival of char fingerlings will improve further, etc.

The conclusion reached was that the intensified exploitation was in fact responsible for the stunting of the char. Filipsson and Svärdson recommended a new management, principally favouring the trout. One of the available techniques is the introduction of the opossum shrimp (*Mysis relicta*), which has been found to give the trout a substitute for *Gammarus* (Fürst 1972). Table 1 summarizes the effect so far obtained in Lake Blåsjön. The trout has increased and the char, consequently, has dwindled. The quality of the char has been very much improved—which was the main object of the *Mysis* introduction—but in fact the strong shift in the trout-char balance surprised the Swedish fishery biologists.

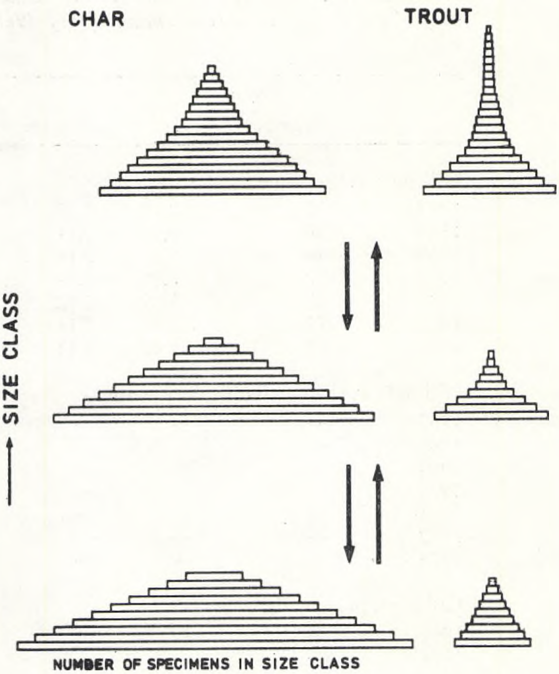

Fig. 6. Model for shifts in the trout/char balance, suggested by Filipsson and Svärdson (1976) as a basis for a new mode of management.

Arctic char versus Whitefish (Coregonus sp.)[1]

Ekman (1910) pointed out the role of man in modifying the fish fauna in northern Scandinavia. He mentioned six Swedish lakes in which the char had heavily decreased in numbers, or had died out completely, following the introduction of whitefish. Huitfeldt-Kaas (1918) mapped the distribution of freshwater fish in Norway. Dis-

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[1] The Scandinavian whitefish complex comprises six sympatric species and a multitude of introgressed populations (Svärdson 1957, 1970 and unpublished). Dominance of the more planktivorous species is very prominent within the group. However, in order to shorten the main discussion, the whole complex is treated in this paper as one superspecies.

Table 1. *Catch of experimental fishing, Lake Blåsjön, where the introduced opossum shrimp, Mysis relicta, was abundant from 1968. Note the reduction of char and expansion of trout.*

	Trout			Char		
	Numbers	Kg	Average weight	Numbers	Kg	Average weight
Gill nets at the shore						
1967	30	2.19	0.07	307	27.38	0.09
1968	56	6.14	0.11	349	36.19	0.10
1969	46	6.41	0.14	211	19.84	0.09
1970	22	2.96	0.14	174	20.23	0.12
1971	43	5.19	0.12	172	13.78	0.08
1972	72	10.31	0.14	244	25.41	0.10
1974	83	9.40	0.11	76	8.58	0.11
Gill nets at the bottom in deep waters						
1967	—	—	—	352	32.99	0.09
1968	—	—	—	230	26.43	0.12
1969	—	—	—	94	8.52	0.09
1970	—	—	—	148	13.92	0.09
1971	—	—	—	136	12.56	0.09
1972	—	—	—	74	6.63	0.09
1974	—	—	—	81	7.33	0.09
Gill nets, pelagically						
1967	—	—	—	25	1.94	0.08
1968	—	—	—	33	3.02	0.09
1969	—	—	—	10	1.14	0.11
1970	—	—	—	16	1.38	0.09
1971	—	—	—	18	2.01	0.11
1972	—	—	—	27	2.78	0.10
1974	—	—	—	18	2.23	0.12

cussing the ways of dispersal and the role of man, HUITFELDT-KAAS pointed out that char had disappeared after the introduction of whitefish.

FILIPSSON and SVÄRDSON (1976) discussed the interaction between char and a number of other species. They listed nearly 30 Swedish lakes into which whitefish was known to have been introduced during the last century and where the effect on char was more or less disastrous.

Lake Övre Björkvattnet, Ume river, was converted into a reservoir in 1963. A downstream lake, with whitefish and perch, was dammed up and included in Övre Björkvattnet, which was a trout-char lake (*cf.* NILSSON and FILIPSSON 1971 for the two species of char in the lake).

The catch on experimental gill nets performed in Övre Björkvattnet by the Freshwater Institute is given in Figs 7 and 8. At the shore, on bottom nets, there has been an expansion of the new whitefish which has reduced the char (Fig. 7). In the open water, on pelagic gillnets, the reduction of char by whitefish has been more pronounced (Fig. 8). This is the habitat where the two species compete for plankton. In weight the percentage change of pelagic biomass has been most evident; the whitefish is approaching 80 % after a mere dozen years (Fig. 9).

Since the knowledge of the effect of whitefish introductions on char has been widely spread, it may seem curious that so many lakes have been destroyed. However, it is only in recent times that char has come to be evaluated so much higher than whitefish. Formely, when food production was more important, the whitefish was rated higher as it expanded to a greater biomass in the lake. The regional distribution of char and whitefish lakes (Fig. 10) also stimulates whitefish introduction to slightly more elevated lakes in the same watershed.

The char-whitefish relation is a classical case in Scandinavian fisheries biology, side by side with the brown-trout/char interaction. But it

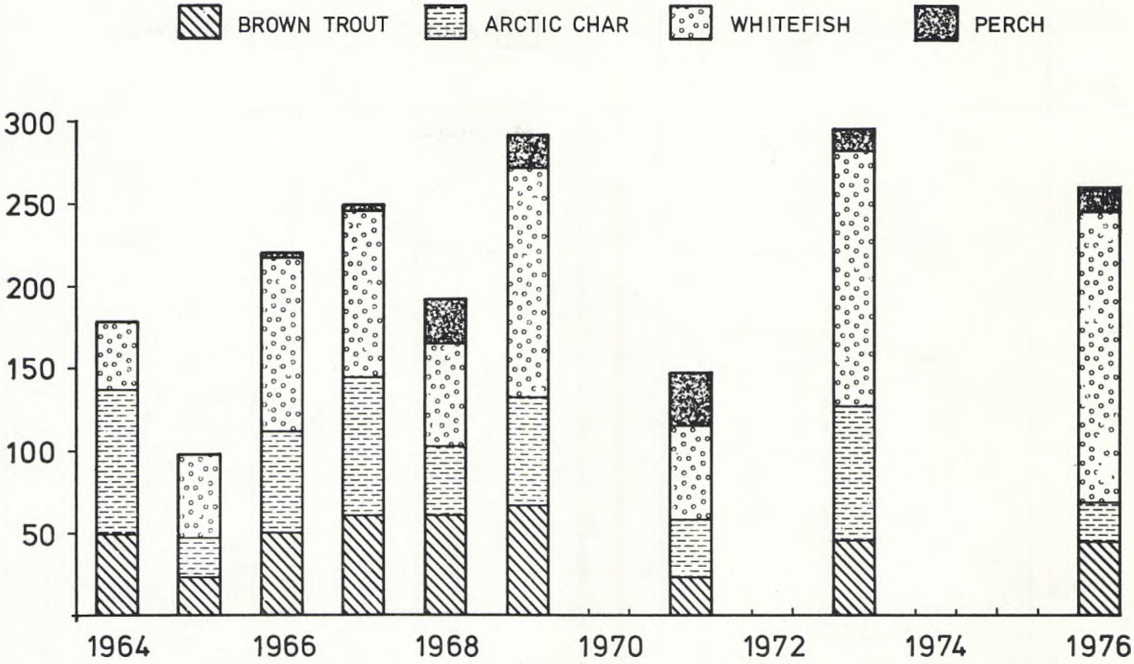

Fig. 7. Catch on gill nets at the shore, Lake Övre Björkvattnet. Whitefish and perch were introduced 1963 by damming up a lower lake.

was only recently that the mechanism of extermination, *i.e.* competition for plankton and the capacity of the whitefish to live on smaller plankters, was demonstrated (Lötmarker 1964, Nilsson and Pejler 1973).

According to the terminology proposed in this paper, the whitefish is clearly dominant over the arctic char. If char is to survive at all, sympatrically with whitefish, it must adapt itself as a deep-living population, and this may or may not develop its predatory tendencies. Char and whitefish do live sympatrically when the lake is large and deep. Cases are known where a sparse char population had lived together with two or even three species of whitefish, only to be wiped out in a short time when a further species of whitefish was introduced.

Lake Vättern, the second largest lake in Sweden and the fifth largest in Europe (1,900 km^2) was supposed to be an exception to the dominance of the whitefish over char. Vättern produces an annual catch of some 50 tons of excellent and highly-priced big char side by side with an even bigger catch of whitefish (Grimås *et al.* 1972). It was found, however, that there is a significant negative correlation of the annual catches (Svärdson 1963). Thus the dominance is still operative, after a sympatric existence of some 10,000 years. The whitefish of Lake Vättern has increased in recent times and it was found (Svärdson 1963, Svärdson and Freidenfelt 1974) that the recent peak catches were due to rich year classes born in 1953 and 1966. In both those years there was an anticyclone in early June, giving rather hot and calm weather during a period when the whitefish fry starts feeding.

Though the richer production of plankton in 1953 and 1966 would no doubt also have favoured the char (perhaps after a year's delay, since the young char is deep-living), the net effect of the climate was negative on char but positive on whitefish. This divergent reaction to the climate seem to be caused by the dominance of the whitefish.

The generally large biomass of *both* whitefish and char in Lake Vättern is further discussed later on (page 167), as it is probably based on the buffer effect of a third species.

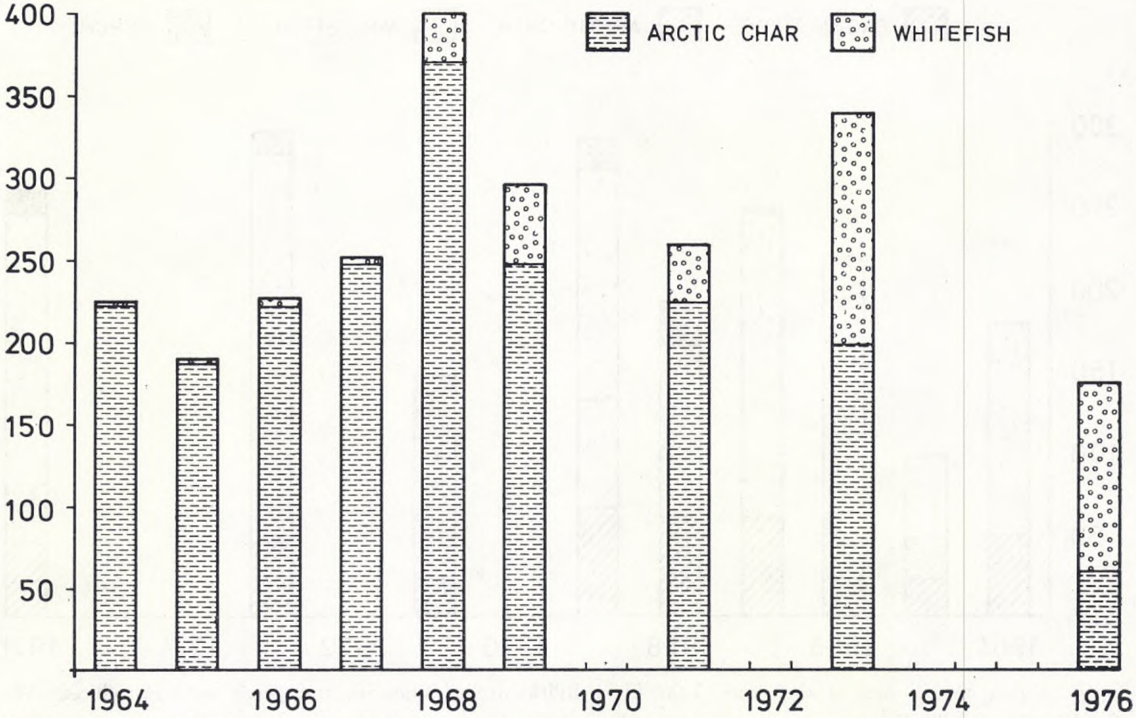

Fig. 8. Catch on pelagic gill nets, Lake Övre Björkvattnet. A good start towards the future extermination of char by whitefish has been made in a decade.

Perch (Perca fluviatilis) versus Whitefish

In small lakes the littoral perch preys on fish fry to such an extent that the whitefish is unable to survive. In the period 1930—45, when fry plantings were extremely abundant in Sweden, it was common knowledge that whitefish fry, planted in small lakes, were reduced to extinction by perch.

In larger lakes, however, the more pelagic

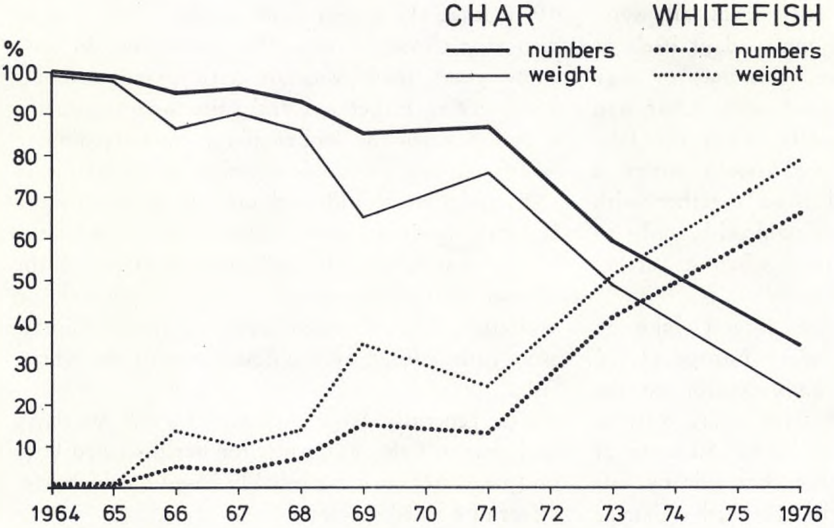

Fig. 9. Char and whitefish catch, per cent, on pelagic gill nets, Lake Övre Björkvattnet.

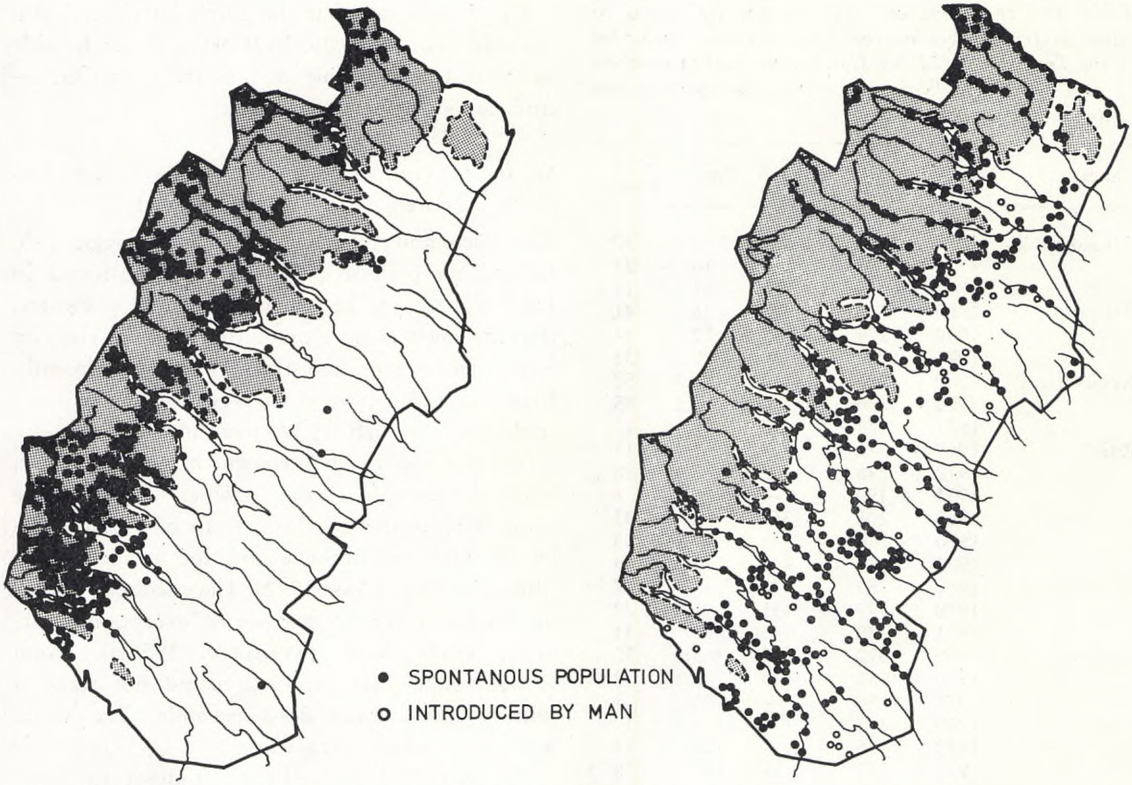

Fig. 10. Samples of char lakes (left) and whitefish lakes (right) in the province of Swedish Lappland (modified after Berg 1963).

whitefish has a fair chance of surviving. The colder the lake, moreover, the more dominant the whitefish become.

It was reported (Svärdson 1951) that introductions of Baltic whitefish fry into several lakes in Malå parish, province of Västerbotten, were successful and were followed by a drastic reduction in the number of perch. The growth rate of the perch improved greatly.

Conversely, Petersson (pers. comm.) found that heavy fishing for stunted whitefish in a number of lakes of the Idijoki river (tributary of the Torne river) during three seasons caused a decline in the number of whitefish (and roach) caught but led to a general increase in the perch. Most of the perch were yearlings. A smaller experimental fishing some years afterwards proved that the perch had increased its standing crop (Table 2).

Statistics from one fishing-industry port on Lake Vänern (courtesy Mr Robert Karlsson) show a significant reversed correlation of the landings of whitefish and perch (Fig. 11). Nümann (1970, 1972) reported a similar reversed correlation between perch and whitefish from Lake Constance. He was, however, in doubt as to which of the two species was really the dominant one and he pointed out that the whitefish had poor year classes when there were many adult perch in the lake.

It is known that perch and char often live sympatrically (Filipsson and Svärdson 1976), a circumstance which indicates that the perch is a rather poor plankton predator. The whitefish is a more efficient predator and interferes with the plankton fauna. Apart from having this competitive edge as far as plankton is concerned, the whitefish fry, aged a couple of weeks, are also voracious predators on newly-hatched perch fry

Table 2. *Experiment on fish removal by means of seine hauls in lakes of the Idijokki river, tributary to the Torne river (72°N). Catch/seine haul in numbers of fish specimens. Note the increase of perch when two other species are reduced.*

Lake	Year	White-fish	Roach	Perch	Seine hauls
Aikalompolo	1969	53	1,496	4	30
	1970	28	463	16	24
	1971	6	288	61	11
Fatijärvi	1969	343	368	26	41
	1970	274	90	12	44
	1971	181	106	70	31
Ruoksajärvi	1969	423	23	1.3	52
	1970	236	7	0.2	85
	1971	174	3	14	17
Raisjärvi	1969	376	34	1	17
	1970	246	2.9	3.3	28
	1971	190	—	26	8
Kätåjärvi	1969	206	354	2	43
	1970	246	226	0.6	65
	1971	136	448	65	45
Kuortajärvi	1969	153	245	37	47
	1970	199	155	1.7	22
	1971	79	343	81	34
Idijärvi	1969	390	13	(65)[1]	30
	1970	451	13	3	52
	1971	68	—	46	7
Mertajärvi	1969	395	—	—	10
	1970	666	1.5	30	84
	1971	131	—	117	38
All lakes	1974	178	200	104	106

[1] Estimated from weight, probably too high.

(Tägtström 1937). Moreover, whitefish of some 400—600 grammes prey on fingerling perch: up to 15 perch fingerlings have been found in a single whitefish (Stenlund 1947). Finally the adult perch, of course, preys on whitefish fry and yearlings. The outcome of all these possible modes of interaction seems to be that whitefish is the dominant species in large lakes (having a considerable pelagic volume) as well as in cold lakes, while perch is more adapted to small or warm lakes.

Svärdson and Molin (1973) found that climatic deterioration was probably responsible for the decline of the sander stock in Lake Vänern. Fig. 11 indicates that the long-term trend of the perch/whitefish balance has changed accordingly. The more cold-adapted whitefish has gradually increased in abundance, while the perch has become less numerous. No doubt the effect of climate on perch was added to by the dominance phenomena.

Fig. 7 indicates that the perch introduced into the cold lake Övre Björkvattnet will not be able to expand in the same way as the whitefish, introduced in the very same year.

Smelt (Osmerus eperlanus)[1] *versus Cisco (Coregonus albula)*

The cisco and the smelt are both pelagic fish, feeding on plankton. Nilsson (1974) found in Lake Vänern, as have earlier authors elsewhere, that the smelt is more predatory than the cisco on larger crustaceans and fish fry. It was recently found in Lake Ivösjön, however, that the cisco could prey on smelt fry (Almer, unpublished).

The smelt more often spawns in running water, while the cisco is a lake spawner, except in the lower parts of the cold Lule, Kalix and Ume rivers in the Gulf of Bothnia and the Laagen river, Mjøsa, Norway (Aass 1972). The cisco may ascend or descend rivers in periods of exceptional turbidity from floods (Svärdson 1956 a). Järvi (1950) found that the cisco could not stand a salinity higher than 2—3 permille. The smelt, however, is more tolerant.

Ekman (1922) mapped the Scandinavian distribution of smelt (Fig. 12) and found the species to be a relict. Nowhere had it passed above the highest shores of the different stages (fresh or marine) of the Baltic Sea. Cisco, however, does occur above the highest shores in the southern highlands. Svärdson (1966) suggested that the cisco penetrated north-running rivers from the flooded lower parts of central Sweden and, when the land slowly tilted to the south in the post-glacial upheaval, some headwaters were caught by south-running rivers. In this way the cisco could reach the interior area of southern Sweden while the smelt did not.

The two species occur in a number of lakes along the Baltic seaboard of northern Sweden.

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[1] The existance of two sibling smelt species in Lake Vänern was suggested by Svärdson (1958 a, 1961 b). There are two growth types, one smelt species being larger and older than the other. Scale readings indicate a growth difference from early life. The situation may correspond to the existence of two smelt types in lakes on the North American seaboard. As far as Sweden is concerned, however, the question of the existence of sibling smelts must be regarded as still open. In any case it has no relevance to the present discussion.

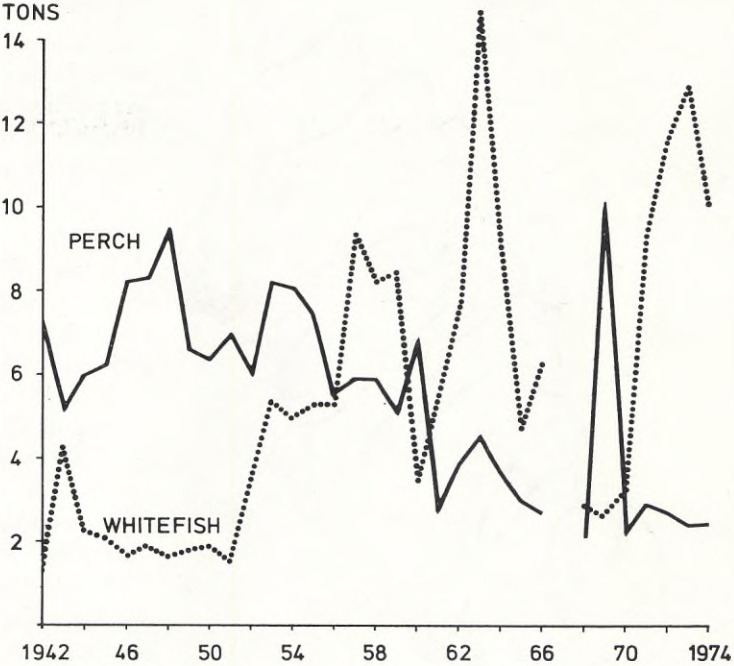

Fig. 11. Lake Vänern, commercial landings in Kristinehamn 1942—74.

The smelt is never found above the highest shores, whereas the cisco has in exceptional cases climbed a few dozen metres:

	> 300 m	299—250 m	249—200 m	199—150 m	149—100 m	< 100 m	Lakes
Smelt	—	—	9	10	10	22	51
Cisco	2	9	14	20	6	20	71

Some small rivers, the whole length of which had risen from the salt Litorina sea, could be colonized only by smelt because of the salinity at the river mouth. Allopatric smelt therefore tends to be found mainly in lakes close to the seaboard. Other lakes, which are in fact only stretches of rivers (deprived of plankton), can also be allopatric smelt lakes.

Out of the 110 lakes inhabited by either cisco or smelt, only 13 are known to have the two species living sympatrically. This fact indicates interaction between the two species. If the cisco had had the same possibilities of invading rivers during all periods of the Baltic as have had the more brackish-water-living smelt, the number of smelt lakes would certainly have been smaller. The numerical dominance of cisco (71 lakes, against 51) would thus have been greater.

Northcote and Rundberg (1970, 1971) found the cisco and smelt of Lake Mälaren to be segregated in depth, the smelt living deeper.

Almer and Larsson (1974) reported from Lake Vänern that the smelt occurred in deeper waters than the cisco. The young specimens of both species were found in higher water layers than the adults and the commercial fishermen in Lake Vänern, trawling for cisco, know that the denser schools of that fish are also horizontally segregated from those of the smelt.

In Lake Hjälmaren, where cisco is absent, smelt abound in spite of the fact that the lake is shallow and warm. Formerly smelt were caught in this lake as a source of oil or, as after drying, food for cattle.

Smelt as a buffer species is further discussed on page 167.

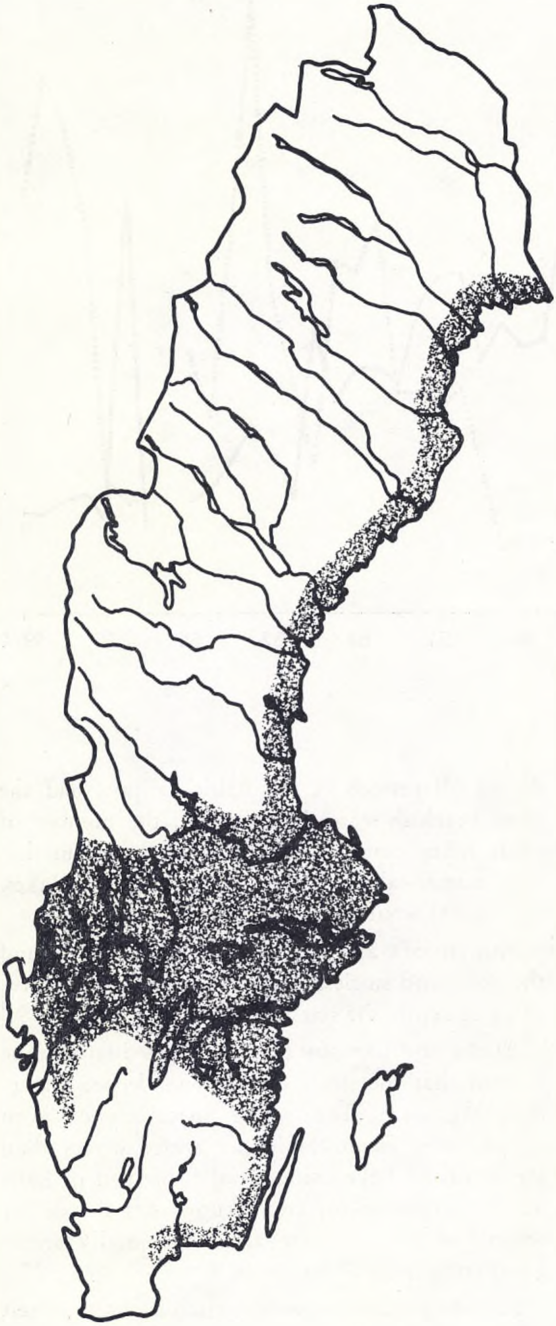

Fig. 12. The geographical distribution of smelt (*Osmerus eperlanus*), in Sweden modified after Ekman (1922).

Whitefish versus Cisco[1]

The cisco is a much more pronounced plankton feeder than any species within the whitefish group. The position of the mouth, the gill rakers and the schooling habits are all adaptations for a true pelagic life. Stomach studies (Vallin 1969, Nilsson 1974) confirm the planktivorous diet of the cisco.

The almost complete absence of cisco above an altitude of 300 metres means that the whitefish species have plenty of lakes in northern Sweden where they can evolve dwarfed populations, the individuals of which are plankton feeders. Actually even species with a rather low number of gill rakers (25 or fewer) can adapt themselves to plankton; it seems as if the small size of the fish (and consequently of the gills) compensates for the fewness of the gill rakers by enhancing their filter effect. Ecologically, these whitefish populations fill the niche of the cisco. It is thus not surprising that, within the cisco region of Sweden, such dwarfed whitefish populations are virtually absent. This indicates the dominance of cisco over even the planktivorous whitefish species.

Filipsson (1975) summarized the evidence on the interaction between whitefish and cisco. He pointed out that ten rivers of southern Sweden all had allopatric cisco populations in the lowest lake. In some of the river mouths the Baltic whitefish were spawning, and thus invasion or reinvasion of the lowest lake by whitefish might easily have occurred. All ten rivers had whitefish in their headwater lakes, in four cases allopatric. This distributional pattern in southern Sweden again clearly indicates the dominance of the cisco.

Filipsson also pointed out the differing pelagic occurrence of whitefish where the cisco is sympatric. In allopatric whitefish populations he regularly found a lot of whitefish on pelagic gill nets. In sympatric cases, however, the pelagic nets catch only ciscoes, the whitefish living at the shore or close to the bottom.

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[1] Cisco is split into two sibling species (Svärdson 1957, 1958 b, 1961 b and unpublished). One is the rare spring-spawning cisco, which is subordinate to the common species and is recorded from four Swedish lakes only. Presumably it is conspecific to a spring-spawning cisco in the Carelian region on the border between Finland and USSR.

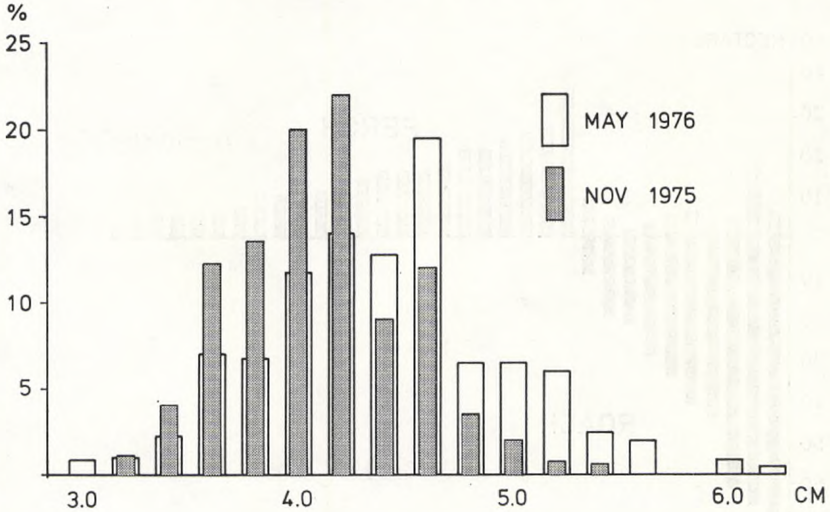

Fig. 13. Size distribution of first-year roach in Lake Mälaren before and after the winter. The late summer of 1975 was very warm and the roach were larger than normal. Despite this, differential size mortality is evident.

Introductions of whitefish have failed in cases where cisco was already present in the lake, while introductions into comparable lakes without ciscoes have been successful. Introductions of the cisco species into whitefish lakes have succeeded in a few cases (in fact only a small number of experiments have been performed), with deteriorating growth of the whitefish as a result.

Fischerström (1785) wrote on the famous whitefish of Lake Mälaren. It was sold, fresh or salted, all over the country. From interviews with a hundred commercial fisherman operating in the lake, Rundberg (1968) could document a steady decrease of the whitefish catch from the early 1920s onwards down to a mere half ton nowadays, while the cisco has, in the same period, risen in the commercial catch from insignificant numbers up to a recent 150—200 tons. In Lake Mjøsa, southern Norway, whitefish has decreased while cisco has tripled in recent years (Aass, pers. comm.)

Perch versus Roach (Rutilus rutilus)

The roach is widely distributed in Sweden but much less so in Norway. The roach was favoured by the amelioration of the postglacial climate and gained access to many lakes just below the mountainous region. There are many isolated small lakes in the woods where roach exist, though the larger lakes downstream have no roach. This fact has puzzled many investigators and it has been suggested that these isolated populations are the result of introductions made by man in order to get bait fish. However, as was pointed out by Alm (1937), these marginal roach populations are probably relicts from the warm postglacial period. This is supported by Nikolskii's (1961) statement that some 5,000 years ago the cyprinid bream was much more abundant in the White Sea basin than it is now and that another cyprinid fish, the rudd, also existed there. Nowadays it is absent.

The permanent existence of roach in shallow bays or at the mouth of nutrient-carrying rivers in large oligotrophic lakes or in shallow small lakes between larger (and colder) ones indicates that food abundance and temperature are marginal for the survival of the roach. Kempe (1962) found that the temperature of late summer was correlated to the strength of the roach year-class and that the total length at the beginning of the second growth period was remarkably stable at some 40—45 mm, in different habitats and years. In the eutrophic Lake Mälaren at sea level and the oligotrophic Lake Särnasjön at an altitude of 422 metres, the overall growth rates were different, while the back-calculated first-summer length was 42 and 41 mm, respectively.

Kempe sampled young-of-the-year roach during the winter and found an apparent growth caused by, as he supposed, selective mortality of the smallest fish. Fig. 13 illustrates this phenomenon on new material from Lake Mälaren during the

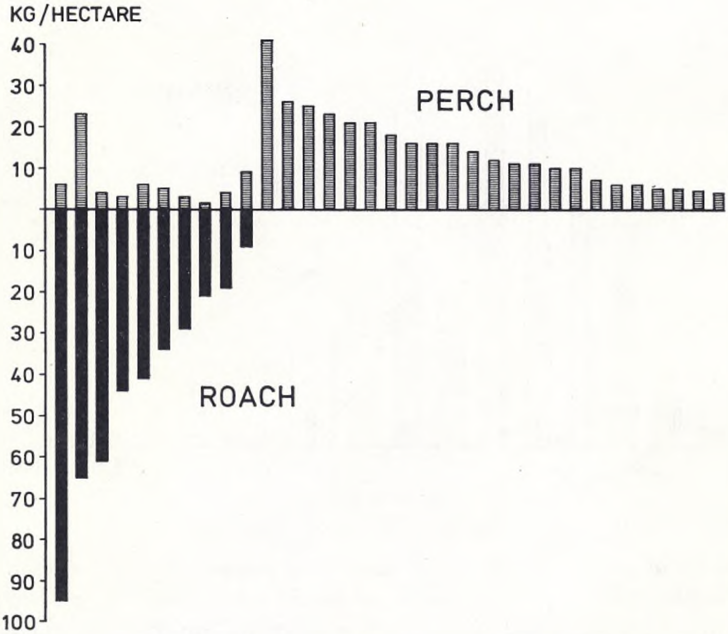

Fig. 14. Biomass kg/ha of 32 small Finnish lakes. Modified after SUMARI 1971.

winter 1975—76. LIND and KUKKO (1974) noted the seasonal variation of roach condition which reached a peak in August—September and was lowest in spring, especially in young fish. LYAGINA (1972) found that fat content decreased from 1.15 % to 0.69 % in roach of the Ruza river (tributary of the Moscow river) from September to May. The remarkable stability of first-summer growth, as indicated by back-calculation from older fish, thus seems to be due to their having the threshold size necessary for winter survival. It follows that a warm summer, or an increased amount of food provided by eutrophication, should result in more fingerling roach having the size and condition that make first-winter survival possible.

Apart from the "shortcomings" of the roach as far as food and temperature are concerned, the species is also susceptible to oxygen deficiencies as well as to soft and too hard waters (ALMER 1972, FRANK 1973, ALMER *et al.* 1974, MILBRINK and JOHANSSON 1975). FRANK found an increased mortality of roach embryos at pH values just below 7, while the Scandinavian authors noted that no reproduction occurred around pH 5.5.

Within these rather wide limits of existence, however, the roach is a formidable competitor. Its relations to the perch are important, since the two species live sympatrically in tens of thousands of Scandinavian lakes.

In the smallest lakes or tarns in the woods, the perch tend to live alone. It would seem that an occasional oxygen deficiency in winter or a too low pH (from bog waters) is responsible for the absence of roach. Where it can survive, it develops a larger biomass than the perch, and reduces the perch population considerably, as illustrated by SUMARI (1971), Fig. 14.

In the Idijoki river system, roach exist in dense populations side by side with the whitefish and, when both were reduced by heavy seine fishing during three summers (Table 2), the perch fingerlings survived much better and produced (temporary) populations. In Lake Aikalompolo, where probably even the whitefish was reduced by the roach, the effect on perch seems to be due to the roach reduction only, while in the other lakes of the river system it is a combined effect.

The perch/roach balance along the shores of Lake Vänern has been investigated in recent years by Mr B. ALMER. He finds that roach and perch are on the whole of equal strength (percentage biomass) but that the perch dominates (2: 1 or

Table 3. *The fish population development of the new Ottmachau Reservoir (1,500 hectares), River Neisse (Oder), Wundsch (1949). Catch in kg.*

Year Species	1934	1935	1936	1937	1938	1939	1940	1941	1942
Anguilla anguilla	36	36	128	112	239	549	334	308	442
Esox lucius	3,187	4,748	5,336	5,183	3,000	1,860	1,789	1,541	971
Abramis brama	82	82	208	1,114	6,027	8,601	8,402	18,227	33,108
Rutilus rutilus	3,640	2,932	4,568	4,780	12,285	22,452	33,774	44,852	75,187
Perca fluviatilis	2,297	1,843	1,920	1,197	1,317	872	1,156	410	7,653
Tinca tinca	1,923	2,689	2,537	2,691	2,410	1,306	893	669	456
Cyprinus carpio	16	103	257	998	591	233	206	476	598
Barbus barbus	—	—	—	—	—	—	509	152	69
Carassius carassius	59	41	32	56	10	1	48	56	23
Stizostedion lucioperca	—	—	—	8	5	3	14	16	396
Salmo trutta	3	3	1	1	2	1	1	—	—
% roach of total catch	32.3	23.5	30.5	29.6	47.4	62.5	71.7	67.2	63.2

3: 1) in bays with no pollution while roach dominates (up to 10: 1) in strongly polluted areas, as in the vicinity of the Slottsbron pulp mill. When this mill was closed in June 1974, the perch began to reinvade the area.

RUNDBERG (1975) presented the seasonal catch in the fixed pound nets of one commercial fisherman in Lake Mälaren. The cisco dominated the catch in May—June and again in October—November, while perch was most prominent in July and roach was completely dominant in August. During the warmest period the roach lives pelagically in the upper water layers (NORTHCOTE and RUNDBERG 1971) and, as the pound nets proved, the perch and cisco went elsewhere.

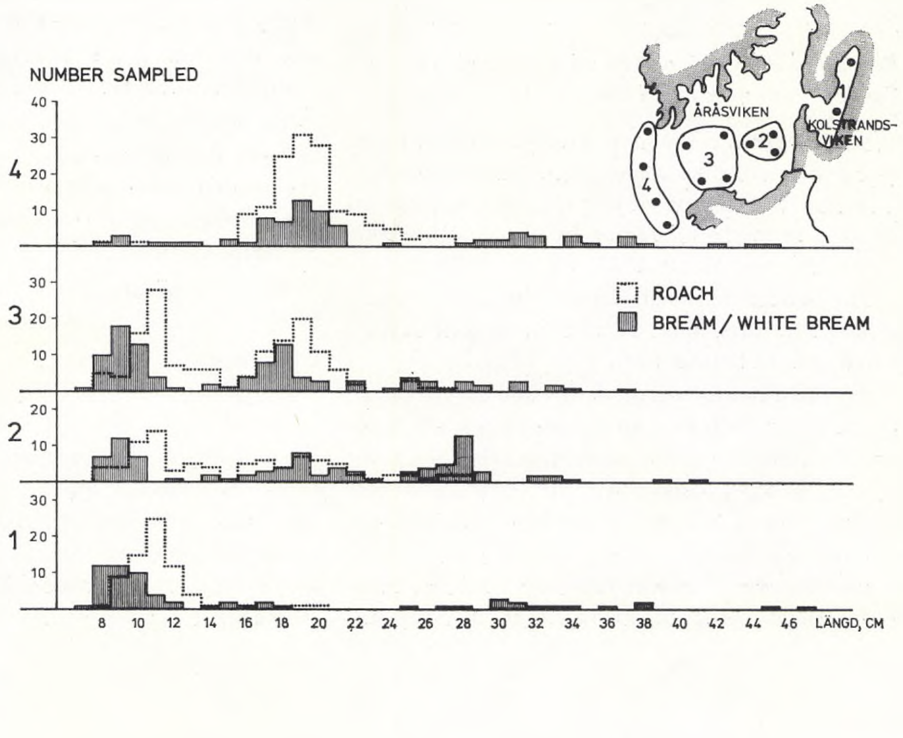

Fig. 15. Size distribution of roach and bream in a bay of Lake Vänern. The larger specimens penetrate into the open oligotrophic lake.

When a new lake is formed, *i.e.* by damming up a river, the roach "takes over" within a few generations. This was described by Wundsch (1949) from the Neisse river (Oder). Since his paper is hard to obtain, Wundsch's data from the Ottmachau Reservoir are given here as Table 3. In less than ten years the roach biomass became some 60—70 % of the total. The remarkable reduction of pike, after a short population expansion, has also been noted in several Swedish river reservoirs.

Ecologically the roach is a very successful species. It is littoral and feeds on phytoplankton as fry, on zooplankton as a young and adult fish, on all sorts of benthos and benthic or free-drifting algae (Otterstrøm 1931). Algae, however, seem to be fed on primarily when animal food is in short supply (Lyagina 1972). When the population pressure intensifies in bays of oligotrophic lakes, the older roach specimens tend to become pelagic. This was illustrated in Lake Vänern (Fig. 15) where the pelagic roach are food competitors to whitefish, cisco and smelt (Nilsson 1974). The same recent change of roach behaviour was reported from Lake Geneva (Laurent 1972) and Lake Constance (Nüman 1972, Brenner 1973), as well as from several lakes within Switzerland (Roth 1970, Roth and Geiger 1972) and lake Mjøsa, Norway.

Perch and Pike (Esox lucius) versus Sander (Stizostedion lucioperca)

While the perch is the most widely distributed fish in Sweden and pike comes second, the sander has a limited distribution in eutrophic warm lakes in an area formerly inundated by the Ancylus lake (Svärdson and Molin 1973).

The sander has well-defined habitat requirements. The water must be turbid and well-oxygenated and the bottom firm.

All three species are predators and all spawn at the shore but shift over to a more pelagic life later on, the pike as stray adult fish, the perch as schools hunting collectively for prey, and the sander early in life as a permanent roaming predator.

Introduction of sander into new lakes has been a favourite mode of management in southern Sweden for a hundred years. Practical experience has proved that introduced sander influences other fish, especially perch, which tends to be heavily reduced (Svärdson and Molin 1973). The Lake Erken case (*op.cit.*) is of special interest since it demonstrates that the introduced sander reduced the pike and the perch of the lake. Since the perch had been a standard prey of the pike, however, the reduction of pike started an avalanche of perch abundance, when the introduced sander had difficulties to reproduce themselves in Lake Erken.

Further evidence on the dominance of the sander is provided by catch statistics from the four big lakes of central Sweden (average annual catch in kg/km^2):

	Vättern	Vänern	Mälaren	Hjälmaren
Sander	0.1	11.3	91.3	239.6
Pike	4.2	19.9	29.2	55.0
Perch	12.6	2.5	7.2	53.1
Sander/Pike	0.24	0.57	3.13	4.36
Sander/Perch	0.08	4.52	12.68	4.51

The lakes are arranged in order of progressive suitability as sander habitats. The more favourable the habitat is for the sander, the more this species tends to dominate the pike, though the pike, too, is favoured by shallower, warmer and more eutrophic habitats. The perch frequency of the lakes is much influenced by the occurrence of smelt, since a diet of smelt stimulates perch growth and produces perch that are marketable. The figures discussed are based on commercial catches.

The long-term trend of sander, pike and perch in Lake Ivösjön was described by Almer (1976). He related the sander expansion, and the subsequent shrinking of the population, to the May—September temperature (Fig. 16).

The role of the smelt as a "buffer species" between the sander and the perch is discussed later (see page 167).

In the last fifty years the sander has spread and increased in the brackish Baltic archipelago outside Stockholm. The turbidity caused by eutrophication is generally presumed to be responsible. The local fishermen complain of a parallel decrease in pike and blame this on the anglers. Dominance of the sander, however, seems more reasonable.

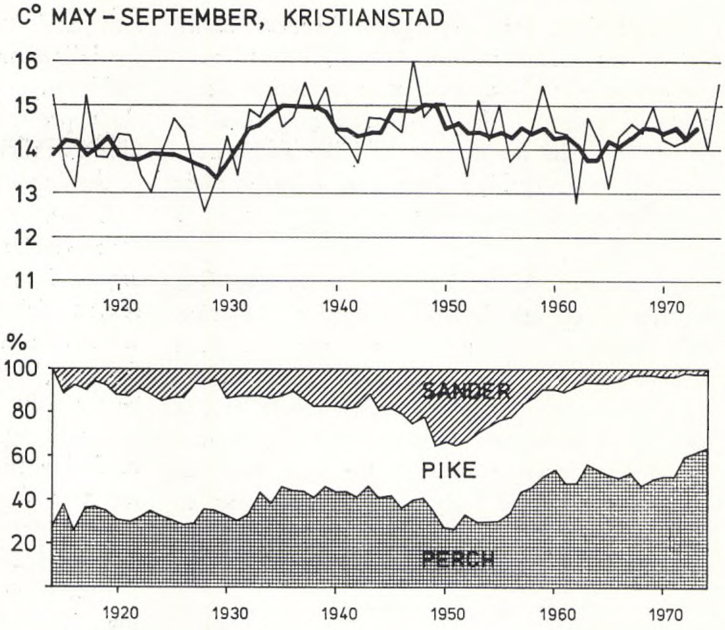

Fig. 16. Long-term catch trend of sander, pike and perch in Lake Ivösjön, province of Scania. After Almer 1976.

Some prey species

There was a peak burbot *(Lota lota)* catch in Lake Vättern of some 60 tons in 1957, when nylon nets were new. After this the annual yield dwindled rapidly to only 2 tons in 1973. It may be that PCB has contributed to the decline of the burbot. Whatever the cause of the burbot reduction, however, the consequences for the prey fish, sharing the deep-water bottom habitat with the burbot, are obvious. The commercial fishermen find the ruffe, *Gymnocephalus* (*Acerina*) *cernua*, much more abundant after the burbot decline. Some evidence also points to a rise of the numbers of four-horn sculpins, *Myoxocephalus quadricornis*.

Experimental fishing by survey nets (with varying mesh sizes) along the shore of Lake Vättern by the Freshwater Institute in recent years indicates an exceptional abundance of ruffe. The catch in three localities in 1974 was as follows:

Rutilus rutilus	335 sp.	40.2 kg
Gymnocephalus cernua	2,112	40.2
Coregonus albula	839	39.2
Perca fluviatilis	409	34.4
Coregonus lavaretus	67	21.1
Salvelinus alpinus	50	17.7
Myoxocephalus quadricornis	174	6.7
Osmerus eperlanus	158 sp.	1.5 kg
Alburnus alburnus	23	0.9
Salmo trutta	1	0.9
Lota lota	1	0.6
Salmo salar (stocked)	1	0.1
Phoxinus phoxinus	2	0.02

Since ruffe are food competitors to young burbot, while adult burbot prey on ruffe, the prey/predator balance may have been shifted by overexploitation. After a too strong reduction of the predatory burbot the further development may have been caused by competition pressure from the expanding prey and competitor, the ruffe. At present this interesting situation cannot be analysed in greater detail because of the shortage of burbot. Theoretically, however, it may be similar to the trout/char balance and thus illustrate one of the most dangerous inherent consequences of overfishing.

The crucian carp (*Carassius carassius*) is a sparsely occurring cyprinid fish in most eutrophic lakes in southern Sweden. It grows to be an old and large, deep-bodied fish, weighing some 0.5—1.5 kg. On the other hand, in small tarns or ponds, with a very low oxygen content and often no other fish, the crucian carp lives in dense, stunted populations where the weights are 50—100 grammes. These different types of crucian carp had their own vernacular Swedish names already in the 18th century. It has, however, been a common experience that after rotenone treatments of eutrophic lakes, crucian carp tend to survive and, in the absence of pike and perch, "explode" to very high abundance. Clearly, their normally sparse occurrence in lakes is due to predation.

The same experience has been found regarding the ten-spined stickleback, *Pungitius pungitius*. This species lives a very secret life in the shore vegetation and must be a rare fish, as it is seldom seen. After rotenone treatment, however, it has "exploded" to enormous numbers, milling around in the open pelagic zone of the lake, and the population pressure has been so intense as to create emigration in thousands, drifting with the outlet (Lake Halmsjön, 39 hectares in the early 1960s).

IV. DISCUSSION

Intraspecific and interspecific interaction pressure

Most freshwater fish in the Scandinavian fauna are non-specialists. The fry tend to have diets and habitats dissimilar to those of the young fish and the latter, again, are partly separated from the adult or older age groups by diet or habitat. This ecological separation of age groups means that most of the environmental resources are open to the species and is selected for.

A counterbalancing selection pressure is established by the interspecific competition, where a second fish species with a similar broad non-specialist ecology utilizes the very same resources of food and shelter. Then a more specialist type of niche is selected for by the subdominant species, either a more rigid diet or a habitat preference.

In principle, evolution should mould two different types of fish, depending on whether the intra- or the interspecific competition is the most forceful agent. The roach is a successful non-specialist: living either in the vegetation, or at a fairly open shore or, in dense populations, leading a rather pelagic life. It feeds on (even small) zooplankton, benthos of all kinds, and algae. The roach is a very dominating species and the related rudd (*Scardinius erythrophtalhmus*) and chub (*Leuciscus leuciscus*) seem to have specialized in living either, as in the case of the rudd, only in the vegetation zone or, as with the chub, preferably in (cold) streams. It seems probable that these specialized habitats evolved because of the dominance of the roach.

A fish species that is heavily preyed upon by other species may evolve a striking tolerance for any environment where predation is low. The ten-spined stickleback is a sparse species, living very secretly in the shore vegetation of eutrophic lakes. Brinck (1965) found the ten-spined stickleback to be the only (albeit sometimes very abundant) fish in small, highly polluted streams in the province of Skåne (Scania). Finally in large oligotrophic northern Swedish lakes, introduced lake trout, *Cristivomer namaycush*, preyed upon the ten-spined stickleback in fairly deep water, again in a habitat where predation had previously been low. The common denominator for these three seemingly very different habitats of the ten-spined stickleback is a low predatory pressure (*cf. Daphnia magna* in fish-free habitats and *Bythotrephes* in those of fairly low fish predation). Clearly, the interspecific interaction has been responsible for the habitat magnitude of the stickleback.

A compromise between the two conflicting selection pressures could be a strong non-genetical flexibility, allowing the species to have a broader ecology when allopatric but a more specialized diet or habitat when sympatric with a dominant species. The brown trout is known to spawn at the shore beside rivers, to roam about pelagically, hunting for plankton, *i.e.* displaying the char type of ecology when living as the only species in a lake (Klemetsen 1967, Nilsson and Pejler 1973). Whether this is an ecological subspeciation or a non-genetic "interactive segregation" (Nilsson 1967) is not known for certain. The growth rate of brown trout in Lake Lillsjouten changed slightly between 1950 and 1973. Young fish (presumably living in streams) grow more slowly, older fish, however, more rapidly. Arctic char was introduced in the lake in the 50's and expanded greatly. A selection pressure on trout for a longer parr life in streams seems probable (Filipsson and Svärdson 1976). The char of Lake Hornavan, in which several species of whitefish live, has been shown to have an avoidance reaction to the whitefish odour (Höglund *et al.* 1975). At present, it is not known whether the char of Lake Sädvajaure upstream of Lake Hornavan, living in a whitefish-free environment for 9,000 years, have the same response. If so, the response has not been enhanced by natural selection for the same period of time.

The local selection seem to have created ecological subspecies (demes) which may have valuable management qualities. The two stocks of brown trout in Lake Vänern have different migration patterns, as is proved by tagging, and growth rates. When hatchery-reared smolts of both stocks were released at an artificially selected starting point, the migrational pattern was modified but there were still migrational and growth differences between stocks (Wickström 1974). The big sea-running trout of the River Vistula, Poland, has been tested since 1960 in Sweden in lakes and in the Baltic. It has proved to have a tendency to grow big, be a long-distance migrant and an early runner in the Dalälven river.

There seem to be three levels of adaptation to the conflicting competition pressures: (1) specific differences, (2) subspecific local genetic adaptations and (3) non-genetic flexibility to change diet, growth or habitat according to the prevailing situation. Only experiments can identify allopatric differences as belonging to either the second or the third of those levels.

What makes a species dominant?

In a lake the littoral zone provides abundant food and shelter for the fish fauna. The pelagic open water offers zooplankton or prey fish as main sources of food, but provides very poor shelter. The larger the lake, the smaller is the proportion of it constituted by the littoral region.

The Scandinavian freshwater fish present an interesting series of littoral species, being dominated by the more pelagic ones. The char obviously is more pelagically adapted than the brown trout and it clearly dominates in normal mountain lakes. Only if the lake is small and shallow, *i.e.* consists of littoral only, can the brown trout be the more common fish.

The whitefish (all species taken as a group) again is more pelagic than the char and dominates that species. The only chance for the char to live sympatrically with whitefish is to adapt the pelagic predator niche, either roaming around for fish in the upper water layers or living in the deepest water, feeding on whatever is available in this cold, dark and food-deprived environment.

Again, the whitefish is dominated by the cisco, which is by far the most evolved planktivorous species of the series. The cisco is clearly more pelagic than any of the whitefish sibling species. The cisco has many gillrakers (40—50) while the smelt has fewer (30—40), indicating that the cisco is a more advanced plankton predator than the smelt.

Among the cyprinids the roach certainly is mainly a littoral species, but the population may shift temporarily to a pelagic life, where the roach can feed on free-living algae but also bring into play its own, excellent capacity to prey on zooplankton. When members of the staff of the Institute of Freshwater Research were mid-water trawling in Lake Vänern in recent years, pelagic roach (and bream) were found in the centre of the lake.

Of the three fish predators, the pike is more littoral than the perch, while the sander is the most pelagically evolved species. It is also the dominating one.

Apart from the circumstance that the pelagic zone comprises more cubic metres than the littoral zone there must exist some adaptational feature common to species leading a pelagic life, that makes them dominant, to explain why an introduced, more pelagic species reduces or even exterminates a sympatric, more littoral species. There can be little doubt that the phenomenon in question is correlated to the capacity to prey on zooplankton, especially the smaller plankters. In the last few years, knowledge of the impact that fish can exert on the plankton fauna has greatly increased.

Pehrsson (1974), studying the food basis of ducklings of long-tailed duck (*Clangula hyemalis*), noted drastic differences in the plankton fauna of Scandinavian high mountain lakes inhabited by fish (mostly char) as compared with barren lakes having no fish.

Species	41 lakes with no fish		8 lakes with fish	
	Number of lakes	Mean [1]	Number of lakes	Mean [1]
Polyartemia forcipata	38	273	—	—
Bythotrephes longimanus	37	74	4	59
Holopedium gibberum	29	323	4	225
Eurycercus lamellatus	23	13	2	2
Daphnia galeata	9	218	2	5
Sida crystalina	8	84	1	89

[1] Mean of ten horizontal hauls with a length of 3 m (net 0.7 m^2, mesh size 1.0 mm).

The anostracan fairy shrimp, *Polyartemia*, is normally found in small lakes only, but it occurred in Pieskejaure (60 km^2) when char was introduced in 1961. Char growth was exceptional in the first few years. *Polyartemia* had completely disappeared by 1968 and the diet — and growth — of the char began to adjust to normal conditions (NILSSON 1972, NILSSON and PEJLER 1973).

Details of the successive changes in plankton fauna in the series of lakes with no fish-trout-char-whitefish were reported by NILSSON and PEJLER (1973). Large or colourful plankters are eliminated through the predation of more powerful pelagic specialists. *Heterocope saliens* gives way to *H. appendiculata*, *Daphnia longispina* to *D. galeata* and this species to *D. cristata*. *Bytotrephes* becomes sparser but the small *Bosmina* becomes more abundant. NILSSON (in print) has summarized the subject in general terms.

Even the final step of the series has recently been proved. EKSTRÖM (1975), studying the zooplankton fauna of those lakes in southern Sweden where char has survived, grouped the lakes according to the presence of cisco populations (Table 4).

Since all the lakes studied by EKSTRÖM were oligotrophic, were situated in the same geographical region and were all char lakes, the obvious plankton-fauna differences according to the presence of ciscoes are significant, in spite of the fact that other species of fish are also involved.

Table 4. *Some plankters in lakes with or without cisco (Coregonus albula).*

	Daphnia cristata	*Daphnia longispina*	*Heterocope appendiculata*
Lakes with ciscoes			
Drögen	++	—	—
Sommen	r	—	+
Vättern	++	—	—
Ören	—	—	—
Mycklaflon	+++	—	—
Östra Nedsjön	+	—	—
Yngen	+++	—	—
Stora Låsen	—	—	—
Norra Hörken	+++	—	+
Lakes without ciscoes			
Skiren	—	—	—
Rödingehultsjön	—	—	r
Ölmehedens Långtjärn	—	—	—
Körttjärn	+	+++	+++
Norra Örsjön	r	++	+++
Södra Örsjön	r	++	+++
Ängsjön	—	r	++++
Trehörningen	r	++	++++
Nyckelvattnet	—	++	++
Östra Skälsjön	—	r	+
Norra Gussjön	—	++++	+++

r = rare
+ = often found
++ = fairly abundant
+++ = abundant
++++ = very abundant

Fry or young stages of most fish species depend on plankton. A superior plankton predator therefore interferes with the survival of another species by reducing the amount of plankton available. Mortality is probably highest in the fry stage, but it should be noted that following introductions of adult char (plankton feeders from mountain lakes) into whitefish lakes in the same climatic region the introduced adult char became heavily stressed, lost weight, and disappeared in some months (SVÄRDSON 1961).

In littoral species the competition between fry, young and adult of the same species can be reduced by different habitat selection. In pelagic fish species, young may tend to live in higher water layers than adults (cisco and smelt), but since the diet comprises the same plankters (albeit different age groups, *cf.* AIRAKSINEN 1967 for cisco) there should be a competition for food between adults and their fry.

It is an interesting fact that the cisco (SVÄRDSON

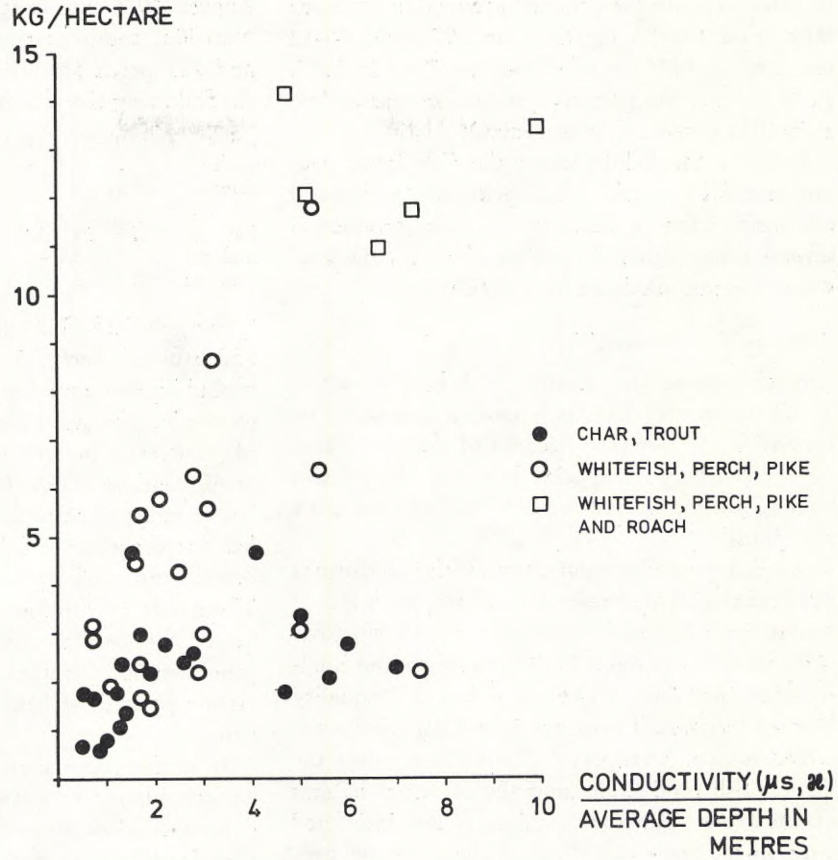

Fig. 17. Yield in lakes with different fish species in northern Sweden. Modified after LINDSTRÖM 1975.

1956 b, AASS 1972) and the sander (SVÄRDSON and Molin 1973) have long been noted for their exceptional year-class fluctuations. Rich year classes of cisco are known to depress the subsequent ones, presumably through food competition. As far as the sander is concerned, climate is more responsible for the origin of rich year classes, but the intraspecific cannibalism may be another contributing factor.

The populations of dominant species, as illustrated by cisco, roach and sander seem to be regulated mainly by abiotic factors (pH, oxygen, temperature) or intraspecific competition, while the subordinate or dominated species are more influenced by interspecific competition for food or predation.

Finally, there is a correlation between dominance, *e.g.* superior plankton preying capacity, and primary production. The elimination of larger species of plankton (some of which are themselves predators on smaller plankters) is followed by a higher abundance of smaller plankters (rotifers included). This may influence the grazing of phytoplankton and hence the primary production of the lake.

Catch records tend to indicate higher production in lakes inhabited by more dominant fish (Fig. 17). The ultimate evidence, of course, is that derived from studying the primary production in the same body of water in a normal state and later, when the fish fauna has been eradicated. Such an experiment was recently performed by STENSON (1976) in the small lake, Stockelidsvattnet, in south-western Sweden. This lake was limnologically surveyed throughout 1973 and 1974, treated with rotenone in November 1974, and further surveyed during 1975 and 1976. After the treatment, alkalinity fell, the visibility was doubled and the primary production per hour sank from 15—20 mg C/m^3 in 1973 and 8—12 mg C/m^3 in 1974 to only 1—3 mg C/m^3 in 1975. In 1976, too, the primary production was as low as in 1975 (STENSON, pers. comm.).

In Lake Stockelidsvattnet the fish fauna was dominated by roach, which was then ultimately responsible for a primary organic production several times higher than when the same body of water was not inhabited by any fish.

Stress on fish communities.

Any change of the abiotic conditions in which a fish community lives is bound to generate alterations in the biomass. Because of the dominance phenomena between species, however, the relative biomass of the various species will change more profoundly.

When a mountain trout-char lake is transformed by damming into a reservoir, where the water is stored in the summer and autumn, the brown trout is found to suffer most, both in numbers and quality. The char tends to be stunted, and its quality also deteriorates. The stress, involving greatly enlarged annual water-level fluctuations, ruins the littoral fish food fauna and the principal habitat of the trout. The char habitat is not interfered with to the same extent, since the plankton production may continue. The result is a serious decline of the trout fishery, part of which is caused by the increased pressure of competition from the char. Recently it was found that turning an allopatric trout lake into a reservoir did not cause the same serious decline, since there was no additional char influence (NILSSON and ANDERSSON 1967, NILSSON and FAGERSTRÖM 1973).

Because of industrial air pollution, acid rains have lowered the pH of many Scandinavian lakes and rivers (DICKSON 1975). The detrimental effects on the fish fauna have been studied by ALMER *et al.* (1974), DICKSON *et al.* (1975) and LEIVESTAD *et al.* (1976).

The roach is more sensitive to acid water than are several other sympatric species (ALMER *et al.* 1974). Because of the dominance of the roach, however, some species, such as perch, may expand their population as a reaction to the disappearance of the roach. In one stage of acidification, therefore, the fishery for perch may be excellent. In August 1976 an experimental netting in Lake Nättsjön, south-western Sweden, gave one pike and 211 perch (15.5 kg), a sample of which had the following size distribution:

cm	10	11	12	13	14	15	16	17	18	19
males	1	4	4	6	4	2	3	6	2	1
females	3	1	1	3	3	—	4	6	2	8

cm	20	21	22	23	24	25	26	27	28	29
males	2	3	—	—	1	—	—	—	—	—
females	2	5	5	9	3	1	2	1	1	1

Formely, Lake Nättsjön was crowded with roach and stunted perch. Reproduction of roach has probably not occurred since 1965, and so the species has now vanished. From a fisherman's point of view, the present status of the lake is very good (courtesy Mr AURELL and Mr ALMER).

The stress of eutrophication on fish communities has in recent times become an issue in the economic and political discussion in Scandinavia. Thousands of millions of crowns have been invested in order to clean up polluted lakes. The generalization is often made that increased nutrient standard of lakes constitutes a menace to fish.

It is the dominance of roach and bream that has contributed to a general notion that an overall deterioration of commercial fish accompanies eutrophication. In many oligotrophic lakes, however, the phosphorus and nitrogen are beneficial to the fishery and it is the biocids and heavy metals that give cause for alarm.

In order to analyse more deeply the consequences of eutrophication of different lakes, the dominance phenomena must be taken into account. The whitefish populations of the four largest Swedish lakes constitute an interesting example.

There has been a gradual increase of whitefish landings in the two largest and most oligotrophic lakes, *i.e.* Vänern (Fig. 12) and Vättern (GRIMÅS *et al.* 1972). There are temporal peaks in the catch, caused by rich year classes produced in warm summers. The trend upwards, however, cannot be related to summer climate, which has deteriorated during the same period of time. Consequently, the eutrophication of the lakes is, probably correctly, blamed or praised for the whitefish population expansion.

Lake Mälaren, the third largest lake, is more eutrophic than Vänern and Vättern, and its whitefish has very clearly *decreased* during the last 50 years (Rundberg 1968). This seems to be at variance with the interpretation given for Vänern and Vättern. However, Lake Mälaren cannot be too eutrophic for whitefish, as the fourth largest lake, Hjälmaren, is very warm, shallow and eutrophic and still produces some 7 tons of whitefish annually, while the Mälaren catch nowadays is less than one ton.

The most plausible interpretation at present is that which gives the cisco the major role. The cisco is supposed to have only slightly increased its abundance in Vänern (average catch 190 tons) and Vättern (40 tons), but it has definitely increased enormously in Lake Mälaren, where the catch has mounted from a few tons in the 1920s to an average of 160 tons in the last few years. The inversed correlation between whitefish and cisco in Lake Mälaren over a period of 50 years makes sense, as the cisco is known to dominate the whitefish. And the surprising occurrence and high catch of 7 tons of whitefish in the warm Lake Hjälmaren can be understood only when one knows that cisco *does not occur* in this lake. Thus, a slight eutrophication of Vänern and Vättern has so far stimulated whitefish more than cisco, while the more intensive eutrophication of Lake Mälaren has triggered of a great positive cisco reaction, with adverse effects on whitefish.

The relatively low number of ciscoes in the highly oligotrophic Vättern and their non-existence in the eutrophic Hjälmaren should also influence the smelt in those lakes. The smelt is known to be very abundant in these two lakes and forms the prey basis for salmonids (char, trout, stocked salmon and rainbow) in Lake Vättern and for sander in Lake Hjälmaren. The perch, which feeds on smelt and then becomes large enough for the commercial market, is also landed in interesting quantities (Vänern 2.5 kg/km^2, Vättern 12.6, Mälaren 7.2 and Hjälmaren 53.1 kg/km^2). The paradox of the occurrence of the best perch catch in the warmest and the coldest of the four lakes is probably related to the abundance of smelt, a phenomenon which in turn depends on the cisco.

The smelt also seem to serve as a "buffer species", smoothing the interaction of whitefish and char in Lake Vättern as well as sander and perch in Lake Hjälmaren. In both lakes, a negative correlation is known to prevail between landings of the interacting species; yet *both* species are abundant in the two lakes. The buffering effect of the smelt comes from the fact that it is the most sought-after prey for (even small) char, sander and large perch. The hypothesis of the smelt as a buffer prompted suggestion for management (Filipsson and Svärdson 1976) to the effect that smelt should be introduced in southern lakes where char has been almost exterminated by whitefish, cisco, roach or other competitors and in the mountain lakes to stop the stunting of char there, after excessive human exploitation of the (predatory) brown trout.

In October 1903 six hundred adult ciscoes were brought from Lake Mälaren in an effort to introduce the species into Lake Hjälmaren (Ekman 1904). Lake Hjälmaren was isolated during the salt Litorina period and its rivers are too small to supply the cisco with upstream sanctuaries like Lake Mälaren. The 1903 introduction failed, but recently the question has been discussed of making a second attempt with the aid of modern technology. On the basis of what is now known, however, the proposal is not to be recommended. If the hypothesis here discussed is accepted, the following prognosis for Lake Hjälmaren is suggested if the cisco expands: the whitefish will disappear (7 tons), the perch will be stunted and become unsaleable (25 tons), and a heavy reduction of the sander from 240 kg/km^2 towards that of Lake Mälaren (90 kg/km^2) — a loss of some 50—60 tons — will occur. The sander is the backbone of the commercial fishery of the lake. The introduction of cisco thus seems too risky.

The upper tolerance limit to eutrophication *per se* by whitefish and cisco cannot be properly studied when roach is a member of the fish community. This is the case in all Swedish lakes where eutrophication is advanced.

Lake Orrevann in the Stavanger area of southwestern Norway offers, however, a unique possibility. This eutrophic, shallow lake (8 km^2) lies, only 4 metres above sea level, on marine clay and moraine gravel and the transparency is only 20—30 cm, because of very rich nutrients from the surrounding farmland. The fish catch in 1974 was a staggering 52.5 kg/hectar of whitefish (surprisingly of the rare *pidschian* type), 12.5 kg of eel and some 5 kg of cisco and brown trout combined (Vasshaug, in litt). Whitefish and cisco are otherwise met with only in the southeastern part of Norway.

The zoogeographical problem of the isolated two *Coregonus* in Lake Orrevann is probably related to the flushing, in the year 8213 B.C., of the great Baltic Ice Lake (*cf.* ERONEN 1974), when the melting ice withdrew north of the mountain Billingen in southern Sweden. The ice lake then suddenly drained to ocean level and fresh water rushed in a great spate westwards along the ice margin and the Norwegian coast. This flow probably brought drifting whitefish and cisco all the way to the Stavanger area, where they happened to invade some freshwater stream and survived to the present Lake Orrevann.

The Institute of Freshwater Research fished Lake Orrevann in May 1965, searching (in vain) for the spring-spawning cisco. The fishing crew were astonished at the high abundance of whitefish in such eutrophic surroundings. The catch was 33 whitefish, 192 cisco and 2 hybrids on small-meshed gill nets suited only for cisco. Material collected and analysed by PETHON (1974) in 1971 and 1973 comprised 75 whitefish, 91 cisco and 36 hybrids. It seems as if the future of these systematically as well as ecologically most important *Coregonus* populations is threatened by introgression caused by spawning-ground deterioration. Lake Orrevann does indicate, however, that for the whitefish as well as the cisco the tolerance to eutrophication, in the absence of roach, bream, perch and pike, is remarkable. The apparent dominance of whitefish over cisco in Orrevann may be related to the extreme shallowness of the lake (most parts 4 metres only) and the bottom diet of the *pidschian* whitefish. Indirectly, Lake Orrevann is a testimony to the normal dominance of pelagic roach in the final stages of the eutrophication process.

V. SUMMARY

For centuries, the paucity of freshwater fish species in Scandinavian lakes and rivers and the zones of more or less elevated lakes to which natural postglacial spreading of fish was erratic, has stimulated landowners to "enrich" their lakes by introductions of fish from lower regions. These efforts have yielded a great body of experience, which is summarized in the paper. Regional comparisons has added some knowledge about the dominance of some fish species over others.

The interactive relations of the best-known species is presented and some more general conclusions are discussed, regarding evolutionary trends and specific ecological niches, ecological subspeciation and non-genetic "interactive segregation".

There is a trend that specialization on pelagic life contributes to dominance among lake-living fish. The dominance of some fish species seems correlated to their capacity to catch small-sized zooplankton, and this has far-reaching consequences for the plankton fauna and hence primary production.

All kinds of stress on the freshwater fish community trigger off great shifts among species because of the dominance phenomena. The conversion of lakes into reservoirs, acidification and eutrophication are discussed and examples are given. The principle of "buffer species", smoothing the interactions between two antagonistic species, is presented. Some management suggestions are included.

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