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Protein Variations in *Salmonidae*

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Introduction

The structure of proteins is determined by genes through various stages of coding by different forms of nucleic acids. Species specific protein variations are consequently caused by the action of a number of different genes. Techniques for the study of protein variations such as the various types of electrophoretical methods may add considerable information on hereditary divergences between populations and species. The usefulness of electrophoresis in taxonomical work is unquestionable, but the study is complicated by some factors which must be kept in mind, viz. the occurrence of ontogenetic variations and the matter of analogous and homologous genes. Some protein patterns are to wit completely altered in their phenotypic appearance during embryonic development, and they are often radically changed through gradual stages until sexual maturation is attained. Consequently species and population comparisons should be made between individuals of comparable ages. The second problem is whether identical phenotypes are produced by homologous (virtually identical) genes or by analogous genes producing similar appearance. Still another complication to be realized is the case of introgression between sibling species, where an observed polymorphism in one population simply might be due to crossing with individuals of a closely related species.

Biochemical characteristics offer a more stable basis for taxonomic research on fish than was earlier possible when only employing biometric methods. The reason for this is the most common condition of nongenetic (phenotypical) geographic variation in fish, which severly affected many a study of populations when using meristic characters as tools. This phenotypical plasticity, due to a pronounced response to environmental conditions, has long been known (Tåning 1944) and numerous examples are presented elsewhere (Mayr 1963). The process of speciation is even more complicated among most *Salmonidae,* since in these species both anadromous and freshwater forms may occur in different bodies of water. When, for some reason, a population gets landlocked it often switches over to a freshwater life, and hereditary divergence starts due to the quite different environmental conditions and hence different selective forces. A wellknown example is the case with the anadromous and freshwater forms of salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) but even other genera of *Salmonidae* exhibit the same problems (Ricker 1940, Neave 1944, Svärdson 1957). Another problem strongly reflected in above all the blood tissue is the most common phenomenon of drastic changes in the quantitative distribution of the protein fractions. Not only are there seasonal changes (Shell 1961, Kirsipuu 1964) but almost every physiological change, due to for instance type of food, temperature, spawning, disease etc., seems to be connected with altered concentrations of most protein systems present. The difficulties in comparing

blood serum protein patterns should, however, not be overestimated, since they are seldom reflected in the qualitative patterns, i.e. mobility and number of bands.

Still there is some limitation adhering this type of protein taxonomy which must be kept in mind, since this state of affairs is not restricting the morphological investigations. Any pattern visualized must be described as to for instance type of supporting medium, buffer, ionic strength, time of electrophoresis etc., and this makes any kind of comparison between patterns found by different scientists most difficult, unless they are using identical methods — which is not often the case.

One of the first studies of proteins in fish was performed by LEPKOVSKY (1929), but it was not until the development of the different electrophoretical methods that comparative protein investigations started. Various supporting media were investigated as to their contingent value for protein separation and new techniques in histochemistry evolved, capable of demonstrating the zones of enzyme activity in the supporting medium. The most recent electrophoretic investigations make use of above all three types of media in their study of protein variation in fish, viz. agar gel (SICK 1961, RABAEY 1964), starch gel (TSUYUKI 1963, KOCH, BERGSTRÖM & EVANS 1964), and polyacrylamide gel (GOLDBERG 1965).

In the present communication protein variations in several species of the family *Salmonidae* are presented by means of a modified version of the starch gel electrophoresis method first described by SMITHIES (1955).

Material and Methods

Fishes investigated. The fish investigated in these studies were collected and analysed continuously from February 1964 to May 1966. Some 700 specimens belonging to 11 species and 4 hybrid "species" were investigated. Their systematical order is given in Table 1. The hybrids were the offspring of the following species combinations, viz. 1) speckled trout (*Salvelinus fontinalis* MITCHILL) × char (*Salvelinus alpinus* L.), referred to as *bröding,* 2) speckled trout × lake trout (*Salvelinus namaycush* WALBAUM), splake, 3) lake trout × char, *kröding* and finally 4) Atlantic salmon (*Salmo salar* L.) × brown trout (*Salmo trutta* L.), "laxing".

In the hybrid investigations one year old F_1 hybrids of landlocked salmon and brown trout from the River Gullspångsälven were used, and they were compared with one year old specimens of the parental populations. F_2 hybrids of the same species combination were obtained from ova of Irish fish. The study of geographic variation in salmon was based on two year old specimens reared at Älvkarleö (Swedish Salmon Research Laboratory) from ova originating from Canada (Gaspé Peninsula), Sweden (Baltic salmon from the

Table 1.

Family	Genus	Species
Salmonidae	*Salmo*	*S. salar* L. (Atlantic salmon)
„	*Salmo*	*S. trutta* L. (brown trout)
„	*Salmo*	*S. gairdnerii* RICHARDSON (rainbow trout)
„	*Salvelinus*	*S. alpinus* L. (char)
„	*Salvelinus*	*S. fontinalis* MITCHILL (speckled trout)
„	*Salvelinus*	*S. namaycush* WALBAUM (lake trout)
„	*Hucho*	*H. hucho* L. (Danube salmon)
„	*Osmerus*	*O. eperlanus* L. (smelt)
„	*Coregonus*	*C. lavaretus* L. (whitefish)
„	*Thymallus*	*T. thymallus* L. (grayling)
„	*Oncorhynchus*	*O. nerka kennerlyi* WALBAUM (kokanee)

River Lule älv) and Lake Saima (Finland, landlocked salmon). For the study of protein variation in Baltic salmon 200 sexually mature fish were collected from the River Indalsälven (downstream the dam at Bergeforsen), and further specimens from this river, reared under laboratory control and 1 to 4 years of age, were gotten at Älvkarleö. These individuals were compared with fish of the same age from the River Lule älv, reared at Älvkarleö as well. The study of ontogenic variation in different salmon tissues were applied to ova and individuals of different age mostly originating from the River Lule älv.

For the study of hybrids brown trout from the River Gullspångsälven were used (mentioned above). Two other populations of brown trout, both originating from the River Indalsälven, were used in the study of hereditary divergence in brown trout. One population was anadromous (collected at Bergeforsen), the other was "brook-locked" in the small river Bjässjöån, a tributary of the River Indalsälven.

The rainbow trout were all of Danish extraction, but reared at the Källefall rearing station, province of Västergötland.

The char specimens originated from Lake Vättern, some of them were the offspring of fish stripped in Denmark, others were derived from ova stripped and fertilised at Källefall.

Speckled trout (brook trout) were gotten at Källefall and Kälarne, province of Jämtland, where two types were said to exist, viz. a brook spawning type (normal) and a lake spawning one.

Sexually mature lake trout were sampled at the Bonäshamn rearing station, province of Jämtland.

The intra-generic hybrids between speckled trout, char and lake trout were all obtained in Sweden. Splake, gotten at Bonäshamn, were the offspring of five or six successive generations of freely breeding F_1 hybrids introduced into a lake in western Canada. The *bröding* specimens were true F_1 fish produced at Källefall, and the single *kröding* individual was a big

but sexually immature F_1 fish produced and reared at Drottningholm (Institute of Freshwater Research).

Smelt specimens of unknown age were caught near Drottningholm. A few individuals of whitefish were obtained at Bergeforsen and Bispfors, River Indalsälven, and for a comparison one specimen each of hucho (Kälarne), kokanee (Kälarne) and grayling (Bispfors) were obtained.

Tissues investigated. Blood serum, livers and kidneys were analysed in most species and hybrids, and muscle, (*musculus lateralis superficialis*) brain, spleen and small intestine in salmon as well.

Sampling procedure. Blood can be obtained in sufficient quantities from fish down to 8 cm of length. An incision is made in the ventral region near the heart, the mucus and scales first being thoroughly removed at the spot of injection to prevent clotting. The heart is punctured by means of a thin scalpel and the blood is taken from the pericardial cavity in heparinised glass capillaries. The blood is then transferred to the polyethylene tubes of the Beckman Spinco Analytical System and centrifuged for 15—20 seconds in the microcentrifuge of this system. The serum is removed and refrigerated, either in dry ice (—75°C) or in deep freezer at —20°C. No further preparation is needed, the blood serum can be directly used for analysis.

The following procedure was employed for the other tissues to be analysed: The organs were washed in a physiological saline (0.923 g NaCl/100 ml distilled water) to remove excess blood, then buffered (TRIS, see below) and homogenated in a glass homogenator cooled in an ice water mixture. After the homogenisation the tissue "fluid" is transferred to the polyethylene tubes mentioned above, and the cell debris is spun down. The supernatant solution thus received is then used for immediate analysis or stored in the freezer. All organs were removed immediately after sampling the blood and stored in closed glass tubes in dry ice or freezer to prevent denaturation of the proteins and inactivation of the enzymes. Permanent storing of blood serum, for instance, makes it possible to analyse nonspecific esterases after at least one year. Repeated thawing and freezing by sampling, however, accelerate the denaturation and inactivation processes and the zymograms get faint and diffuse. These phenomena call for the necessity of two samples of each tissue, one being kept as a control.

Electrophoresis apparatus. The apparatus employed is a slightly modified version of the apparatus constructed by GEDIN and GAHNE, Inst. of Biochemistry and Dept. of Genetics and Plant Breeding, University of Uppsala (unpublished). Starch is used for supporting medium, and platinum for electrodes. The complete apparatus is cooled by means of cold running water, and the electrode vessels are not attached to the apparatus in order to allow them to be cleaned easily, which is especially important when changing buffer systems. The vessels each hold some 400 ml of buffer. The current is taken from a regulated power supply (Oltronix LS 107), which a max.

capacity of 200 mA and 500 V. This type of electrophoresis box allows analysis of 20—25 samples simultaneously, insuring a good comparison.

Preparation of the gel. 200 ml of buffer is heated to boiling. Another 100 ml of the same buffer is admixed with 31 g of hydrolyzed starch (Connaught Medical Research Laboratories, University of Toronto, Canada). The starch-buffer solution is mixed with the boiling buffer, and after shaking and de-gassing the gelsolution it is evenly poured onto a framed glass plate measuring some 15×30 cm. After 15 minutes the starch is covered by a sheet of thin plastic film. The starch has set after some two hours, faster in a refrigerator, and can be used for further preparation.

Application of samples. For investigation of blood serum proteins a vertical slit is made parallel to the longest side and some 4 cm from the edge. Analyses of organs must be performed in a different way. A vertical slit is made for each sample, by means of a special device insuring uniform slits, in order to prevent interaction between samples, which might else be a problem with these tissues. Filter papers of a standard thickness and measuring some 0.5× 1.0 cm are damped with 10 µl of the solution to be investigated. The filter papers are placed into the slits and the gel is covered with a sheet of Parafilm M (Marathon Menasha, Wis., U.S.A.). The buffer in the electrode vessels is connected to the gel and a constant voltage of 400 V is used, the strength of current ranging from 250 to 90 mA. After 15 minutes all protein components have migrated into the gel and the filter papers are removed. The electrophoresis is performed another 75 minutes. The heat generation makes cooling of the apparatus most necessary. After the completion of the electrophoresis the gel is sliced horizontally by means of a device insuring a standard thickness of the slices, each slice either used for staining of different enzymes or other types of proteins or as a control.

Staining procedures. The buffer systems employed in the studies were those described by POULIK (TRIS, 1957), ASHTON & BRADEN (1961) and a few analyses using acetate buffer (BURSTONE, 1962). Alkaline phosphatases were run in the buffer suggested by POULIK, most of the other enzymes and proteins were run in the buffer suggested by ASHTON & BRADEN. Incubation and staining was performed at room temperature (25°C).

Lactate dehydrogenases: 0.5 g of lactic acid, 16 mg of PMS (phenazin-metho-sulphate), 40 mg of DPN (di-phospho-pyridine-nucleotide) and 10 mg of NBT (nitro-blue-tetrazolium) are diluted in a small amount of distilled water and added to the gel which is incubated in 100 ml of TRIS-HCl (0.2 M, pH 8.1). The gel is stored in complete darkness as NBT and PMS are sensitive to light.

Alpha-glycerophosphate dehydrogenases: 100 mg of alpha-glycerophosphate, 20 mg DPN, 30 mg NBT and 16 mg PMS are diluted in distilled water. Same incubation procedure as above.

Alkaline phosphatases: 100 mg sodium-α-naphthol phosphate, 100 mg Fast Garnet GBC salt and presence of manganese and magnesium ions diluted in distilled water. Incubation in 100 ml Tris buffer (pH 8.6).

Leucine amino peptidases: 100 mg l-leucyl-β-naphtyl amide HCl and 100 mg Black K salt diluted in distilled water and added to an incubation buffer of 0.1 M Tris-maleate of pH 6.0.

Esterases: α-naphthol acetate was diluted to a concentration of 1 per cent in equal amounts of distilled water and acetone. 1 ml of this solution and 100 mg of Fast Red TR salt are diluted further in 50 ml of distilled water, which is added to an incubation buffer of sodium phosphate of pH 7.0 (BURSTONE 1962).

Amido Black and Coomassle Brilliant Blue: 1) The following stock solution is prepared: 300 ml of methanol, 300 ml of distilled water, 60 ml of HAc, 150 ml of glycerine, 5 g of amido black and 2 g of nigrosine. A small amount of this solution is evenly poured onto the gel slice until it is completely covered. After 3—5 minutes the amido black — nigrosine solution is removed by means of a glass staff, and excess dye is removed by incubation in a solution of 5 parts of methanol, 5 parts of distilled water and 1 part of acetic acid. Repeated washing in the solution mentioned is necesssary for rapid visualization. 2) A stock solution is prepared by diluting Coomassie Brilliant Blue R 250 to a concentration of 1 per cent in 7 per cent HAc. Visualization same as above. The time of incubation depended on type of enzyme and time of sample storage. Maximum staining intensity in fresh blood serum esterases was reached in 10 minutes, the common time ranging from 1 to 2 hours, while blood serum proteins dyed with amido black had a range extending to 6 hours.

Of the above mentioned enzymes only the dehydrogenases are so called specific enzymes, i.e. they are demonstrated by the use of naturally occurring, specific substrates. The others are consequently "non-specific" since they are visualized by synthetic compounds as substrates. This distinction between specific and non-specific enzymes is, however, not entirely valid, which was pointed out by SHAW (1965): ". . . while 'natural' substrates are used to demonstrate the presence of dehydrogenases, this is no proof that the metabolism of that particular substrate is the only or even the chief action of that molecule. Conversely, some of the esterases display activity toward a number of synthetic substrates in vitro, whereas in vivo they may have a high degree of specificity."

Results and Discussion

The results are discussed under 14 different headlines A—N, generally one for each species or hybrid "species". In all the schematic pictures the

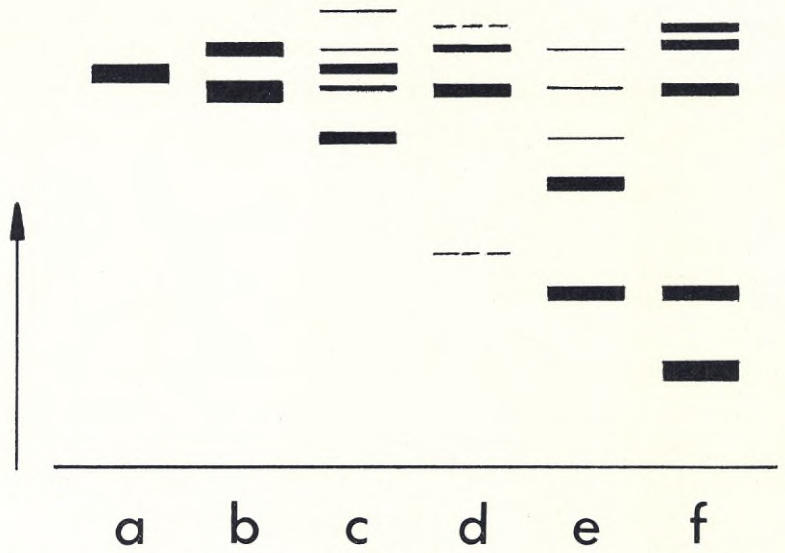

Fig. 1. Esterase patterns in salmon. a) serum, b) kidney, c) liver, d) spleen, e) small intestine and f) brain.

horizontal line represents the starting point and the arrow indicates the direction of the anodic migration.

A. *Atlantic salmon.* Studies on protein variation in salmon tissues are still very few in number. One of the first was performed on a few specimens of hatchery salmon (SCHUMANN 1959) and two components of haemoglobin were shown by means of agar electrophoresis. More recent studies on the haemoglobin of salmon (KOCH, BERGSTRÖM & EVANS 1964 a, b) have revealed a far more complicated pattern. The haemoglobins can be separated into two groups by means of a starch gel electrophoresis method, in each group the patterns are altered by gradual transitions from the juvenile stage to the sexually mature individual. The differences presented are of qualitative as well as quantitative origin. Studies of patterns of salmon originating from 10 rivers have not revealed any inter-population differences so far, no polymorphism noted and the same type of ontogenetic development present in all the populations. One type of protein variation is reported in salmon, however (DRILHON & FINE 1963), by the discovery of a sexual dimorphism in the serum protein patterns.

Protein patterns in sexually mature salmon: The esterase patterns in blood serum and 5 organ tissues are schematically shown in Fig. 11. No "intra-tissue" variation was detected, and 450 investigated specimens had the same one-zone esterase form in the blood serum, indicating a monomorphic esterase. This homogeneity has been used for systematic classification of individuals where the biometric characters of two closely

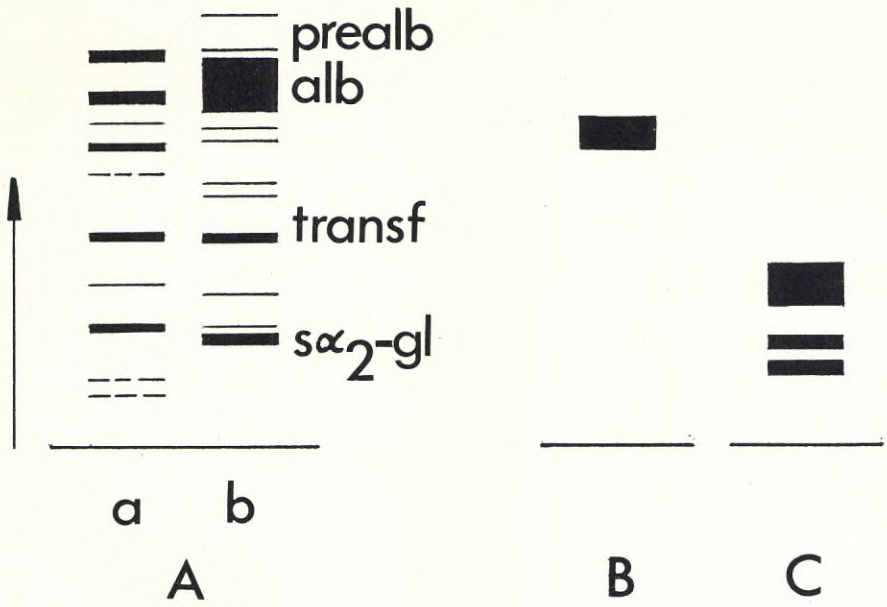

Fig. 2. A) Serum protein patterns in salmon (a) and human (b) blood. prealb=prealbumins, alb=albumin, transf=transferrin and $s\alpha_2$-gl=slow α_2-globulins. B) Serum leucine amino peptidase in salmon. C) Alkaline phosphatases in salmon serum.

related species are almost overlapping in extreme cases, since the protein patterns of the species involved are very different (SVÄRDSON 1966). The organ proteins stained with amido black do not show any variation what so ever, neither of intra- nor interspecific kind. Besides they stain very faint. The opposite condition is present in the serum proteins where the patterns are distinct and species specific. Salmon and human protein patterns are compared in Fig. 2 A. The minor variations in the salmon patterns had a too low rate of reproducibility to be able to serve as tools. The leucine aminopeptidases and alkaline phosphateses in blood serum were only tested in a few individuals and no intraspecific variation was noted (Fig. 2 B, C). Studies of leucine aminopeptidases in salmon, brown trout, speckled trout, lake trout, splake and hucho indicated only one zone of enzyme activity in each species and since there was no pronounced difference in mobility these enzymes were not used for further investigations.

In Fig. 3 the isozyme patterns of lactate dehydrogenases and α-glycerophosphate dehydrogenases are presented. The α-glycerophosphate dehydrogenase pattern in the kidneys and the lactate dehydrogenase patterns in kidneys and serum indicate a tetrameric structure produced by two polypeptide subunits synthesized under the control of two nonallelic genes. This mode of inheritance is explained elsewhere (SHAW & BARTO 1963). More recent studies on lactate dehydrogenases in various species of *Salmonidae,* however, indicate

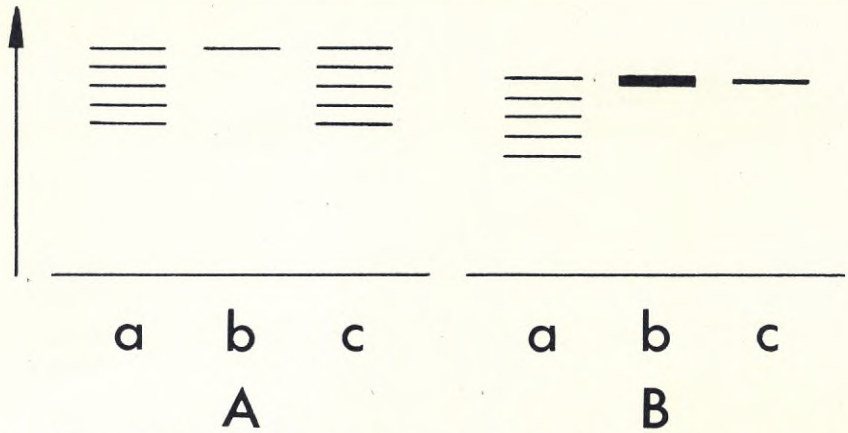

Fig. 3. A) Lactate dehydrogenases in salmon tissues. a) kidney, b) liver and c) serum. B) α-Glycerophosphate dehydrogenases in salmon tissues. a) kidney, b) liver and c) serum.

at least a third subunit in all tissues examined (GOLDBERG 1965, BOUCK 1965). In Fig. 4 the possible underlying genetics of the five electrophoretically distinguishable isozymes is indicated. A and B are the two polypeptide subunits, the bands AAAA and BBBB are consequently different proteins and the three zones in between are hybrid proteins. When enzymes occur in more than one molecular form they are called isozymes (MARKERT & MØLLER 1959).

No association with sex was found in any of the investigated proteins.

Ontogenetic variation in salmon: Analyses of enolase patterns by means of starch gel electrophoresis has been performed in 8 species of the genera *Salmo* and *Oncorhynchus* (TSUYUKI & WOLD 1964), and these studies did not indicate any significant differences between juvenile and sexually

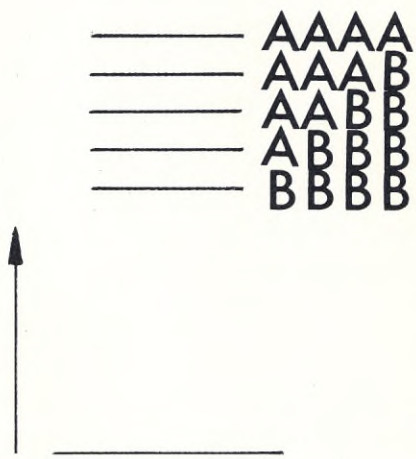

Fig. 4. Supposed genotypic background of dehydrogenases, further explained in the text.

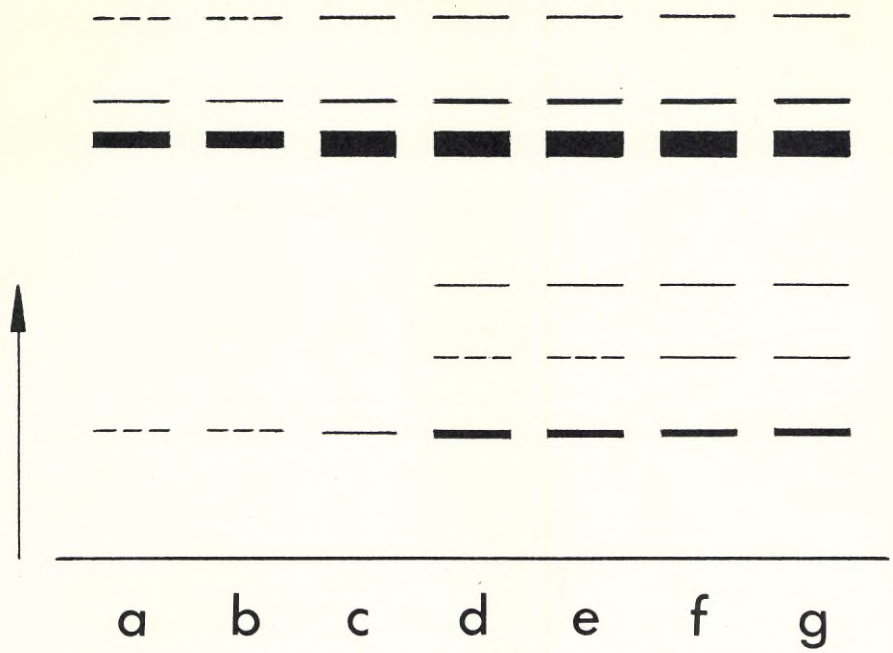

Fig. 5. Differences in salmon muscle esterase patterns, possibly due to ontogenetic development. a) 4 weeks before hatching, b) 3 weeks before hatching, c) newly hatched, d) 1 year of age, e) 2 years of age, f) 3 years of age and g) 5 years of age.

mature fish. In order to find out the state of affairs in Atlantic salmon, muscle proteins (amido black) and muscle esterases were investigated. The muscle esterases (Fig. 5) were investigated in embryos (4 and 3 weeks before hatching), in newly hatched fry and in fish 1 to 5 years of age, all reared under laboratory control at Älvkarleö. Slight but significant differences indicating a gradual increase in the number of zones, and in the plainness of them as well, are evidently due to ontogenetic development. In Fig. 6 more drastic differences are shown in the muscle protein patterns. Four protein "systems" seem to be involved ("system" is only used from considerations of convenience, and does not indicate any genetical correlation between the zones involved). System A is rather uniform in the qualitative distribution of the bands involved, but with a quantitative decrease with age. The B and D systems are probably due to sexual maturation as both of them occur at the age of 2, and they are thereafter constant in the qualitative and quatitative distribution of the bands. The C system is also rather constant, with a quantitative increase at the age of 2+. The muscle proteins evidently indicate a typical example of ontogenetic development, with gradual transitions of the protein patterns and a marked increase in the number of bands when sexual maturity is attained.

Geographic variation in salmon: Geographic variation is a

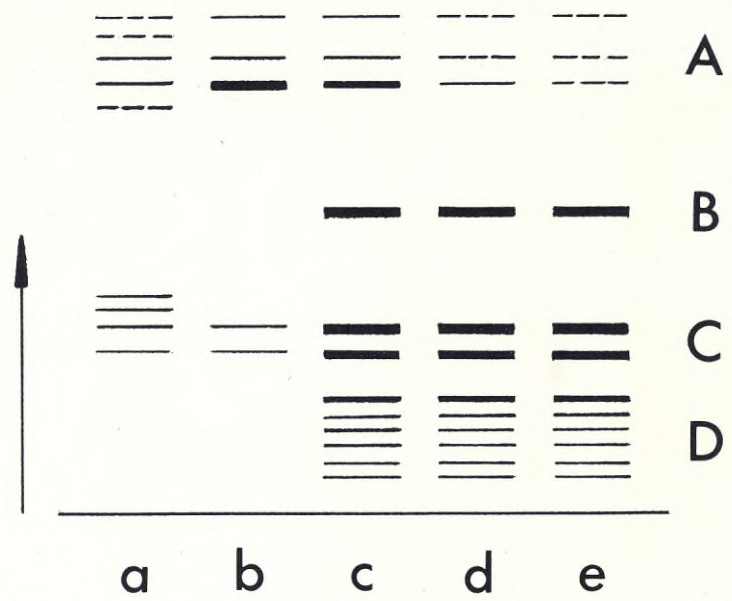

Fig. 6. Differences in salmon muscle protein patterns, possibly due to ontogenetic development. a) newly hatched, b) 1 year of age, c) 2 years of age, d) 3 years of age and e) 5 years of age. A, B, C and D = "systems" explained in the text.

common condition among animals and plants. In fact it has long been known that differences occur between practically all local populations (demes) of a species. These differences may be internal or external, conspicuous or microscopic. In some groups of animals, the lower vertebrates for instance, this geographic divergence is very often due to non-genetic (phenotypical) adaptability, i.e. a response to environmental conditions. In such cases the value of meristic characters as taxonomic tools is uncertain, since there must be incontrovertible evidence for the genetic basis of any given variation. Among fishes (especially freshwater forms) this phenotypical plasticity is very pronounced and has severely affected many a study of speciation, possible occurrence of sibling species and intraspecific variation. An exception was shown by SVÄRDSON (1949, 1950, 1952), who demonstrated the genetic basis of the number of gill rakers in the genus *Coregonus,* which helped to solve the so called *Coregonus* Problem. Among most other fishes, however, the genetic basis of most intraspecific variations, as demonstrated by biometric characters, is rather diffuse.

Since differences in band number and mobility of protein patterns can be demonstrated to have different genetic basis (see below: Salmon×brown trout hybrid), qualitative differences are advantageous for investigating inter- and intraspecific variation. One of the first investigations performed on fish for the study of geographic variation at the protein level was made by SICK

(1961, 1965 a, b). By means of an agar gel electrophoresis method he revealed that the haemoglobins of cod (*Gadus morhua* L.) were polymorphic for two codominant allelic genes, and in his most recent papers he describes the different geographic races observed, as determined by the frequencies of the alleles involved. The present study deals with differences in the protein patterns of salmon from Canada (Gaspé Peninsula) and the River Lule älv (Gulf of Bothnia).

It is of great importance that the compared specimens are of the same age, to avoid possible complications due to developmental differences. Equally important for the study of genetic divergence is the presence of identical environmental conditions for the populations to be investigated, and this can only be maintained under laboratory control. The fish investigated in this study were consequently reared under as far as possible identical conditions in concrete troughs, and were subsequently placed at my disposal by the Swedish Salmon Research Laboratory, Älvkarleö. The influence of the environment would thus be kept at a minimum, and possible differences would be of a genetic origin. Finally one would have to prove that the zones appearing in the zymograms (electropherograms) have a genetic basis and are segregated to the offspring. The significance of the protein band segregation is easily demonstrated in analyses of interspecific hybrids, where the parental species differ in as many protein zones as possible. This state of affairs was demonstrated in the F_1 hybrids between salmon and brown trout (see below), where the hybrids exhibit a summation of the protein patterns present in the parental species.

The differences found in the blood serum protein patterns of salmon from Canada (C) and Sweden (S) are slight but significant, in neither case could any intrapopulation variation be detected (Fig. 7 A). The major band at a) has a mobility some 1.0 mm faster in the Canadian population, and this offers a clear classification when the blood sera are not subjected to haemolysation, as this band is close to the main haemoglobin fraction. The extra band in the "b-system" of Canadian salmon is somewhat diffuse but mostly legible. The faint slow α_2-globulins located at c) in Baltic salmon are also normally fully legible. The specimen from Lake Saima (Finland) was almost inseparable from the River Lule älv individuals, but possibly with a "b-system" similar to Canadian salmon.

The distinct differences in the liver esterases (Fig.7 B) indicate the most easy way of separating the two populations. Furthermore, livers are much easier to obtain than blood, no centrifuge or special preparation needed. The distinct esterase band at a) in Swedish fish is completely missing in Canadian specimens, and the band at b) in Canadian salmon is a bit slower than the corresponding band in Swedish fish. The pattern of the specimen from Lake Saima could not be separated from the Swedish pattern. For future investigations of liver esterases in different populations, performed on

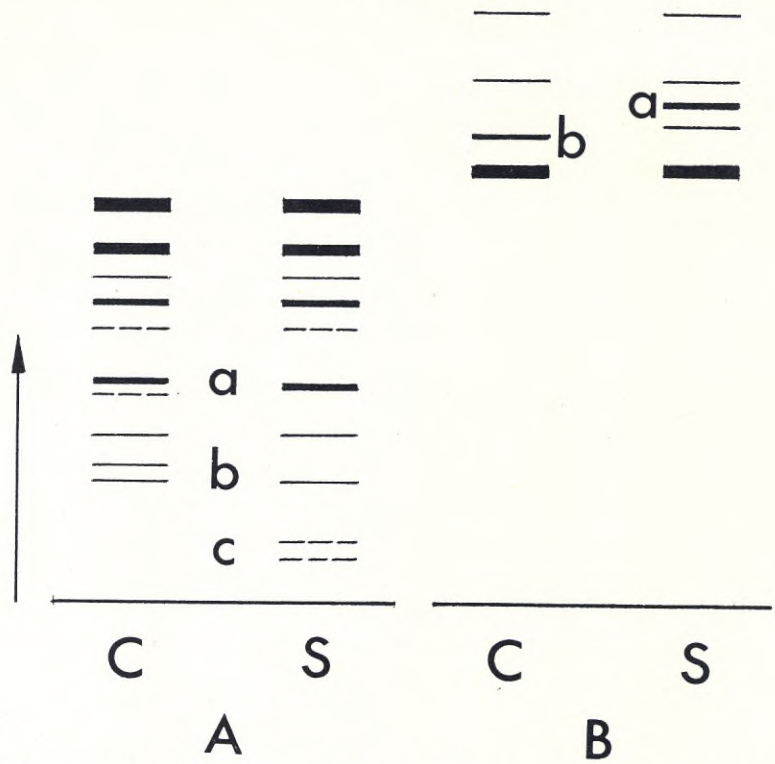

Fig. 7. A) Serum protein patterns in Canadian (C) and Swedish (S) salmon. a, b and c are explained in the text. B) Liver esterase patterns in Canadian (C) and Swedish (S) salmon. a and b are explained in the text.

big fish, it would become unpractical to use whole livers since they are bulky and require much dry ice for freezing. To avoid these complications the livers from two big hatchery reared salmon were divided into 10 sections each. These sections were separately treated in the manner described in Material and Methods, and analysed electrophoretically. No intra-tissue variation was reflected in the esterase patterns, which evidently would allow sampling of small pieces of liver. This experiment seems to justify the use of pieces measuring some 1 cubic cm.

A marked difference in the staining intensity of the serum esterases was noted, that of Canadian salmon being significantly stronger. To find out where the differences were optimal samples were incubated in sodium phosphate buffer of varying pH. Some of the results are presented in Fig. 8 where S stands for Swedish and C for Canadian. The Canadian esterases were superior in staining intensity at all pH values between 6.0 and 7.5, at lower and higher values they both stained faint with about the same intensity. As shown in the figure incubation should be performed at pH 6.5 where the

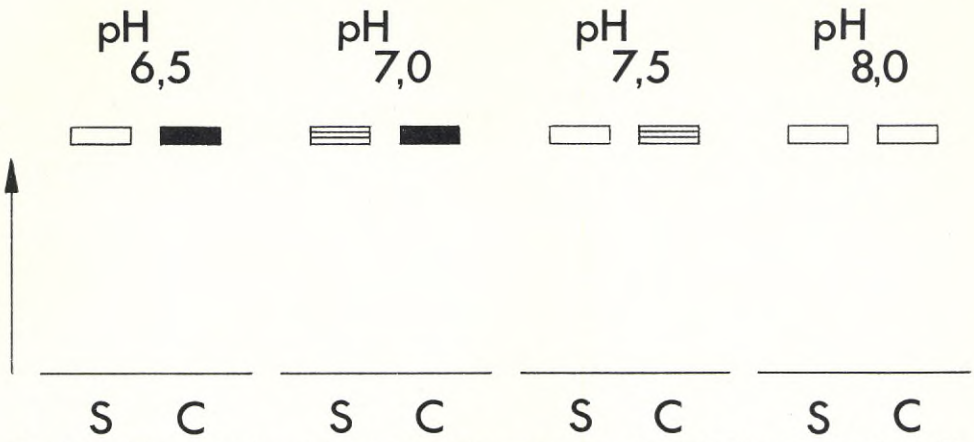

Fig. 8. Staining intensity of the serum esterase zone in Swedish (S) and Canadian (C) salmon at various pH values.

difference reaches a maximum. The Saima specimen seemed to have the same intensity range as the Swedish population.

B. *Brown trout.* Five investigated 1 year old brown trout of the River Gullspångsälven did not differ in their protein patterns from a "brook-locked" population of the small river Bjässjöån. Since the fish from the latter river were sexually mature no development system concerning maturation seems to be present. Anadromous brown trout of the River Indalsälven were, however, different from the freshwater form (Fig. 9 A). As a comparison the normal pattern in salmon is shown. The serum esterase pattern is monomorphic in brown trout (like in salmon) and no mobility differences of the zone in different populations could be detected (Fig. 9 B). A very rare state of affairs is present in the kidney esterase pattern, this too being monomorphic (Fig. 9 C). The liver esterases are indicated in Fig. 9 D. No intraspecific variation was detected in any of the esterases.

C. *Salmon×brown trout hybrid (laxing).* Spontaneous hybridisation between salmon and brown trout seems to be very rare. Despite the fact that salmon and brown trout are thought to be most closely related (ROUNSEFELL 1962), no successful experiments giving fertile hybrid offspring, with a low rate of losses to earlyfeeding fry, was reported until recently (PIGGINS 1965). The main reason for these unsuccessful experiments seems to be the fact that the two species have different chromosome numbers, viz. brown trout 80 and salmon 60 (SVÄRDSON 1945). The F_1 hybrid will consequently have 70 chromosomes, 30 of the salmon karyotype and 40 from the brown trout. The F_1 generation would thus produce a large number of genetically unbalanced gametes, thereby obstructing the rise of an F_2 generation. However, it was reported by ALM (1955) that the choice of brown trout parent was most important for the result of hybridisation. Since the first experiment started

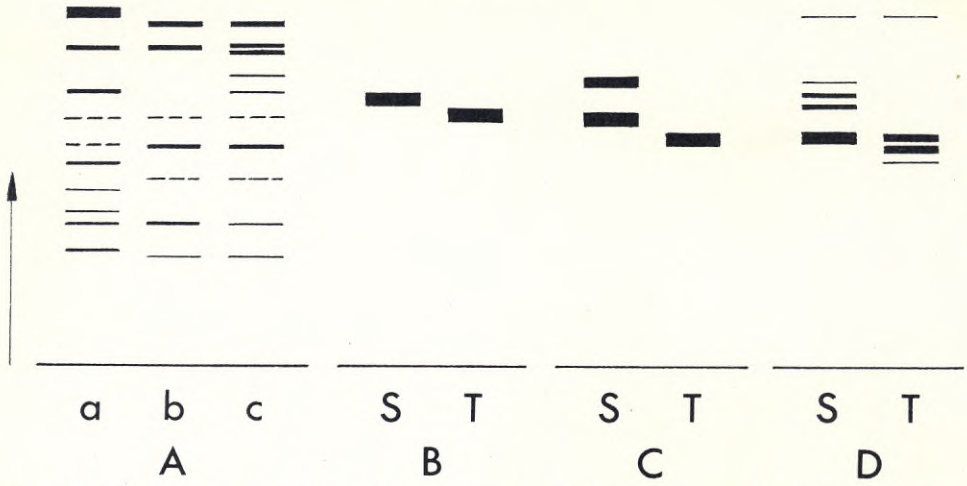

Fig. 9. A) Serum protein patterns in salmon (a), landlocked brown trout (b) and sea trout (c). B) Serum esterase patterns in salmon (S) and brown trout (T). C) Kidney esterase patterns in salmon (S) and brown trout (T). D) Liver esterase patterns in salmon (S) and brown trout (T).

in the autumn 1959, fertile F_1 and F_2 hybrids as well as back-crosses to both parental species giving fertile offspring, have been carried out. Not only is there a high rate of survival but sexual maturity is reached a year earlier than the majority of the parental species, and the growth rate is significantly superior to the parents. These hybrids (F_1 and F_2) evidently show typical signs of hybrid vigor. Since a F_2 batch of these hybrids were sent to Sweden, they were sampled and compared to a F_1 hybrid produced and reared in Sweden, the 1 year old offspring of landlocked salmon and brown trout from the River Gullspångsälven. As the study at once indicated (Fig. 10) the F_1 hybrids had protein patterns which were summations of those in the parents (tissues from the real parents were not gotten, but since no intraspecific variation has been noted in either of the parental populations, this did not seem to be so important). The serum esterases (Fig.10 B) in salmon and brown trout are monomorphic, consequently all F_1 fish would exhibit the same pattern, with both parental bands segregated to the offspring, if none of the genes determining the proteins is selected against. No such selection is evidently present since all the F_1 specimens show the same pattern, which is a summation with about half the concentration of the zones in the parents. The same is true for the serum proteins dyed with amido black (or Coomassie Brilliant Blue). Here a few bands seem to be determined by the same genes in both parental species, only one band present in the hybrid with equal concentration as the parents (Fig. 10 A). The same type of summation exists in the liver esterases (Fig. 10 C). An exception is indicated in the kidney esterases (Fig. 10 D), where one of the bands in salmon is not segregated

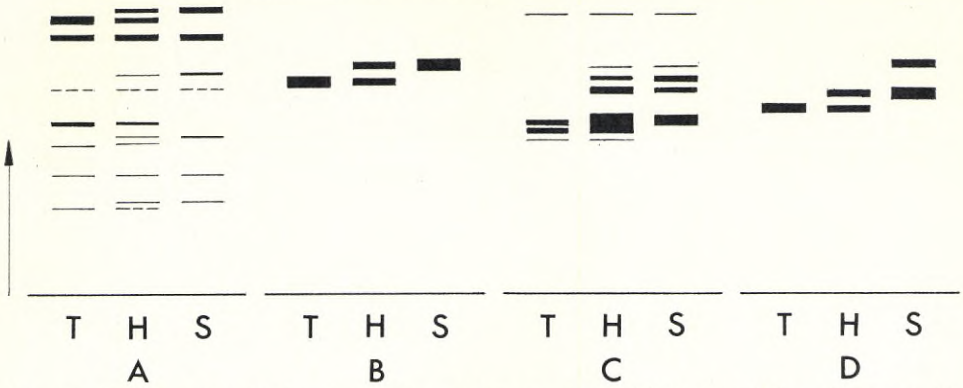

Fig. 10. Protein patterns of various tissues in brown trout (T), hybrid (H) and salmon (S). A) Serum proteins, B) serum esterases, C) liver esterases and D) kidney esterases.

to the hybrid. The reason for this exception is not fully understood, some type of selection evidently taking place, or some kind of irregularity at meiosis since the parental species have different chromosome numbers.

The F_2 hybrids, being the offspring of F_1 fish originating from anadromous salmon and brown trout from western Ireland, indicated that some sort of selection, evidently a very effective one, had taken place against the salmon proteins. The four protein systems investigated, viz. serum proteins (amido black), serum esterases, liver esterases and kidney esterases, were consequently identical in F_2 fish and brown trout (a similar trend is reported below: Speckled trout×lake trout hybrid). This state of affairs is evidently not present in all tissues, as indicated in studies of blood groups in salmon, brown trout and the F_1 and F_2 hybrids (ALABASTER & DURBIN 1965). The trend towards one of the parental species in the appearance of the protein patterns is besides followed by a meristic trend in the same direction. Meristic studies of the F_1 fish show a majority of characters within the trout range, F_2 specimens are still more trout-like, and the trend seems to be continued in a recent F_3 generation (PIGGINS 1966, personal communication). One thing diminishing the value of the results of the protein investigations is the absence of samples from Irish fish. This state of things can perhaps explain why no salmon characters were found, since there might be more proteins common to trout and salmon in Irish than in Swedish populations, and the patterns can be somewhat different in other respects as well. Further investigations of Irish salmon, brown trout and the different hybrid generations will be carried out.

D. *Rainbow trout.* Studies of protein patterns in different rainbow trout tissues have been performed during the last two years. At least 9 LDH isozymes have been found in the blood plasma (BOUCK 1965), and recent studies of serum proteins, haemoglobins and muscle myogens (TSUYUKI & ROBERTS 1965), separated by means of polyacrylamide gel (serum proteins) and starch

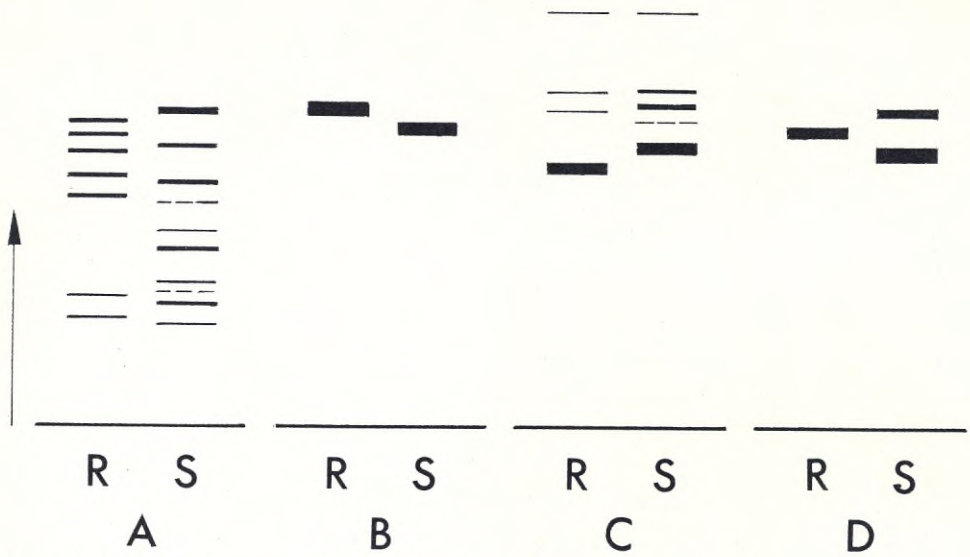

Fig. 11. Protein patterns of rainbow trout (R) and salmon (S). A) Serum proteins, B) serum esterases, C) liver esterases and D) kidney esterases.

gel (haemoglobin, muscle myogens) have been reported. The protein patterns of the three specimens investigated by TSUYUKI & ROBERTS are very different from those separated in this study by means of starch gel electrophoresis. Complete conformity is present in the population used in this study, the rainbow trout pattern besides being very different from the other *Salmonidae* (Fig. 11 A). The serum esterases (Fig. 11 B) seem to be monomorphic like in salmon and brown trout, since 25 investigated specimens were identical. Still there is a chance that they may be polymorphic, with a very low frequency of the other allele involved. This state of things is indicated in the study of cod haemoglobin by SICK (1965) where sample no. 56 had a frequency of the rare allele of 0.01, with only 1 heterozygous pattern observed of a total of 80. The liver esterases have a very pronounced major zone of activity (Fig. 11 C) with faint minor bands, and the kidney esterases are evidently monomorphic (11 D) like in brown trout.

E. *Char*. In Fig. 12 the serum esterase patterns of char are presented, compared to the pattern in salmon. Three distinct electrophoretic patterns were observed in the char of Lake Vättern. Similar esterase configurations have been described in other species of fish (NYMAN 1965). The char esterase patterns may evidently be explained by adopting a hypothesis of two allelic codominant genes responsible for the segregation of the three patterns. If these alleles are termed F (fast) and S (slow), the pattern with one fast band would be the phenotypical appearance of the homozygous F-allele, i.e. with a supposed genotype Est^F/Est^F, where "Est" stands for esterase. The pattern

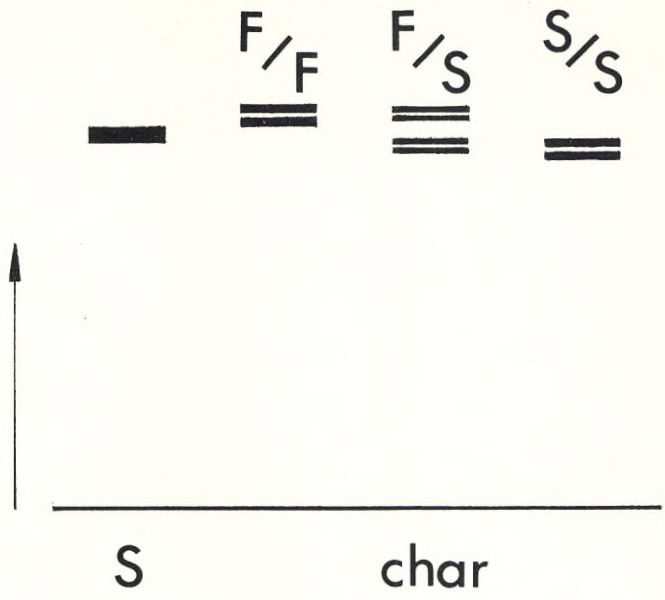

Fig. 12. Serum esterases in salmon (S) and char, and the possible genotypical composition of the three patterns of char.

with the single slow band would thus be due to the segregation of a homozygous S-allele, i.e. with a genetical composition Est^S/Est^S. The genetical background of the pattern with both bands would consequently be Est^F/Est^S indicating the heterozygote. The observed frequencies of the three patterns were compared to the expected distribution as calculated according to the HARDY-WEINBERG law. This law is based on the assumption that random mating pertains and that the two alleles involved have no selective effect on the survival and fitness of the zygote or the growing individual. If these assumptions are fulfilled the population will be in a state of genetic equilibrium. This state of affairs is, however, rare since probably all genes have certain selective influence, and also due to the rate of spontaneous mutation from F to S or reversed. As is indicated in Table 2 the char of Lake Vättern coincide very well with the expected number of individuals in the three possible classes according to the HARDY-WEINBERG law. This fact may give

Table 2. Frequencies of the supposed genes determining the esterase patterns in a sample of char from Lake Vättern, as calculated according to the HARDY-WEINBERG law.

Fenotype	F	F/S	S	Total	Freq. of alleles	χ^2	Probability of a greater value
Genotype	F/F	F/S	S/S				
observed	51	40	9	100	p (F) = 0.71 q (S) = 0.29	0.082	0.75—0.90
expected	50.4	41.1	8.4	100.0			

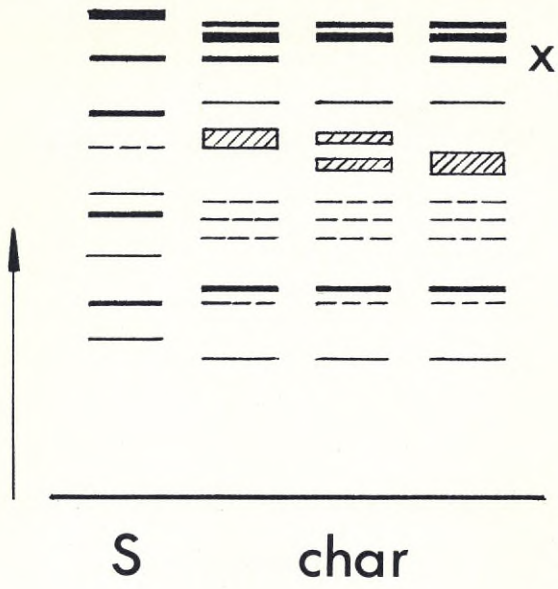

Fig. 13. Serum proteins of salmon (S) and char. The polymorphisms of char proteins are explained in the text.

us important information as to a few biological properties of the population, if it is assumed that the frequencies of F and S are kept in genetic equilibrium (LEWONTIN & COCKERHAM 1959). Since there obviously is no excess of either homozygotes or heterozygotes, the sample has not been taken from different subpopulations but from a single homogeneous population. Furthermore there does not seem to be any kind of heterosis (i.e. selective superiority of heterozygotes) due to overdominance. No higher fitness of the heterozygote over the homozygotes thus seems to prevail.

The serum protein patterns are shown in Fig. 13. As is indicated in the diagram the possible transferrin fraction seems to be polymorphic for the same patterns as the esterases, thereby indicating the same genetic background, i.e. two allelic codominant genes. These patterns are, however, rather diffuse when making use of this type of staining and electrophoresis, and consequently they are not very good tools for population investigations. The main albumin fraction is also polymorphic, with two possible types due to the presence of an extra band (×) in about 50 per cent of the individuals.

Significant differences in liver glycogen levels at various occasions of the year between salmon fed on pellets and fresh food have been described recently (WENDT 1965). In order to examine if there were any differences in the protein patterns of char, also divided in two groups fed on pellets and fresh food respectively, samples from these groups were investigated as to liver proteins (amido black) and liver esterases. Despite the very different appearance of the two groups of livers, pellet-fed fish had light yellow livers—fresh food group had dark brown, no significant differences in patterns or enzyme activity could be detected. Not only were there diffe-

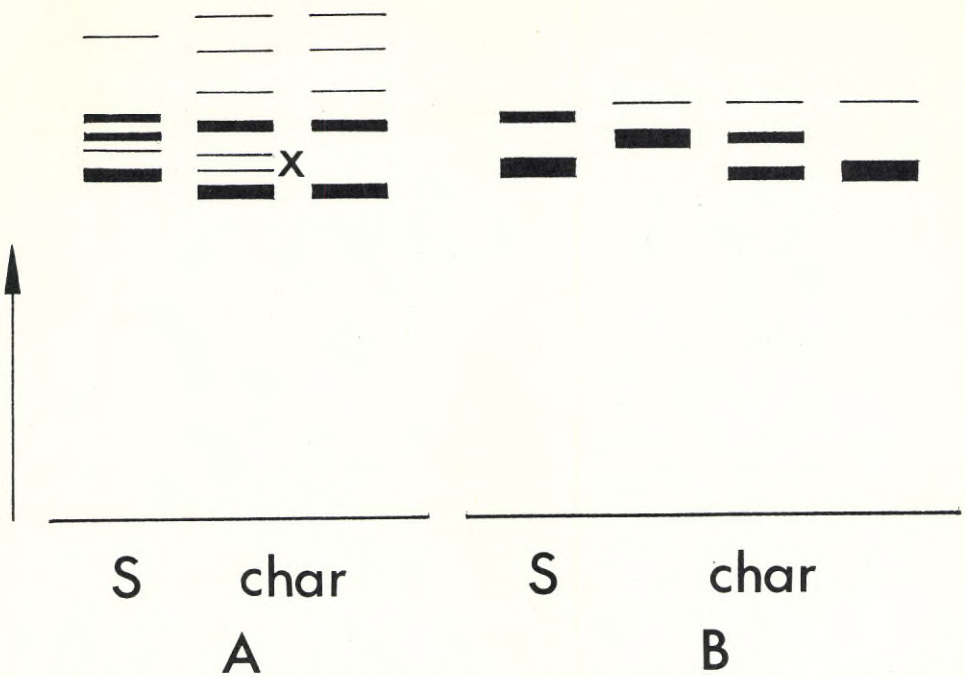

Fig. 14. A) Liver esterase patterns of salmon (S) and char. The minor bands at "x" are absent in some individuals. B) Kidney esterases in salmon (S) and char (with observed polymorphism).

rences in color but the light livers had a very loose structure compared to the compact organ of the fish fed on fresh food. Some intraspecific variation in the liver esterase pattern was, however, detected (Fig. 14 A), since the minor bands at ×) were visible only in a few specimens. Another polymorphism was detected in the kidney esterases (Fig. 14 B). Since only 10 kidneys were investigated nothing conclusive can be stated as to gene frequencies, genetic equilibrium and consequently type of segregation, but the three patterns are similar to the serum esterase configurations which probably are due to the segregation manner mentioned above.

F. *Speckled trout.* Electrophoresis of various proteins in speckled trout (brook trout) is reported recently (TSUYUKI & ROBERTS 1965). The serum proteins were separated by means of polyacrylamide gel, but the patterns received were not very similar to those obtained in the present study using starch gel. The only intraspecific variation noted in samples from three different populations of speckled trout is indicated in Fig. 15 A. Still there might be other differences both of inter- and intrapopulation origin but this question could not be answered since only 15 specimens were available. The serum esterases seem, however, to be monomorphic like in most *Salmonidae* (Fig. 15 B). An interesting fact is shown in the mobility of the esterase zone,

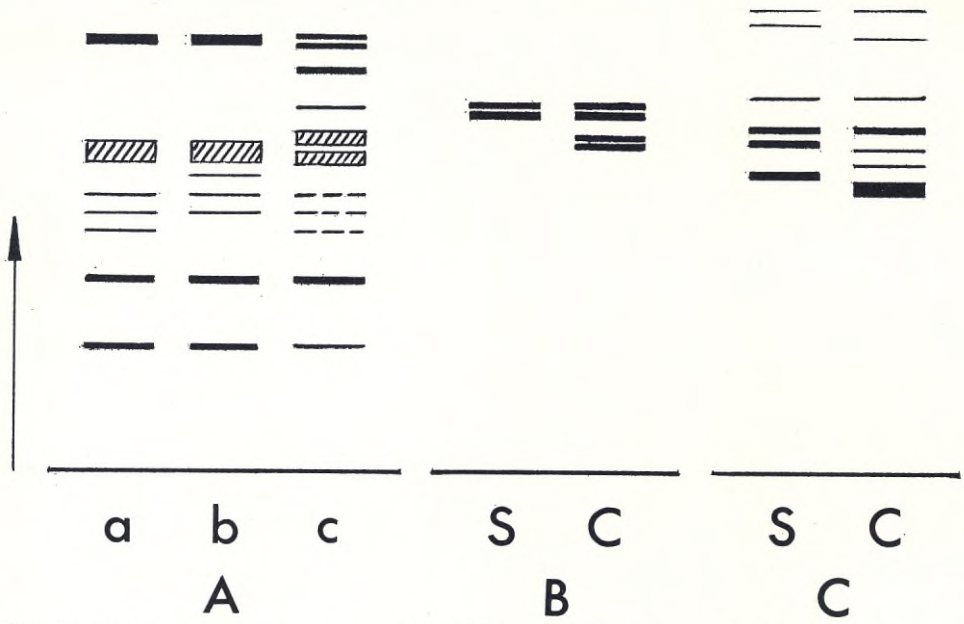

Fig 15. A) Serum protein patterns of speckled trout (a and b) and char (c). B) Serum esterases of speckled trout (S) and char (C). C) Liver esterases of speckled trout (S) and char (C).

this being identical to the Est^F allele in char. It is also essential to point out that there are further facts indicating similar genetical coding for the identical esterase mobilities in the three *Salvelinus* species investigated and in *Hucho hucho* as well, at least at pH 8.7 (cp. *Lake trout* and *Hucho hucho*). One is elucidated in the three hybrids with only one zone of activity and still another in the conformity of all the patterns when the electrophoresis is performed at different pH. The different mobilities of the esterase zones in for instance the three *Salmo* species (see above), however, do not indicate that these species are more distantly related than the *Salvelinus* species, since the differences may only be due to the substitution of a single amino acid altering the charge of the protein. Longer or shorter distance between protein zones is consequently no indication of the degree of relationship. Save for the albumins even the serum proteins of char are quite similar to those of speckled trout. The liver esterases of the two species are schematically pictured in Fig. 15 C, indicating a close similarity and the same state of affairs is indicated in the kidney esterases (Fig. 16), where the two *Salvelinus* species are compared to the kidney esterase patterns of the three *Salmo* species investigated.

G. *Speckled trout×char hybrid* (*bröding*). These hybrids were F_1 fish reared at Källefall and all being 1 year of age. Since the parent species have equal chromosome numbers (84) and belong to the same genus it can be

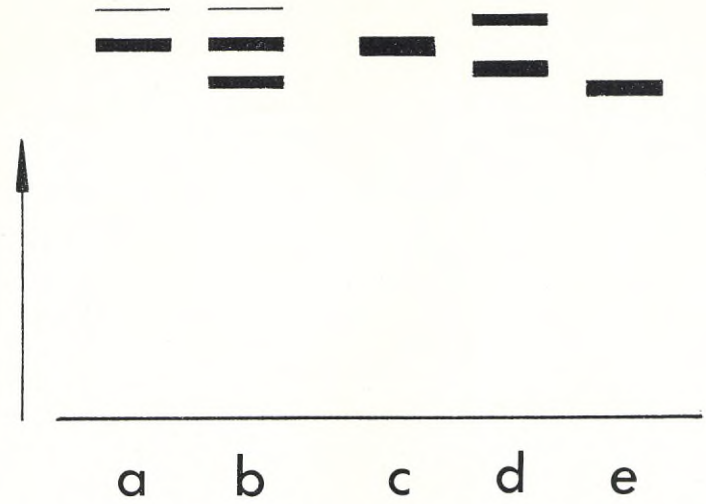

Fig. 16. Kidney esterase patterns in various salmonids. a) speckled trout, b) char (heterozygous pattern), c) rainbow trout, d) salmon and e) brown trout.

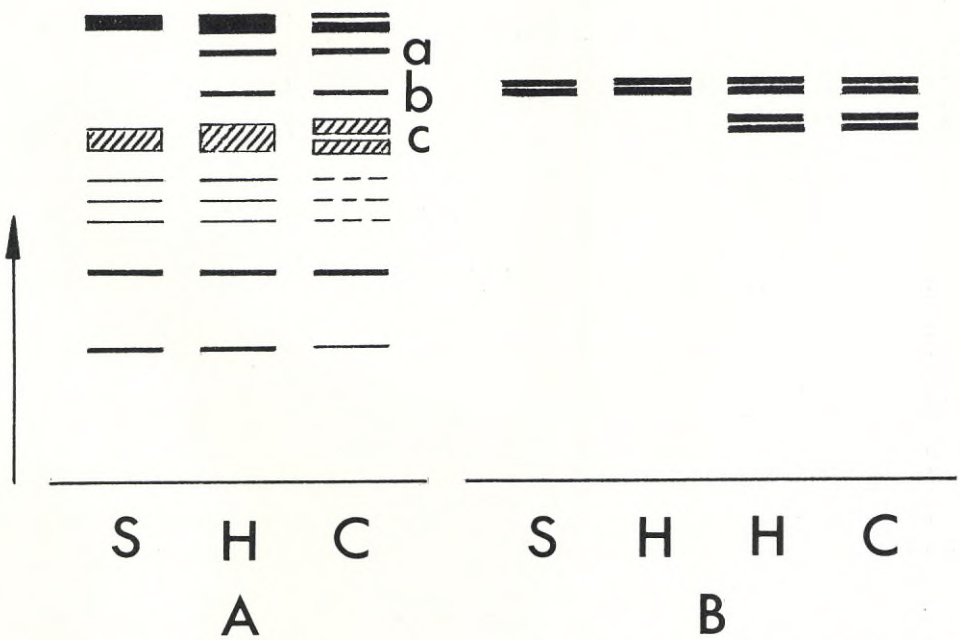

Fig. 17. A) Serum proteins of speckled trout (S), hybrid (H) and char (C). The major differences between the parental species are indicated at a, b and c. B) Serum esterase patterns of speckled trout (S), char (C) and the hybrid (H) with two possible patterns.

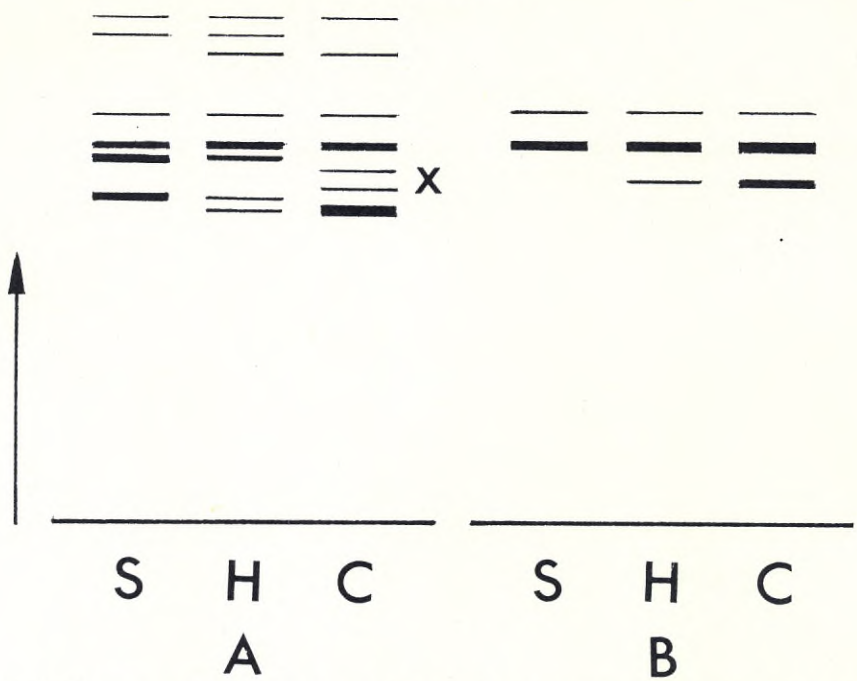

Fig. 18. A) Liver esterase patterns in speckled trout (S), hybrid (H) and char (C), with the minor bands at "x" absent in some individuals. B) Kidney esterase patterns in speckled trout (S), hybrid (H) and char (C).

assumed that fertile F_2 specimens would be easy to produce (compared to salmon×brown trout F_2). The serum protein patterns of the parental species and the hybrid are indicated in Fig. 17 A. Of the three zones separating the parental species, two were segregated to the hybrid offspring (a, b), but the third zone which is diffuse in both species is even more blurred in the hybrid (c). In Fig. 17 B the serum esterase patterns of the parent species and the hybrid are indicated. Since there are evidently two alleles responsible for the esterase patterns in char and only one in speckled trout, two possible patterns would occur in the hybrid if the Est^F zone in char and the single zone in speckled trout had identical mobility. These two possible patterns were also obtained. The liver and kidney esterases (Fig. 18 A, B) indicate an almost complete summation in the hybrid, save for the minor bands at ×) in char. This might either indicate a parent lacking these bands, or some kind of selection against the segregation of the zones to the F_1 generation, like in the kidney esterase pattern of the salmon×brown trout hybrid.

H. *Lake trout.* The lake trout, formerly referred to as a monotypic genus (*Cristivomer namaycush*) is nowadays by most taxonomists included in the genus *Salvelinus*. Many factors account for this state of things. Amongst the most important is the chromosome number (84) shared with all other *Salve-*

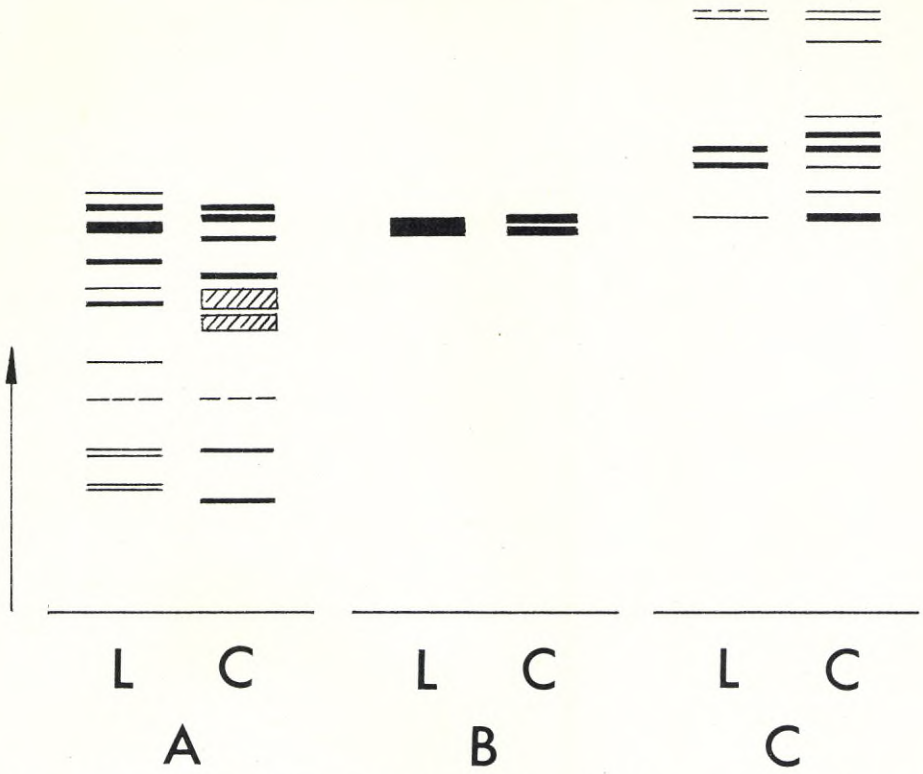

Fig. 19. Protein patterns in lake trout (L) and char (C). A) Serum proteins, B) serum esterases and C) liver esterases.

linus species investigated (SVÄRDSON 1945, WRIGHT 1955, 1956). Another criterion is given in the simplicity of obtaining fertile hybrids with other species of the same genus. The serum protein pattern of lake trout differs only slightly from that of char (Fig. 19 A), the main differences in the "doubled" slow α_2-globulins of lake trout. Since only 3 specimens of lake trout were available nothing can be stated as to intraspecific variation, but the individuals investigated were, however, identical in their protein patterns, although they measured from 26.0 to 46.0 cm. The serum esterase pattern (19 B) indicated the same mobility as the other *Salvelinus* species, with a single zone in the three specimens. Even the liver esterases reveal a pattern almost indistinguishable from speckled trout and char (Fig. 19 C).

I. *Speckled trout×lake trout hybrid* (splake). This hybrid is reported to have the same chromosome number as the other *Salvelinus* species, viz. 84 (WRIGHT 1955, 1956). As the splake here examined were no F_1 hybrids but probably the offspring of a freely interbreeding population of some successive generations, they were not expected to show the same good combination of the patterns in the parental species as did the F_1 generations described

(*laxing, bröding*). But as the first results indicated these few specimens were indistinguishable from speckled trout in all the protein patterns investigated (cp. above '*Speckled trout*'), consequently the same state of affairs as is already reported in F_2 *laxing*. This case may be explained by some kind of selective trend towards speckled trout characters, due to external and/or internal environment. Some ecological factors may possibly account for part of this trend: The generation cycle of speckled trout is 2—3 years, but that of lake trout is 4—5, or even a few years more. Consequently, random mating within a hybrid swarm of splakes tends to increase the number of speckled trout components in the population for each generation. Another difference between the two parental species to give an advantage to the speckled trout is the habit of covering the eggs, a case which is not observed in lake trout. Lake trout eggs are consequently more subjected to predation. As the factors determining these differences must be hereditary there should be pronounced differences in the spawning behavior as well as in attainment of sexual maturity already in the "extremes" gotten in the F_2 generation. These factors may, however, show opposite effect in some lakes having other ecological factors compensating for the disadvantages, and thus give rise to a selection trend favouring the lake trout components, to form an equilibrium or even an increase for them.

J. *Lake trout×char hybrid* (*kröding*). This hybrid seems to be the less well balanced of those described in the present investigation. The only specimen obtained was produced and reared at the Institute of Freshwater Research, Drottningholm. It was a big, 44 cm, male with juvenile gonades, probably fully sterile. This male specimen could be seen to perform spawning behaviour towards other male specimens, and investigation of the inner organs revealed not only juvenile gonades but also for example a pronounced enlargement of the spleen, this normally very small organ being as big as the liver. The serum protein pattern of the hybrid is indicated in Fig. 20 A. Examination of the patterns reveal a very incomplete protein summation in the hybrid. The serum esterase pattern indicates a homozygous Est^F/Est^F char parent, as only one zone of enzyme activity is present (Fig. 20 B). In the liver esterase pattern the summation is better, but still not complete, although the parents only differ in a few bands (Fig. 21 A). The kidney esterases exhibit an interesting comparison, since the two bands in the hybrid coincide in mobility with the two most rapid zones of the char pattern and consequently are identical with those of the speckled trout pattern (Fig. 21 B). This state of affairs may indicate two things, viz. that speckled trout and lake trout patterns are identical (no lake trout kidneys were, however, obtained to prove this case), and secondly that a homozygous "fast" allele in char is responsible for the hybrid pattern. Evidently there may exist identical patterns in the three species examined of the genus *Salvelinus,* the same state of things that has been mentioned above in the serum esterases.

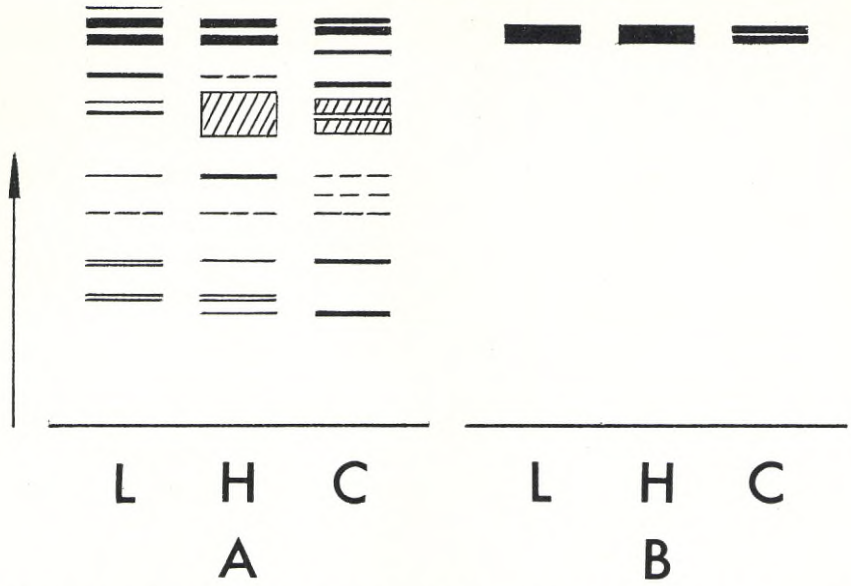

Fig. 20. Protein patterns in lake trout (L), hybrid (H) and char (C). A) Serum proteins and B) serum esterases.

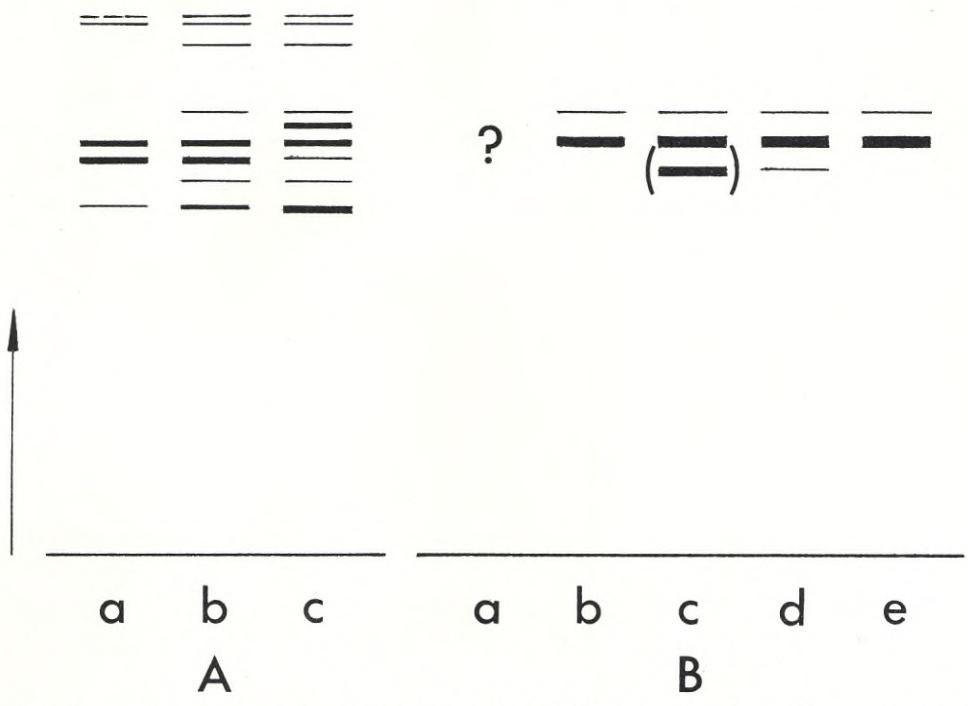

Fig. 21. A) Liver esterases in lake trout (a), hybrid (b) and char (c). B) Kidney esterases in b) *kröding,* c) char, d) *bröding* and e) speckled trout. The figure is further explained in the text.

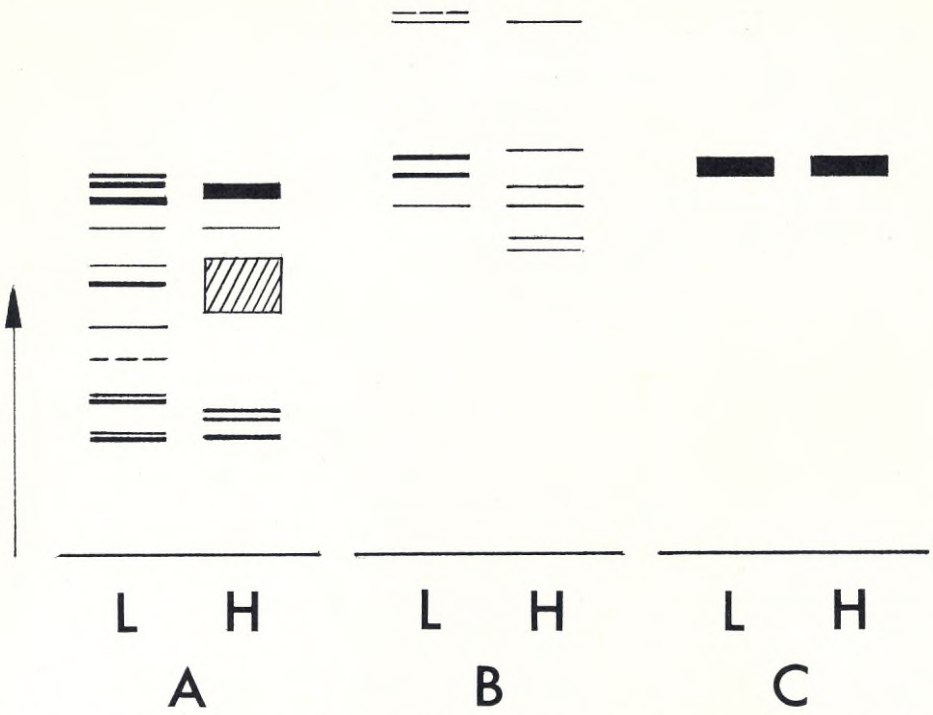

Fig. 22. Protein patterns in lake trout (L) and hucho (H). A) Serum proteins, B) liver esterases and C) serum esterases.

K. *Hucho* (Danube salmon). Only one individual of this species was obtained, originating from Yugoslavia, reared at Kälarne and 26.0 cm of length. This species is by some taxonomists believed to be a remnant population of a formerly circular overlap of a single ancestor, nowadays including the *Hucho taimen* of Siberia and the lake trout of North America. A comparison with lake trout protein patterns would thus be interesting, due to the above reported similarities of the three species examined of the genus *Salvelinus*. The protein patterns do not show any pronounced similarity, however, (Fig. 22 A), and this case is indicated in the liver esterases as well (Fig. 22 B). In one respect, however, the hucho was indistinguishable from the lake trout, viz. in the serum esterases (Fig. 22 C). These patterns were obtained when using the buffer system suggested by ASHTON & BRADEN, the electrophoresis being performed at pH 8.7. When, however, other buffer systems were used, for instance acetate buffer (BURSTONE 1962), the mobilities of the esterase zone in all the *Salvelinus* species and their hybrids were identical, at least down to pH 4.0, but then the hucho esterase zone differed with a slightly lower speed of migration. If the similarity between hucho and lake trout is due to mere chance or indicates a close relationship can not be determined

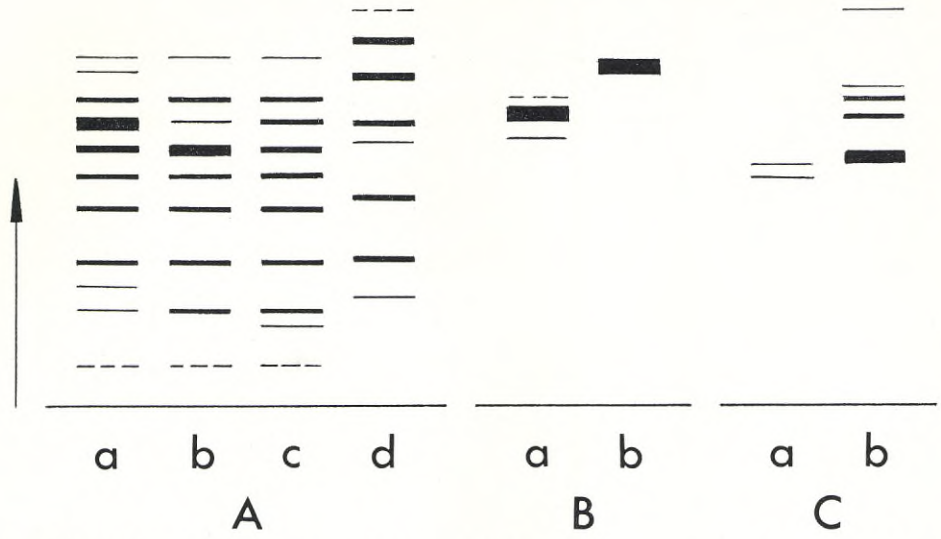

Fig. 23. A) Serum proteins in smelt (a, b and c) and salmon (d). B) Serum esterases in smelt (a) and salmon (b). C) Liver esterases in smelt (a) and salmon (b).

by this study, since no efforts to hybridize lake trout and hucho have been reported, as far as I know.

L. *Smelt.* The electropherograms of smelt serum proteins are quite different from the salmon pattern (Fig. 23 A). Some intraspecific variation was noted, but the most frequently occurring pattern is indicated in type c, with the serum proteins rather evenly distributed among 7 zones. No polymorphism was noted in the serum esterases, these showing the slowest mobility of all *Salmonidae* here examined, and differing from the others in having two minor zones close to the main zone of activity (Fig. 23 B). The liver esterase pattern in smelt is the most simple hitherto examined, with only two faint zones of enzyme activity (Fig. 23 C). No kidneys were obtained from this species.

M. *Whitefish.* The six individuals of whitefish investigated in the present study may well elucidate the above mentioned (SVÄRDSON) complexity of this genus, due to the presence of morphologically very similar species. Since no counts of gill rakers were performed on these fish, the variance found can not be connected to any special species involved. Almost every fish, however, had a unique pattern in some respect (Fig. 24 A). The only esterase with intraspecific or maybe intrageneric similarity was the monomorphic serum esterase (Fig. 24 B). Even the liver esterases were different with various minor bands at $\times$), elucidated in Fig. 25 A, and the same state of things was revealed in the zymograms of kidney esterases (Fig. 25 B).

N. *Grayling and kokanee.* As only one specimen was obtained from each of these species, nothing can be stated as to intraspecific variation. Since

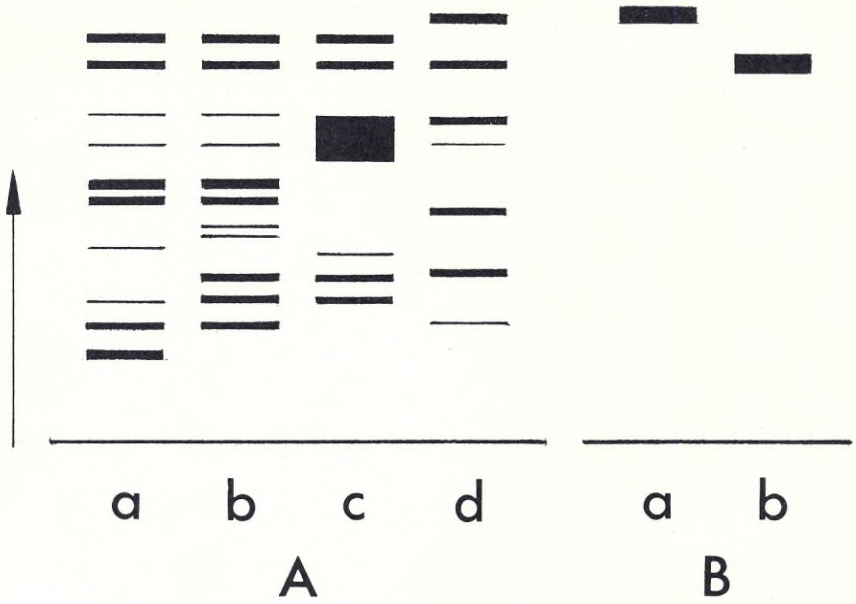

Fig. 24. A) Various serum protein configurations in whitefish (a, b and c) compared to the normal salmon pattern (d). B) The monomorphic serum esterases of whitefish (a) and salmon (b).

Fig. 25. A) Liver esterase patterns of whitefish (gwyniad) with variations in the minor bands at "x", compared to the salmon pattern (S). B) Kidney esterase patterns of whitefish (gwyniad) with variations due to the presence of faint bands in some individuals, compared to the salmon pattern (S).

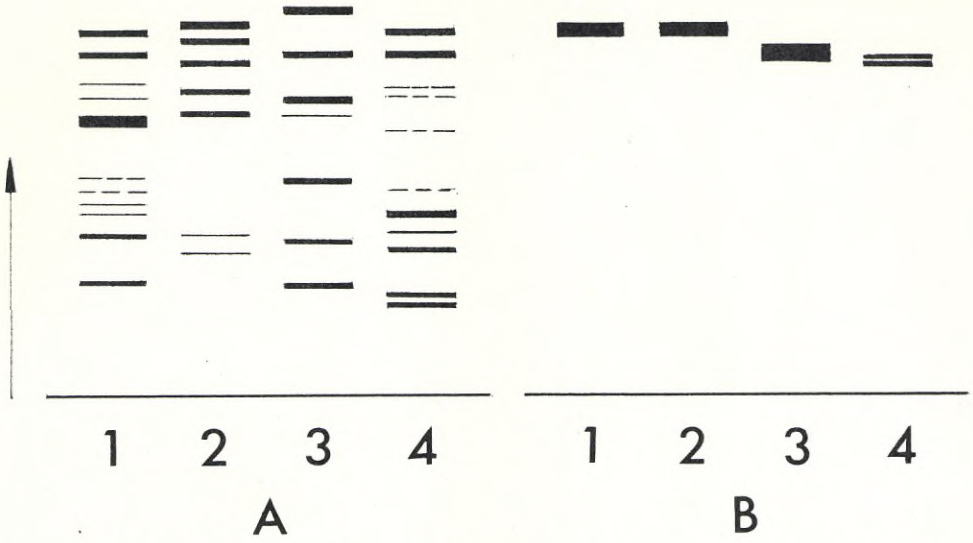

Fig. 26. A) Serum protein patterns in kokanee (1), rainbow trout (2), salmon (3) and grayling (4). B) Serum esterase patterns in kokanee (1), rainbow trout (2), salmon (3) and grayling (4).

Fig. 27. Liver esterase (A) and kidney esterase patterns (B) in kokanee (1), rainbow trout (2), salmon (3) and grayling (4).

some investigators of phylogeny suggest that the genus *Oncorhynchus* has evolved from the genus *Salmo* (e.g. NEAVE 1958, TSUYUKI & ROBERTS 1963) a comparison between kokanee and the only member of the genus *Salmo* in the western part of North America, viz. rainbow trout, might prove interesting. The serum protein patterns of kokanee and rainbow trout are not very similar to each other as is indicated in Fig. 26 A. The grayling pattern (A 4) was easily distinguishable from the other species investigated. In the serum esterase zymograms (Fig. 26 B), two things can be noted, viz. only one zone of enzyme activity in the kokanee with the same mobility as the rainbow trout esterase, and secondly that the esterase zone in grayling is composed of two bands, very close to each other (the same condition seems to prevail in the char and speckled trout serum esterase zones). Even in the liver and kidney esterase patterns (Fig. 27 A, B) some mobility resemblance seems to exist between kokanee and rainbow trout, both patterns anyhow being species specific. The liver and kidney esterase zymograms of grayling are distinctly species specific, with no close resemblance to any other species.

Summary

By means of a starch gel electrophoresis method, described above, water soluble proteins and enzymes were investigated in 11 species and 4 hybrid "species" of fish belonging to the family *Salmonidae*. Examples of species specificity, ontogenetic variation, geographic variation and various polymorphisms are presented and discussed, together with problems concerning the segregation of proteins in hybrids.

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Terrestrial Insects in Lake Surfaces. Their Availability and Importance as Fish Food

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Introduction

Many investigations have shown that fishes utilize terrestrial insects as food to a considerable extent (Allen 1938, 1941, Dyk 1934, Hunt 1959, 1965, Metzelaar 1929, Needham 1930, Nilsson 1955, 1957, 1961, 1965, Schiemenz 1909, and others).

After consultation with the Institute of Freshwater Research, Drottningholm, the author has studied the occurrence of such insects at the surfaces of a series of lakes (Tab. 1) with Lakes Storuman, Blåsjön and Ankarvattnet in northern Sweden as the main objects of investigation.

An account of the conditions in the Blåsjö region has been given earlier (Norlin 1964) and a brief summary of the work done so far has also been given in the handbook "Vattenkraft-fiske" (Norlin 1966).

Here we shall mainly detail the general conclusions drawn from the investigations and give certain primary data of general importance.

Origin of the drifting fauna

Apart from the fauna which has its natural habitat there, the surfaces of lakes always contain a considerable quantity of floating organogenic material. The dominant feature in this drift consists as a rule, of plant remains, but we also find many different animals, most of them insects. These insects are partly those that undergo their larval development in the water and then pass through the surface on hatching, but a rich component of purely terrestrial insects also occurs there. The latter enter the water to some extent by being washed out from the shores, but are mostly there after having fallen from the air. The quantity of terrestrial insects floating on the water, the drifting fauna (Norlin 1964), is in direct proportion to the size of the population of insects drifting in the air and the frequency of their falling. In order to understand the drifting fauna, it is therefore also necessary to consider the occurrence of the so-called "aerial plankton" (Berland 1933). The study of the composition and frequency of the latter has caught the interest of many entomologists, mainly those dealing with agricultural and forest entomology, but it has also been studied from the point

Table 1. The distribution of the sampling.

Lake	Number of samples	Number of collected animals	Sampling period
Abelvattnet	4	153	aug. 1961
Ankarvattnet	34	1,079	20.6—10.8 1962
„	22	140	1957
Arnensee	1	28	25.9 1963
Blåsjön	46	1,209	1957—1959
„	63	7,195	20.6—13.10 1962
„	47	3,488	13.8—6.11 1963
„	16	1,788	26.5—18.6 1964
Engstlensee	1	2,298	30.9 1963
Grundfors	12	557	3.7—2.8 1963
Landösjön	20	39	31.7—8 9 1962
Latnjajaure	(only qualitative mtrl)		1965
Matsdal	1	21	22.7 1963
Nysele	7	245	3.7—2.8 1963
Oeschinensee	5	638	27—29.9 1963
Semmingsjön	3	17	25.7, 28.6 1963
Skalvattnet	4	63	25.7—9.8 1960
Storuman	9	186	2—4.9 1962
„	118	8,158	20.6—2.8 1963
Tarfalasjön	12	526	11—26.7 1961
Tåsjön	11	46	16.8—16.10 1962
Vänern	14	732	juni 1964
Överuman	22	99	27.7—29.9 1962
„ älven ..	4	16	15—26.8 1962
Total	476	28,721	

of view of the ecology of dispersal (FELT 1928, GLICK 1939, HARDY and MILNE 1938, HOLDHAUS 1929, HURD 1920, JOHNSSON 1951, 1955, JOHNSSON and TAYLOR 1955, 1960, JOHNSSON, TAYLOR and SOUTHWOOD 1962, LEWIS and TAYLOR 1965, LUTZ 1927, PALM 1949, PALMÉN 1944, 1950, TAYLOR 1958, 1960 a, 1960 b, 1963, UVAROV 1931, WEBSTER 1902).

From the available literature it can be seen that the process controlling the introduction of terrestrial insects into the surface layers of the water can be considered to consist of three main phases:

1. The insects must in some way, either actively or passively, ascend from their natural place in the vegetation. Factors influencing this change and thus the occurrence of species in the atmosphere are, in part, the behaviour of the different species in their choice of biotope, biology of feeding, diurnal rhythm in flying, etc., and in part, the existing weather conditions which, in the special environments of the different species, regulate their level of activity in different ways.

2. After the insects have been induced to fly, a great variety can be found in the atmosphere. Some come there by active flying, but the majority are subject to aerial transport in which they play a more or less passive role. This is due to the fact that all insects are liable to be overcome by air currents when flying normally, within some twenty or thirty metres of the

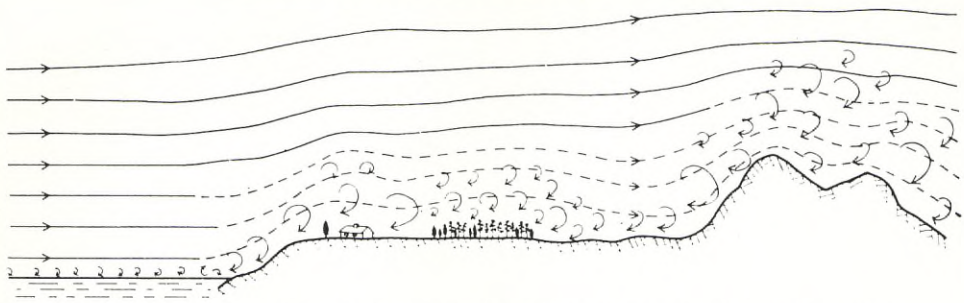

Fig. 1 A. Dynamic turbulence conditioned by friction against the ground surface. (From LILJEQUIST 1962.)

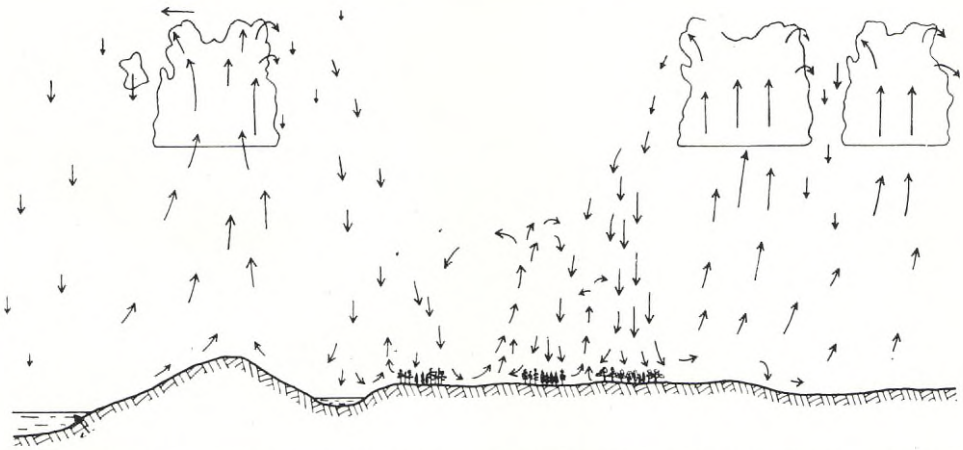

Fig. 1 B. Termic turbulence or convection produced by varying heat absorbing abilities of different ground surfaces. (From LILJEQUIST 1962.)

ground. They are then unable to orient actively and are transported passively to an extent depending on the circulation of the air in the lower layers. This circulation, within the turbulence layer of the atmosphere, is determined to a large extent by the nature of the underlying landscape: both the topographical configuration of the land and varying heat-absorbing abilities of different ground surfaces may contribute (Fig. 1). Rising airmasses may transfer the insects into more wide-spread atmospheric circulations, depending upon the existing macro-climatic weather conditions. Unstable temperature layers favouring such rising movements are particularly common after an influx of cold air, and within masses of warm air in thundery conditions and in conditions with strong insolation. Under normal conditions the density of individuals in the aerial plankton diminishes as the height above the ground increases (Fig. 2), but the absolute density depends ultimately upon the density of the population in the underlying terrestrial environments which act as the source of supply.

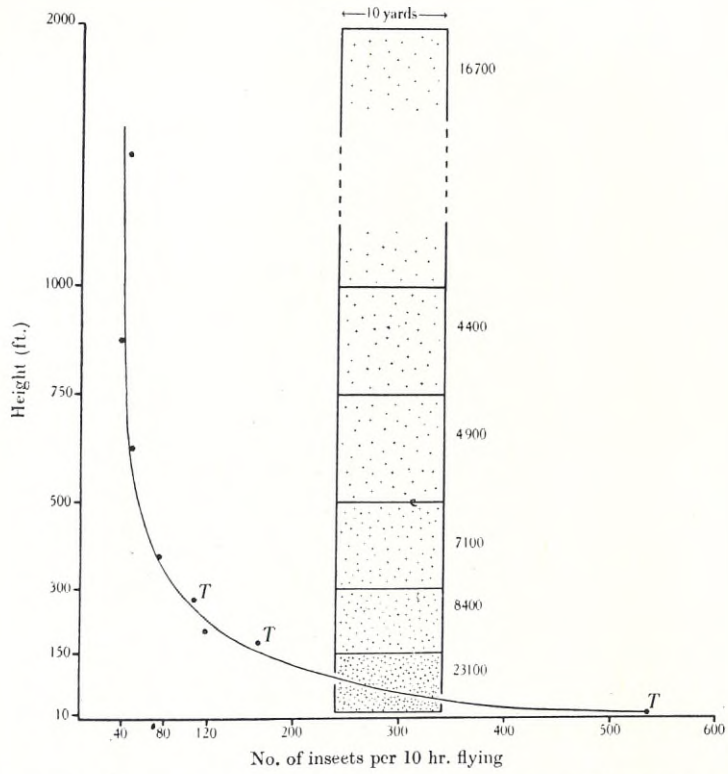

Fig. 2. Graphic representation of the aerial plankton at different heights. (From HARDY and MILNE 1938.)

3. The air-borne insects fall when the air masses have reached stabilization, and when the cooled air sinks. This may happen above portions of the landscape which are cooler than their surroundings, e.g. cold lakes, but takes place especially during the nights, when the atmosphere becomes practically drained of aerial plankton.

Factors influencing the distribution of the drifting fauna on the water surface

Qualitative comparisons between different collecting localities on the same lake (NORLIN 1964) show that material collected off sections of the shore with entirely different types of vegetation are nevertheless remarkably similar. This is due to transport in the surface water when it is agitated by the wind. The velocity of this movement has been estimated by WHIPPLE (1927) to be 3 per cent of the wind velocity in feeble winds, and 1 per cent in strong winds. BIGELOW and EDMONDSSON (1947) have suggested a value of

2 per cent of the wind velocity. Using the latter figures as an average, and assuming a mean wind velocity of 3 metres sec., we find that animals floating on the water surface may be transported at least 5 kms in 24 hours; this is a minimum estimate since the animals protrude above the water and may move faster if they catch the wind.

The result of this surface movement is that original qualitative differences between parts of the lake with different insectfauna in the bordering shore biotopes disappear. At the same time, however, great quantitative differences may be produced. The drifting fauna is not uniformly spread over the lake. When it is blowing strongly, the wind may produce streaks of foam parallel to its direction on the water surface. The bubbles of the foam tend to be adhesive, so that organogenic material is often gathered in these streaks. Breaking waves are required, however, for the production of foam, and for this reason the phenomenon is most frequently observed upon very exposed lakes.

The floating material eventually reaches the windward shore and the greatest quantities of drift-material thus collect there. The collecting stations on Storuman were disposed in such a way that one station was always exposed to the wind; 80 per cent of the largest catches were made at this station. The exceptions were derived mainly from one locality, where wingless ants (*Formica rufa* L.) were washed out from the shore.

The fate of the drifting material depends on the configuration of the shore; it may either be washed on to the land, as happens when the shore is flat or, as on steeply inclined shores, it may remain in the surface water until it sinks to the bottom. Its ability to float has been studied by several authors. SCHWARZ (1890) has shown that insects with strong elytra, such as beetles, are best able to resist a period in the water. *Hymenoptera* are also mentioned as being very resistent. Investigations by FREY (1937) and PALMÉN (1944), as well as experiments carried out by the present author, demonstrate that, under laboratory conditions, most species may survive floating for at least five days, and often longer.

Along steep shores it can be observed that the drift is not pressed right against the land, but remains as a drift line parallel to the shore and at some distance from it. This is caused by the formation of echo waves, when incoming waves strike the shore. The gathering capacity of this type of shore makes it especially important as it forms an easily accessible larder for those species of fish which search the surface for their food. Drift lines and greater or smaller "islands" of drifting material can also occur off flat shores, but most material tends to be cast ashore under these circumstances. This essential difference between these two types of shore was studied most conveniently at Blåsjön, where, with the rising water, the shore-line was shifted from flat sedimentary regions to steep rocky areas.

Qualitative results

The collected material comprises about 29.000 animals. A remarkable amount, 48 per cent, consists of terrestrial insects. In other words, the supply of terrestrial insects can be compared with that of semiaquatic ones, e.g. chironomids which are largely utilized by fish during the time that they hatch in the surface layer.

The material of terrestrial insects contains representatives of fifteen orders. Among them *Homoptera, Coleoptera, Lepidoptera, Diptera,* and *Hymenoptera* dominate both in numbers and quantity; representatives of the remaining orders occur only in smal quantities.

Some 70 families have been distinguished from the dominant orders (Tab. 2).

One of the aims of the qualitative studies made was to determine which type of environment supplied the most important components of the drifting fauna. Examination shows that many of the species which are abundant and often occur in several collecting sites are common and are found over extensive areas all over the country. This makes it difficult to establish their immediate origin. It is, however, possible to note certain characteristic features which, among others, suggest that their origin is, in fact, the immediate neighbourhood of the lakes.

1. Many types are thus found in moist localities, e.g. shores of lakes and watercourses: *Cicadula* spp. (*Homoptera*).: *Arpedium brachypterum* GRAV., *Mycetophorus brunneus* MARSH., *Tachyusa atra* GRAV. and *Podistra* spp. (*Coleoptera*); *Clinocera* spp. *Hilara* spp., *Eristalis tenax* L. *Phaonia aeniventris* ZETT., *Spilogona* spp., and *Coenosia* spp. (*Diptera*), etc.

2. At Blåsjön there are meadows adjoining the lake; at Storuman these occur only in some isolated spots along the shore. This probably explains the fact that samples from Blåsjön contained a much greater number of meadow- and grass-dwelling species than those from Storuman, e.g.: *Agallia brachyptera* BOH., *Euscelidae* spp. (*Homoptera*).

3. In the Oeschinensee, where droppings from cattle were found everywhere along pathways and on the small meadows above the lake and close to it, animals living in excrement were remarkably numerous, e.g.: *Anechura bipunctata* FABR. (*Dermaptera*); *Philontus marginatus* STRÖM., *Aphodius alpinus rubens* COM., and *A. depressus* KUG. (*Coleoptera*).

4. When a species occurred in very great numbers in the water surface, it could also be caught in great numbers on land, e.g.: *Camponotus herculeanus* L., (*Hymenoptera*) was abundant in Storuman and also appeared frequently in MALAISE traps on land. *Oporinia autumnata* BKH. (*Lepidoptera*) was also caught beside Blåsjön in great numbers using ultra-violet lamps. These lamps also attracted many *Diptera,* e.g. the muscids *Spilogona* and species of *Coenosia.*

Table 2. Total number of terrestrial insects from different families within the dominating orders.

	Number of animals	Observed in number of samples	Observed in number of Lakes
Homoptera			
Cercopidae	7	6	3
Euscelidae	473	82	3
Typhlocybidae	3	1	1
Araeopidae	20	10	3
Psyllidae	795	100	11
Aphididae	3,891	154	16
Ortoziidae	3	3	2
Coleoptera			
Carabidae	35	24	14
Silphidae	1	1	1
Liodidae	1	1	1
Staphylinidae	247	82	13
Scarabaeidae	20	5	4
Byrrhidae	8	7	2
Elateridae	12	10	3
Cantharidae	189	52	9
Nitidulidae	1	1	1
Erotylidae	1	1	1
Cryptofagidae	2	2	2
Colytidae	1	1	1
Coccinellidae	3	3	2
Cerambycidae	5	3	2
Chrysomelidae	12	9	7
Curculionidae	17	12	4
Scolytidae	19	14	4
Lepidoptera			
Geometridae	174	44	6
Diptera			
Anisopedidae	2	2	1
Psychodidae	6	6	1
Ceratopogonidae	5	3	9
Thaumelidae	2	1	1
Bibionidae	460	49	9
Scatopsidae	7	2	1
Mycetophilidae	1,625	205	14
Cecidomyidae	69	23	5
Stratiomyidae	2	1	1
Rhagionidae	32	17	4
Tabanidae	1	1	1
Asilidae	3	3	2
Empididae	605	148	14
Dolichopodidae	9	6	4
Phoridae	243	104	12
Pipunculidae	2	2	2
Syrphidae	34	11	6
Psilidae	34	19	5
Platystomidae	2	2	1
Trypetidae	5	5	4
Sepsidae	16	7	4
Sciomyzidae	5	3	1
Lauxanidae	243	29	2
Chamaemyidae	1	1	1
Agromyzidae	311	46	6
Heleomyzidae	7	6	1
Borboridae	6	2	4
Ephydridae	46	26	6
Chloropidae	60	17	8
Calliphoridae	2	2	1
Muscidae	393	103	12
Hymenoptera			
Pamphilidae	1	1	1
Tenthredinidae	87	23	4
Cynipidae	41	21	5
Ichneumonidae	317	63	9
Braconidae	938	93	12
Proctotrupidae	66	27	4
Chalcididae	846	96	13
Mymaridae	11	3	2
Formicidae	870	63	8
Vespidae	4	3	3
Sphecidae	1	2	1
Apidae	4	3	3

5. The Lakes Tarfalasjön and Latnjajaure are situated above the treelimit. For this reason their surroundings may be expected to harbour only a limited number of species. If foreign species are carried there by the wind from distant places, it should be easy to trace them. The species found in these two lakes seem, however, to have their natural habitat in the neighbourhood of the lakes, e.g. *Coccinella trifasciata* L., and *Amara alpina* FABR. (*Coleoptera*); *Lycora borealis* RÜBS. and *Spilogona contractifons* ZETT. (*Diptera*).

Quantitative results

The weight of material for quantitative studies has been determined to an accuracy of 0.1 mg. Weighings have been performed both upon the entire samples and upon different systematic units within each sample.

The distribution of the biomass among the five dominant orders in samples from Ankarvattnet, Blåsjön and Storuman is given in Table 3. Table 4 shows the distribution by weight among families and orders in these lakes, while the biomass for each sample taken in Ankarvattnet, Blåsjön, Storuman, the reservoir at Grundfors and the Swiss lakes is accounted for in Table 5. Fig. 3 shows the distribution of the total material among different weight classes. The strongly unbalanced distribution with the highest frequencies being found in the lowest weight classes is a characteristic feature for all the above-mentioned lakes and the collecting localities in them; on the other hand, the frequency among the higher weight classes is subject to considerable variation. The majority of the samples are thus derived from water surfaces with a comparatively small density of insects.

A calculation based on all the material shows that the median[1] lies at 1.0 mg/m², and Q1 and Q3 at 0.5 and 3.0 mg/m², respectively, implying that 75 per cent of the total material consists of samples weighing less than 3.0 mg/m².

Although a comparison between the different waters shows only a slight deviation of the median from 1.0, it can be noted that it exceeds this value by some tenths for the Lakes Blåsjön and Storuman, while in the reservoir at Grundfors it reaches only 0.7 mg/m². Later investigations have shown that most of the terrestrial animals in rivers and reservoirs are transported as drift below the surface of the water, after being dragged down by turbulence. The main differences between lakes and reservoirs thus seem to be the way in which the terrestrial insects are exposed, e.g. to predation by fish, rather than being differences in quantity.

Table 3. The distribution of the biomass of insects on dominating orders. Weight in mg.

	Ankarvattnet		Blåsjön		Storuman		Total	
	Weight	%	Weight	%	Weight	%	Weight	%
Homoptera	53	5.0	535	3.5	923	2.7	1,511	3.0
Coleoptera	160	15.1	1,369	8.8	373	1.1	1,902	3.7
Lepidoptera	—	—	5,888	38.0	20	0	5,908	11.6
Diptera	423	40 0	5,481	35.4	428	1.3	6,332	12.4
Hymenoptera	422	39.9	2,128	13.7	32,492	94.7	35,042	68.9
Total	1,058	100.0	15,401	99.4	34,236	99.8	50,695	99.6

[1] A non-parametrical statistical method, where the median (M) is the middle item in the array, the quantities Q1, Q3 separating the lower and the upper quarter, respectively, from the rest of the sample array (Cf. SNEDECOR 1956).

Table 4. Distribution of the weight of different families within dominating orders. Weight in mg. Percentage < 1 % is indicated with +. In Lake Storuman the overwhelming single occurence of fam. *Formicidae* is not counted.

	Ankarvattnet		Blåsjön		Storuman		Total	
	Weight	%	Weight	%	Weight	%	Weight	%
Homoptera								
Cercopidae	—	—	9	+	6	+	15	+
Euscelidae	45	4.3	325	2.1	418	23.0	788	1.5
Typhlocybidae ..	—	—	1	+	—	—	1	+
Araeopidae	—	—	7	+	10	+	17	+
Psyllidae	2	+	65	+	243	13.4	310	+
Aphididae	5	+	125	+	245	13.5	375	+
Ortoziidae	—	—	3	+	1	+	4	+
Coleoptera								
Carabidae	33	3.1	251	1.6	43	2.4	327	+
Liodidae	—	—	4	+	—	—	4	+
Staphylinidae ...	18	1.7	269	1.7	9	+	296	+
Scarabaeidae ...	—	—	26	+	33	1.8	59	+
Byrrhidae	—	—	22	+	35	1.9	57	+
Elateridae	21	2.0	113	+	19	1.0	153	+
Cantharidae	65	6.1	313	+	166	9.2	544	1.1
Nitidulidae	—	—	2	+	—	—	2	+
Erotylidae	—	—	5	+	—	—	5	+
Cryptofagidae ..	—	—	—	—	0	+	0	+
Colytidae	—	—	2	+	—	—	2	+
Coccinellidae ...	—	—	40	+	—	—	40	+
Cerambycidae ..	—	—	254	1.6	9	+	263	+
Chrysomelidae ..	12	1.1	27	+	—	—	39	+
Curculionidae ..	—	—	42	+	23	1.3	65	+
Scolytidae	12	1.1	—	—	37	2.0	49	+
Lepidoptera								
Geometridae	—	—	5,888	38.0	21	+	5,909	11.6
Diptera								
Anisopedidae ...	—	—	5	+	—	—	5	+
Psychodidae	—	—	2	+	—	—	2	+
Ceratopogonidae	1	+	2	+	—	—	3	+
Bibionidae	16	1.5	1,718	11.0	4	+	1,738	3.4
Scatopsidae	—	—	2	+	—	—	2	+
Mycetophilidae ..	25	2.4	229	1.5	66	3.6	320	+
Cecidomyidae ...	2	+	122	+	4	+	18	+
Stratiomyidae ...	—	—	14	+	—	—	14	+
Rhagionidae	44	4.1	282	1.8	9	+	333	+
Tabanidae	—	—	63	+	—	—	63	+
Asilidae	—	—	95	+	—	—	95	+
Empididae	56	5.3	434	2.8	205	11.3	695	1.4
Dolichopodidae	—	—	10	+	3	+	13	+
Phoridae	15	1.7	62	+	24	+	101	+
Pipunculidae ...	—	—	1	+	—	—	1	+
Syrphidae	—	—	22	+	5	+	27	+
Psilidae	11	1.0	108	+	3	+	122	+
Platystomidae ..	—	—	0	+	—	—	0	+
Trypetidae	—	—	8	+	—	—	8	+
Sepsidae	—	—	7	+	0	+	7	+
Sciomyzidae	—	—	16	+	—	—	16	+
Lauxanidae	—	—	220	1.4	7	+	227	+
Agromyzidae ...	2	+	126	+	3	+	131	+
Heleomyzidae ..	—	—	46	+	—	—	46	+
Borboridae	—	—	5	+	—	—	5	+

Table 4 continued.

	Ankarvattnet		Blåsjön		Storuman		Total	
	Weight	%	Weight	%	Weight	%	Weight	%
Ephydridae	—	—	16	+	13	+	29	+
Chloropidae	1	+	47	+	11	+	59	+
Calliphoridae ...	—	—	106	+	—	—	106	+
Muscidae	251	23.7	1,823	11.8	71	3.9	2,145	4.2
Hymenoptera								
Pamphilidae	43	4.1	—	—	—	—	43	+
Tenthredinidae	188	17.7	787	5.1	296	16.3	1,271	2.5
Cynipidae	2	+	10	+	5	+	17	+
Braconidae	0	+	93	+	70	3.8	163	+
Proctotrupidae ..	1	+	16	+	3	+	20	+
Chalcididae	17	1.6	60	+	45	1.9	112	+
Mymaridae	—	—	—	—	0	+	0	+
Formicidae	2	+	9	+	31,927	84.3	31,939	62.8
Apidae	—	—	472	3.0	139	7.7	611	1.2

A comparison of Q3 for the different lakes shows that there tends to be a change in distribution towards higher weight classes when lakes with high and steep surroundings are compared to those in lowland areas. Blåsjön thus has more than double the lowest value found (in Storuman), while the highest values are obtained in the Swiss lakes. The topography of the surrounding country seems to assume especial importance during periods with a weather situation favouring high activity level of the insects. The terrestrial insect material transported to the lakes is not only directly proportional to the mass of insects produced in the surroundings, but is also strongly dependent upon the energy that can be developed by aerial turbulence in the neighbourhood, as shown above.

Annual variation

Sampling in Blåsjön has covered the time from the breaking-up of the ice to the formation of a permanent cover of snow in the autumn. This material therefore forms the most suitable basis for study of the temporal variation (Fig. 4). The result corresponds well to the general fluctuation of the insect population in terrestrial environments: the first values are derived from over-wintering individuals which lay the first eggs. In June follows a period when the populations slowly accumulate and then become re-established. Their peak is reached at the end of July. By the end of August, however, the populations become reduced to a minimum; this is followed by the rise of another generation and also of species that fly in autumn and deposit eggs for over-wintering. During all autumn and until the beginning of winter 1—2 mg of terrestrial insects/m^2 were available. There was, on the whole, no correlation between the distribution in Fig. 4 and the temperature curve

Table 5. Biomass per sampling 1962—63 in different lakes, expressed in 0.1 mg/100 m of sampling.

A. Blåsjön and Ankarvattnet

	Blåsjön		Ankarvattnet	
	Station B1	Station B2	Station A2	Station A1
May 26	5,907	412	—	—
29	7	1	—	—
June 1	1	1	—	—
2	1	1	—	—
4	3	2	—	—
8	1	7	—	—
11	130	59	—	—
15	1	1	85	—
18	8	14	71	—
20	20	11	—	—
25	—	—	121	923
July 4	1,897	176	24	198
9	22	4	119	1,273
14	1,168	2,361	545	203
17	1,858	2,861	177	204
23	6,462	4,003	1,282	902
25	3,090	9,360	1	524
30	2,766	8,222	110	673
Aug. 3	553	3,542	—	—
6	1,566	—	2,605	382
10	1,041	903	1,439	766
13	1,247	557	—	—
15	1,002	2,558	—	—
19	113	2,031	—	—
21	218	342	—	—
25	514	508	—	—
27	210	346	—	—
29	7,452	263	—	—
30	834	9,785	—	—
Sept. 1	1,121	5,789	—	—
3	14,586	15,524	—	—
6	2,471	2,869	—	—
8	346	2,032	—	—
10	425	193	—	—
11	2,283	1,751	—	—
14	593	279	—	—
17	772	298	—	—
19	2,458	1,488	—	—
24	1,038	3,077	—	—
27	433	222	—	—
30	29	2,181	—	—
Oct. 3	1,532	168	—	—
5	65	613	—	—
7	82	359	—	—
9	111	336	—	—
13	654	811	—	—
17	1	309	—	—

Table 5 continued.

B. Storuman

	Luspholmen		Långholmen		Umstrand	
	1	2	1	2	1	2
June 28	3,324	1,618	1,342	4,174	—	—
July 3	748	72	178	222	280	348
5	875	312	425	69	—	—
8	379	1	11	38	231	787
10	242	32	537	78	—	—
12	974	2.211	114	66	—	—
15	340	1,462	679	106	571	59
17	570	92	392	144	—	—
19	2,406	27	940	569	—	—
23	353	82	566	761	8	96
25	112	430	201	—	—	—
30	388	754	2,386	439	107	193
Aug. 1	937	361	193	57	—	—

C. Grundfors reservoir

	Grundfors		Nysele
	1	2	
July 1	664	—	1
11	950	128	265
17	20	298	227
26	363	740	176
Aug. 1	319	1,606	130

D. Lakes in Switzerland

Sept. 27	2,348
28	1,117
29	16,819
	8,166
30	26,547

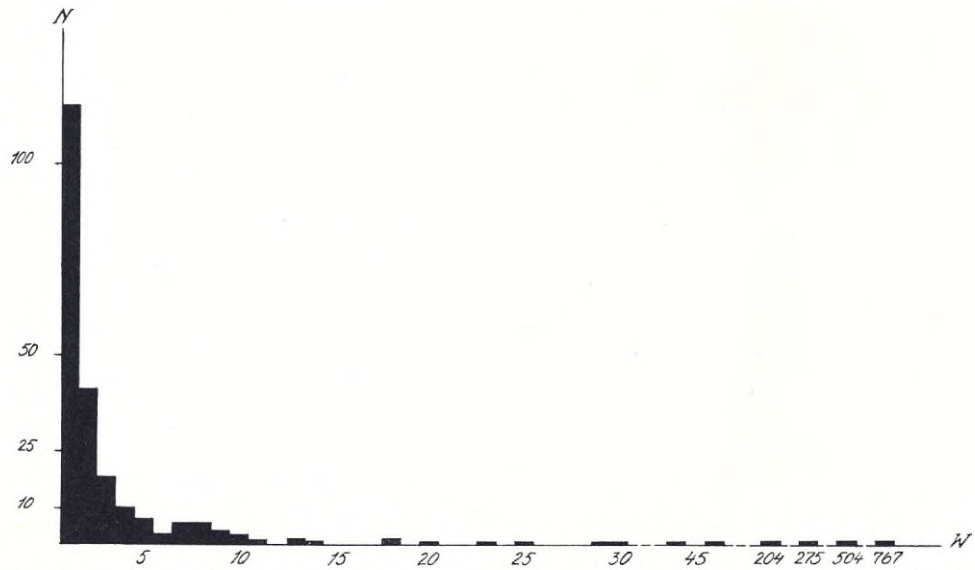

Fig. 3. The distribution of the total material among different weight classes. N=frequency, W=weight classes of 1 mg/m².

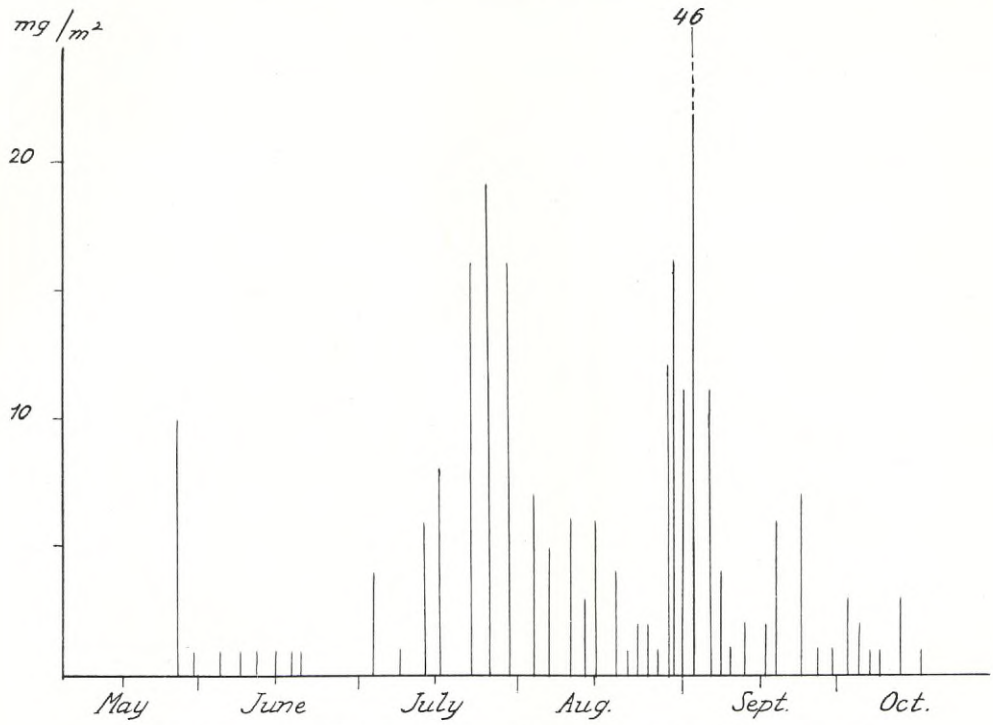

Fig. 4. Temporal variation of biomass in Blåsjön. W=weight in mg/m².

for the same period, however, the effect of certain periods with a high air temperature and consequent increased insect activity can be seen in the results of the sampling. The lack of correlation between the development of the temperature and the mass of the catches may be partly due to the fact that in early summer the temperature of the water is lower than that of the surroundings. This favours the downfalling of insects over the water. In late summer the temperature of the water exceeds that of the surroundings (cf. GRIMÅS 1961) and counteracts this.

The role of the introduction of terrestrial insects in the eco-system of the lake

The contribution supplied by the drifting fauna to the energy budget of the lakes is of particular value on account of its easy availability to predators and also on account of its introduction at a high trophic level, i.e. directly to the comsumers, viz. the fish.

A comparison between the biomass of bottom organisms in regulated mountain lakes, (GRIMÅS *1964, 1965*), *and the biomass of aerial insects shows the mass of the bottom organisms to be about one thousand times greater*

than that of the drifting fauna. A comparison, on the other hand, of the contribution of these organisms to the diet of the fish shows that in Blåsjön, for example, the share of the bottom animals is only about eight times greater than that of the terrestrial food, (NILSSON 1955). The share in the diet of the fish is thus not proportional to the content of the environment, the fish prefering the terrestrial contribution to a certain extent. The reason for this has to be sought in the availability of the different foodstuffs (cr. ALLEN 1941, 1942, GRIMÅS 1963) which results in a difference in the degree of utilization. The great availability of the drifting fauna results from the fact that it is gathered in a concentrated layer, and even occurs compressed into narrow streaks. It lacks the protection and possibilities for escape which the bottom organisms have, being instead clearly visible against the surroundings, viz. dark against a light background when the sun is high, and light against a dark background when the sun is low.

The fact that the drifting fauna is introduced at a high trophic level prevents its comparison with, for instance, the production of planktonic organisms. One must compare it instead with organisms serving as food for benthivarous fish such as the larger crustaceans. A comparison of this kind, based upon material from mountain lakes (NILSSON 1955), shows that in regulated lakes the importance of the drifting fauna and of these crustaceans as food organisms is equivalent. Thus *Gammarus lacustris* and terrestrial insects provided equal shares, about 10 per cent each, in Blåsjön in 1955.

The results support the assumption that nutrition provided in the shape of terrestrial insects forms an important component in the nutrition complex of the lakes, and that it has its greatest importance in the regulated lakes.

Of the three types of fish food, viz. bottom fauna, plankton, and the terrestrial contribution dealt with in this paper, the latter seems to suffer least from interference in connection with water-power regulation. Such interference has no effect on the regions for the regeneration of the drifting fauna on a large scale, nor does it affect the topography of the landscape to an extent that could be disadvantageous for the supply of terrestrial food. On the other hand, the bare zone of the shore which is often found between the water's edge and the vegetation belt can influence the supply of this kind of food in a negative way. This is due to some extent to the fact that spreading over short distances from regions near the shore is partly eliminated; it is also due to the fact that rising thermal air currents originating above such bare regions form a barrier to air-borne transport towards the lake.

Acknowledgements

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The work has been carried on in the Department of Entomology of the Zoological Institute in Uppsala, and I should like to express my gratitude to my supervisor Assoc. professor Bertil Kullenberg, for the positive atmosphere which has surrounded my work. At the Department it has been possible for me to hold discussions with Dr Ulf Grimås almost every day; his deep insight experience, and enthusiasm have been of the greatest benefit to me and have formed the basis for my work. I also wish to thank all the others at the Department for fruitful discussions and assistance with qualitative determinations.

Summary

1. The occurrence of terrestrial insects in the water surface, the drifting fauna, has been examined in a number of lakes in the high mountain regions of Sweden and Switzerland.

2. The supply of these insects seems to depend in the first place upon the production of insects in the immediate neighbourhood of the lakes and upon the capacity of the region to create transporting air currents. In 75 per cent of the samples the biomass falls short of 3.0 mg/m^2, while the median samples, both from the individual lakes and the total material, deviate little from 1.0 mg/m^2.

3. The biomass, which is small, for example in comparison with the bottom fauna, is by way of compensation easily available as prey. This explains the high degree of utilization of the drifting fauna as fish food. The importance of this type of allochthonous contribution in regulated lakes is accentuated by the fact that, contrary to many other comparable fish food organisms, it is little influenced by the interference resulting from regulation of the water level.

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Das Latnjajaureprojekt

Untersuchung eines fischfreien Sees vor und nach dem Einsatz von Fisch[1]

Von Arnold Nauwerck

Einleitung

Die vorliegende Schrift soll über ein Forschungsprojekt informieren, das der Verfasser in Zusammenarbeit mit einer Anzahl anderer Forscher und Institute im Herbst 1963 eingeleitet hat. Ausserdem sollen an dieser Stelle teils eine Übersicht über publizierte und unpublizierte Arbeiten gegeben, teils die bisherigen Resultate zusammengefasst werden, die mit dem Projekt direkt in Zusammenhang stehen.

[1] Mitteilung I des Latnjajaureprojektes.

Abb. 2. Der Latnjajaure gesehen vom Latnjatjårro. Rechts oben Kåppasåjve, im V
Påketjårro. (P

Das Forschungsprogramm

Physikalische, chemische und biologische Milieufaktoren und die Produktionsverhältnisse sowie Voraussetzungen und Möglichkeiten für Fischleben in einem extrem nahrungsarmen und langzeitig eisbedeckten See sollen während mehrerer Jahre studiert werden. Danach soll der See mit Fisch besetzt und dessen Entwicklung und Einwirkung auf das Milieu im Laufe einiger weiterer Jahre beobachtet werden.

Als geeignetes Objekt für die Untersuchungen bot sich der See Latnjajaure (Latnjavaggejaure) im Abiskogebiet im nördlichen Schwedisch-Lappland an. Der See ist von Natur aus fischfrei und hat ein nährstoffarmes Wasser, enthält aber ein verhältnismässig reichliches Plankton, das sich aus relativ wenigen Arten zusammensetzt. Der See ist ferner aus Nützlichkeitsgesichtspunkt ziemlich uninteressant und daher nicht in Gefahr, den Eingriffen wirtschaftlich interessierter Gruppen zum Opfer zu fallen. Er liegt oberhalb der Baumgrenze, ziemlich isoliert, ist von einfacher Form, hat ein begrenztes Einzugsgebiet und ist während fast 10 Monaten des Jahres eisbedeckt.

Da der See ein sehr einfaches Ökosystem darstellt, darf man erwarten, dass ein Eingriff von aussen schnell in einer relativ kräftigen und leicht messbaren Veränderung seiner biologischen Komponenten resultieren wird,

grund die noch unfertige limnologische Feldstation, auf der entgegengestzten Seite der A. Nauwerck).

die mit grosser Sicherheit mit dem Eingriff verbunden werden kann. Nicht nur die einfache Beschaffenheit und Überschaubarkeit des Sees, sondern auch die Nähe der Bahn und der Naturwissenschaftlichen Station in Abisko machen den Latnjajaure besonders geeignet für das Projekt. Ausserdem war der See schon früher Gegenstand wissenschaftlicher Untersuchungen und ist zur Zeit einer der drei wichtigsten Seen im Hochgebirgsprogramm des Limnologischen Instituts der Universität Uppsala.

Das Latnjajaureprojekt ist ein Teil des Forschungsprogrammes des Limnologischen Instituts in Uppsala betreffend Produktion und Milieuverhältnisse in verschiedenen Gewässern und hat in diesem Zusammenhang den Charakter reiner Grundforschung. Weiter soll das Projekt die regionale Limnologie mit Vergleichsmaterial von einem extrem nahrungsarmen Gewässer bereichern. Schliesslich soll mit dieser begrenzten aber relativ intensiven und allseitigen Untersuchung ein Beispiel für die Möglichkeiten der angewandten Limnologie gegeben werden.

Die Initiative zu diesem Projekt ergriff der Verfasser im Jahre 1963, sie geht aber zurück auf Anregungen von Professor SVEN EKMAN und Professor WILHELM RODHE. Der Hauptteil der Arbeiten obliegt dem Limnologischen Institut in Uppsala, jedoch ist eine Reihe anderer Institute und Forscher an dem Projekt beteiligt, so vor allem das Sötvattenslaboratorium Drottningholm, die Institute für Zoologie, Botanik und Geographie der Universität Uppsala sowie Sveriges Meteorologiska och Hydrologiska Institut (SMHI) in Stockholm. Ausserdem ist der See aufgenommen in das Oberflächen- und Bodenwasser-Projekt des Schwedischen Naturresourcenkomittees.

Die Durchführung des Projektes wird ermöglicht durch ökonomische Unterstützung des Schwedischen Naturwissenschaftlichen Forschungsrates. Dank finanzieller Beiträge des KEMPE-Fonds, der Stadt Kiruna und der HIERTA-RETZIUS-Stiftung sowie einer Donation der BASF in Ludwigshafen konnte die wichtigste Voraussetzung für die Arbeiten, die Feldstation am See geschaffen und ausgerüstet werden.

Frühere Literatur

Monographisch ist der See Latnjajaure, dessen äussere Bedingungen EKMAN (1957, pp. 112—115) beschrieben hat, noch nicht untersucht. Ausführlich sind nur seine Rotatorien durch PEJLER (1957, pp. 18—19) und seine Planktonalgen durch SKUJA (1963, p. 363) behandelt worden. Verschiedene Einzelangaben finden sich bei RODHE (1962, 1963) und RODHE et al. (1967), besonders betreffend Primärproduktion und Biomasse, sowie bei LOHAMMAR (1963) und NAUWERCK (1966). Bereits im Rahmen des Projektes durchgeführt sind die Arbeiten von PALM und TÖRMÄ (1965), KARLSSON (1967), TAUBE (1966) und BODIN (1966).

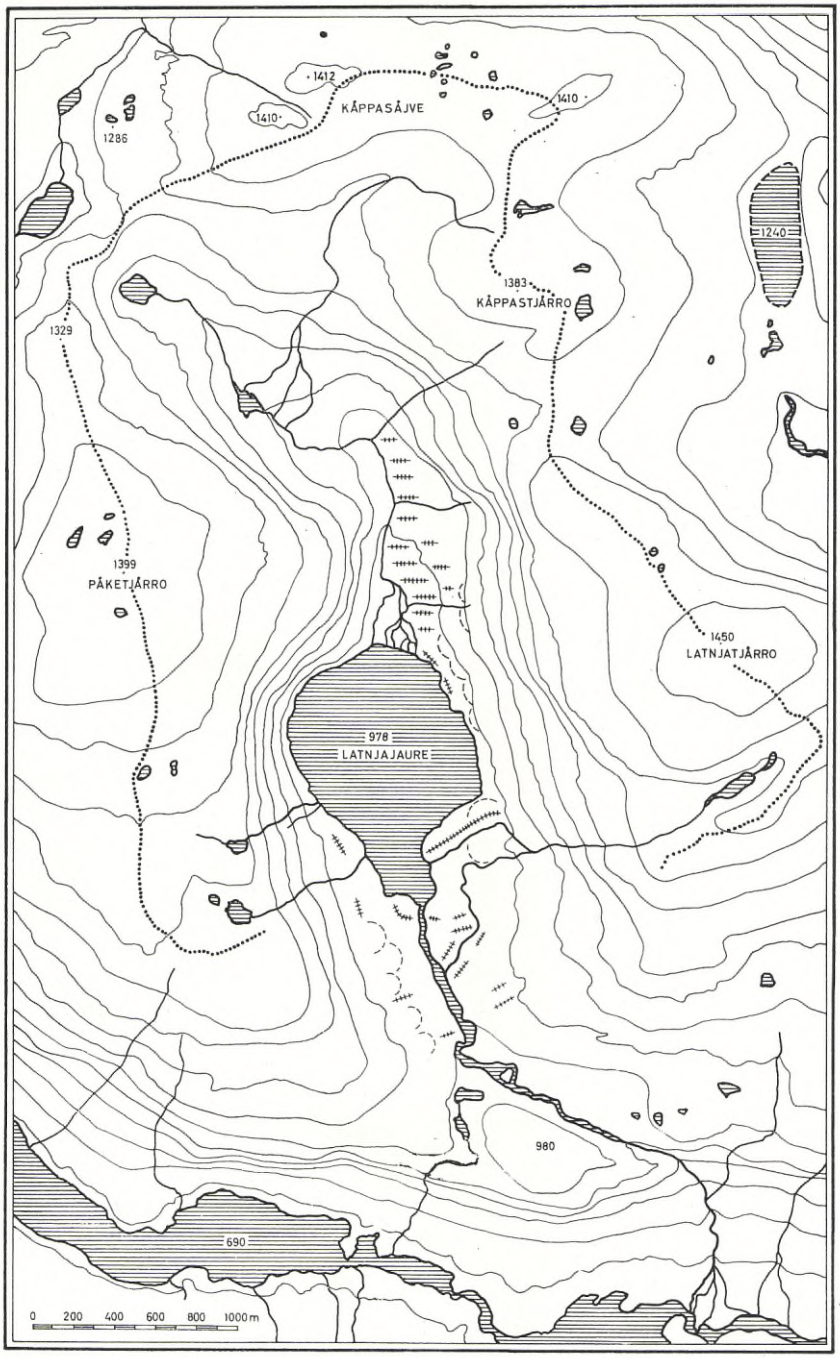

Abb. 1. Das Einzugsgebiet des Latnjajaure (umgezeichnet nach PALM und TÖRMÄ). ·····=Wasserscheide, +++++=Moränen, - - - - -=Fliesserdewülste.

Die folgende Beschreibung des See stützt sich in erster Linie auf die oben zitierten Arbeiten. Sie umfasst ferner Beobachtungen aus der ersten Arbeitsperiode des Projekts und ist ergänzt mit einigen unpublizierten älteren Resultaten.

Der See

a) Geographie und Geologie

Diesem Abschnitt zugrunde liegen die Arbeiten von PALM und TÖRMÄ (1965), von EKMAN (1957) sowie mündliche Mitteilungen von B. PALM, S. TÖRMÄ, J. KARLSSON, K. BODIN samt eigene Beobachtungen und Berechnungen.

Der Latnjajaure liegt ca. 12,5 km in genau westlicher Richtung von der Touristenstation in Abisko in 978 m. ü.M. Seine Lage ist gekennzeichnet durch die Positionsangaben N 68°21′, E 18°37′. Das Einzugsgebiet des Sees umfasst reichlich 9 km² und ist begrenzt von den Höhen des Kåppasåjve (1412 m) im Norden, und des Påketjårro (1399 m) und Latnjatjårro (1450 m) im Westen und Osten (Abb. 1). Etwa 20 % dieses Gebietes bestehen aus Almwiesen und Mooren, etwa 8 % entfallen auf den See selbst, weniger als 1 % sind Tümpel und Kleinseen. Der Rest besteht aus offen zutage liegenden Schutthalden oder anstehendem Gestein aus Glimmerschiefer und Granatglimmerschiefer mit eingesprengten Quarzgängen und fleckenweise eisenhaltigen Konglomeraten. Etwa 10 % des Gebietes können als permanent schneebedeckt bezeichnet werden.

Das Latnjavagge, ein Hochtal glazialen Ursprungs, erstreckt sich etwa 5 km in südöstlicher und südlicher Richtung, von den Höhen des Kåppasåjve bis zum Kårsavagge, in das es durch einen scharf ausgeschnittenen Cañon einmündet. Der See selbst liegt in der Mitte des Tales in einer Nische, gebildet aus den Steilabhängen des Påketjårro und des Latnjatjårro und ist im Süden durch einen Moränenwall abgeschlossen (Abb. 2). Seiner Entstehung nach ist der See als ein übervertieftes Glazialbecken anzusehen. Sein Alter lässt sich auf ca. 6000 Jahre schätzen.

Betreffend die Bodenbeschaffenheit des Seebeckens gilt folgendes. Die Uferzone besteht zum grössten Teil aus Steinblöcken und grobem Geröll. Am Fusse der Steilwand des Påketjårro setzen sich die Geröllhalden der Taluskegel bis in die grösste Tiefe des Sees fort. Auch der Boden des flachen Durchbruchssiels durch die Moränenbarriere im Süden und die weniger tiefen Partien des unterseeischen Rückens, der den See in seiner Längsrichtung durchschneidet und wahrscheinlich eine Restmoräne eines früheren Påkejårrogletschers darstellt, sind überwiegend mit Steinen bedeckt. Im Gebiet des Einflussdeltas des Latnjajåkk und in der südwestlichen Bucht findet man Sand, ebenso in allen weniger steil abfallenden Gebieten bis etwa 10 m Tiefe. In grösserer Tiefe besteht das Sediment zunehmend aus Kiesel-

algen- und Gletschergyttja. Im Nordosten des Sees sind grössere Flächen des Bodens mit Limonit ($Fe(OH)_3$) bedeckt. Fleckenweise finden sich Ausfällungen von See-Erz auch in den südwestlichen und südöstlichen Teilen des Sees.

b) Morphometrie und Hydrographie

Diesem Abschnitt zugrunde liegen Messungen und Berechnungen von PALM und TÖRMÄ (1965) und von mir selbst sowie Beobachtungen von K. BODIN und I. TAUBE.

Die Form des Sees ist einfach, fast rund mit einem flacheren Abflussiel. Die grösste Tiefe liegt gleich unterhalb der Steilwand des Påketjårro im Westen, nur etwa 100 m vom Strand entfernt und beträgt 43,5 m. Die mittlere Tiefe des Sees ist 16,5 m, sein Volumen beträgt etwa $12{,}1 \cdot 10^6 m^3$, die Oberfläche deckt 0,73 km^2, die Uferlinie ist 3,8 km lang (Abb. 3).

Seinen Zufluss empfängt der See in erster Linie aus dem Latnjajåkk, der einem kleinen See (B 17 bei EKMAN) dicht unter der Passhöhe zwischen Latnjavagge und Kuoblavagge—Låktatjåkko entspringt, der seinerseits von einem Schneefeld gespeist wird. Der Bach macht etwa 80 % der Wasserzufuhr des Sees aus. Der Rest verteilt sich auf eine Anzahl kleinerer Bäche, die zum grössten Teil nur kurzfristig Wasser führen („njiras"), einige Grundwasserquellen, hauptsächlich im Südwesten des Sees, sowie Niederschläge direkt auf die Seeoberfläche.

Die durchschnittliche Wasserführung des Abflussbaches beträgt ca. 200 l/sec während der Monate Juni bis September. Das Maximum liegt im Juli und dürfte etwa 1 m^3/sec betragen. Von September bis Mai sind Zuflüsse und Abfluss so gut wie versiegt. Der Wasserstand im See ist am höchsten unmittelbar nach dem Eisbruch Ende Juli—Anfang August und sinkt im Laufe des Sommers bis zur Eislegung Ende September—Anfang Oktober um 20—25 cm.

Die Niederschläge im Gebiet betragen (expoliert aus den Sommerwerten im Vergleich mit den Daten des SMHI von Abisko und Riksgränsen) etwa 480 mm pro Jahr. Die mittlere Jahrestemperatur (ermittelt auf die gleiche Weise) liegt zwischen —3,5° und —4,0°C. Positive Durchschnittstemperaturen haben die Monate April bis August, aber im Hinblick auf die mittlere Höhe des Niederschlagsgebietes (1125 m) muss man damit rechnen, dass nur während der Monate Mai bis Juli die Niederschläge als Regen fallen. Das entspricht etwa 1/3 der gesamten Niederschlagsmenge. Schneetransport durch den Wind in das Einzugsgebiet des Sees hinein oder aus diesem hinaus können von Jahr zu Jahr erhebliche Verschiebungen des theoretischen Wasserbudgets verursachen. Aus der Differenz zwischen Niederschlagsmenge und Abfluss lässt sich für das Jahr 1965 ein Verlust von reichlich 40 %

Abb. 3. Tiefenkarte des Latnjajaure und Einflussdelta des Latnjajåkk (umgezeichnet nach PALM und TÖRMÄ).

berechnen, der zum grössten Teil durch Verdunstung, zum geringeren Teil durch Schneeverwehungen verursacht sein dürfte.

Die theoretische Erneuerungsgeschwindigkeit der Wassermasse des Sees beträgt etwa 4 Jahre.

c) Licht- und Temperaturverhältnisse

Diesem Abschnitt liegen zugrunde Messungen und Beobachtungen von W. RODHE, G. LOHAMMAR, PALM und TÖRMÄ (1965) und mir selbst sowie Einzelmessungen verschiedener Besucher des Sees.

Die Einstrahlungsverhältnisse sind gekennzeichnet durch Mitternachtssonne im Sommer (Ende Mai bis Mitte Juni) und Polarnacht bzw.-dämmerung im Winter (Anfang Dezember bis Mitte Januar). Der Lichtgenuss des Sees wird indessen stark eingechränkt durch Beschattung von den Bergen, durch anhaltende Bewölkung und Nebel und durch die Eis- und Schneedecke, die den See die längste Zeit des Jahres bedeckt.

Die Transparenz des Wassers ist bedeutend. Die Sichttiefe variiert zwischen 17 m und mehr als 30 m und liegt im Durchschnitt bei 20—25 m. Die 1 %-Grenze des Oberflächenlichts schwankt zwischen 30 m und (theoretisch) 80 m Tiefe. Die Farbe des Wassers erscheint blau oder blau-violett, jedoch ist die grösste Transparenz für den Wellenbereich von Grün festzustellen.

Eine Temperaturschichtung ist im See nur ganz selten zu finden. An der Oberfläche in geschützten Buchten können ausnahmsweise 10°C gemessen werden. Normalerweise erwärmt sich der See nicht über 6—7°C. Die Jahresmitteltemperatur beträgt 1,5—2,0°C. In der Regel herrscht Homothermie mit einem Gradienten, sommers negativ, winters positiv, von wenig mehr als 1°C von der Oberfläche bis zur Tiefe des Sees.

Die Eisdecke des Sees erreicht zwischen 80 cm und 150 cm Mächtigkeit. Die Eislegung im Herbst erfolgt meistens nicht auf einmal. Heftige Stürme können auch ziemlich dicke Eisdecken noch einmal aufbrechen. Bei solchen Gelegenheiten kann der See auf nahe an 0°C abgekühlt werden. Bergstürze und Lawinen vom Påketjårro können ebenfalls feste Eisdecken wieder zerstören. Im Winter 1964—65 sprengte ein Bergsturz die ganze Eisdecke des Sees, die bereits 20 cm Dicke erreicht hatte. Auch der Eisbruch im Sommer geht in Etappen vor sich. Grosse Eisschollen können noch Wochen nach Beginn des Eisbruchs im See umhertreiben, und in kalten Sommern kann landfestes Eis am Westufer überhaupt liegen bleiben.

Die Dicke der Schneedecke ist stark vom Wind abhängig. Grosse Teile des Sees können von den Fallwinden vom Påketjårro zeitweise kahlgefegt werden, während am Ostufer Schneewehen von ein paar Metern Dicke antreiben.

d) Wasserchemie

Diesem Abschnitt zugrunde liegen hauptsächlich die Analysen der chemischen Abteilung des Limnologischen Instituts in Uppsala unter Leitung von T. AHL, ferner Einzelanalysen von L. KARLGREN, Ö. LINDGREN und G. LOHAMMAR.

Der pH des Sees is schwach sauer, er schwankt in der Regel nur wenig um den Mittelwert 6,3. In Bodennähe kann er während der winterlichen Stagnationszeit auf 5,8 sinken und direkt unter dem Eis bis auf 7 ansteigen, solange das Ausfrieren von Salzen anhält, d.h. bis April—Mai. Auch die Mittelwerte sind im Hochwinter am höchsten.

Die Leitfähigkeit, gemessen in $\varkappa_{20} \cdot 10^6$, ist nieder, im Durchschnitt 18—20. Sie erreicht ihre höchsten Durchschnittswerte ebefalls zur Zeit der stärksten Ausfrierung, wo die Werte in den obersten Wasserschichten bis über 27 betragen können. Auch in Bodennähe findet man meistens höhere Werte, jedoch nicht über 22. Am niedersten sind die Werte für den ganzen See unmittelbar nach dem Eisbruch im Juli, wo sie auf 15 sinken können. Im Laufe des Sommers steigt die Leitfähigkeit wieder langsam auf 18.

Der O_2 liegt zu allen Jahreszeiten nahe am Sättigungswert. Gegen Ende des Winters sinkt die Sättigung in Bodennähe auf 90 %, im Sommer ist in der Tiefe gelegentlich eine schwache Übersättigung feststellbar, deren Ursache die Bodenflora sein dürfte (vgl. S. 69).

Für die grösseren Konstituenten genügt es, zur Charakterisierung des Wassers ihre durchschnittlichen Grössenordnungen anzugeben. Sie betragen für Mg: 0,4 mg/l, Ca: 1,7 mg/l, Na: 0,6 mg/l, K: 0,4 mg/l und Cl: 0,9 mg/l. Von Interesse sind auch Si mit etwa 0,5 mg/l im Durchschnitt, sowie Sulfat mit etwa 5 mg/l und Fe mit etwa 0,01 mg/l. Je nach Art des Sediments (vgl. S. 61) können die Fe-Werte in Bodennähe erheblich zunehmen.

Der PO_4-Phosphor liegt meistens unter der Messbarkeitsgrenze, d.h. unter 1 µg/l. Die höchsten Werte sind im Sommer und im Spätsommer festzustellen. Sie liegen bei etwa 4 µg/l und finden sich in grösserer Tiefe. An der Oberfläche ist der PO_4-Gehalt praktisch immer kleiner als 1 µg/l.

Auch der Totalphosphor zeigt mit der Tiefe zunehmende Tendenz, ist aber im allgemeinen gleichmässiger verteilt als der PO_4-Phosphor. Der Jahresmittelwert liegt bei 3—5 µg/l, der bisher höchste festgestellte Wert ist 13 µg/l, die niedersten Werte sind im Spätwinter und um den Eisbruch zu finden.

Starke Schwankungen in Zeit und Raum zeigen die Konzentrationen des Stickstoffs. Zwar liegt das Maximum meistens an der Oberfläche, jedoch kommen von Probenahmentiefe zu Probenahmentiefe (in der Regel 10 m Distanz) nicht selten Differenzen von 10 : 1 oder 1 : 10 vor.

Die Durchschnittswerte für die Summe $NH_4+NO_2+NO_3$-Stickstoff liegen im Mittel bei etwa 30 µg/l. Sie schwanken aber von unter 1 µg/l bis über 100 µg/l nicht nur von Datum zu Datum, sondern auch innerhalb einer

Probenserie von verschiedenen Tiefen. Zufällige Oberflächenmaxima sind nicht selten. Nach unten nehmen die Werte meistens ab. Die höchsten Durchschnittswerte sind im Winter, die niedersten in der Regel Ende des Sommers festzustellen.

Der organische Stickstoff zeigt ebenfalls starke Schwankungen. Sein Jahresmittelwert liegt bei etwa 50 µg/l. Das Maximum findet sich im Sommer und an der Oberfläche, über 200 µg/l, das Minimum im Hochwinter, etwa 10 µg/l. Im grossen und ganzen verlaufen die Jahreskurven für organischen und anorganischen Stickstoff etwa spiegelbildlich.

Für die Nährstoffversorgung des Sees ist die Chemie seiner Zuflüsse von Interesse. Die umgebenden Tümpel und Kleinseen, die direkt oder indirekt in den See entwässern, zeigen durchweg bedeutend niederere Leitfähigkeit als der See, nämlich zwischen 4 und 13. Ihr pH schwankt zwischen 5,5 und 7,0, liegt aber im Durchschnitt in der gleichen Grössenordnung wie das des Sees. Dagegen liegen Leitfähigkeit und vor allem Stickstoffgehalt des Hauptzuflusses, der in seinem Delta ein Moorgebiet passiert, wenigstens in den Sommermonaten höher als im See, während das pH gleichzeitig markant niederer liegt. Besonders während der Schneeschmelze ist der Materialtransport in den See (durch den Wind während des Winters auf dem Schnee abgelagerter Staub und organisches Débris) bedeutend.

Von nicht zu unterschätzender Bedeutung sind auch Fäkalien von Lemming und Ren, die sich im Winter auf und unter dem Schnee ansammeln. Da der Boden, soweit es sich nicht um nackten Fels handelt, lange Zeit gefroren bleibt, werden diese Fäkalien ebenfalls mit der Schneeschmelze abgespült und auch die oberen Bodenschichten können durch das abfliessende Wasser ausgelaugt werden. Auf dem Eis liegendes, aus der Umgebung zugeführtes Schmelzwasser, das sich durch braune oder grüne Färbung vom Schmelzwasser der Eisdecke selbst deutlich abhebt, kann doppelt so hohe Konzentrationen von anorganischem Stickstoff aufweisen, wie das Wasser des Sees.

Natürlich bedeuten auch die Bergstürze eine ständige Zufuhr von anorganischem und organischem Material.

e) Plankton

Phytoplankton

Diesem Abschnitt zugrunde liegen meine eigenen sowie H. Skujas Untersuchungen.

Skuja gibt für den Latnjajaure eine Artenliste von über 60 Arten, einschliesslich unpublizierter Funde verzeichnet er etwa 90 Arten, zum überwiegenden Teil Arten des Netzplanktons. Die wichtigsten Arten sind, in fallender Ordnung nach Skuja, *Tabellaria flocculosa, Synedra ulna, Mougeotia* sp., *Oocystis submarina* v. *variabilis, Melosira distans* v. *alpigena,*

M. ambigua, Gloeococcus Schroeteri, Chlamydomonas arctoalpina, Ch. lapponica, Ankistrodesmus falcatus, Peridinium aciculiferum, P. inconspicuum, P. pusillum, Gymnodinium lacustre, Cryptomonas obovata.

Meine eigenen Funde, die hauptsächlich quantitativen Probenahmen entstammen, umfassen eine Liste von etwa 130 Arten, in erster Linie Arten des Nannoplanktons. Dass nur 40 Arten der beiden Listen identisch sind, erklärt sich in erster Linie aus der Probenahmetechnik, in geringem Masse wohl auch aus langfristigen Fluktuationen im Planktonbild. Quantitativ am wichtigsten sind jedenfalls die Chrysomonaden mit *Dinobryon acuminatum, D. americanum* v. *sociale, Chrysolykos Skujai* und *Kephyrion boreale,* die Grünalgen mit *Chlorella,* mehreren *Chlamydomonas*-Arten und *Oocystis submarina* v. *variabilis* sowie die Panzerflagellaten mit *Peridinium inconspicuum* und verschiedenen kleinen Gymnodalen. Weniger wichtig sind die Cryptomonadinen mit hauptsächlich *Rhodomonas minuta, Cryptomonas Marssonii* und *Sennia parvula* sowie die Kieselalgen mit *Melosira distans* v. *alpigena.* Ohne Bedeutung, wenn auch vereinzelt repräsentiert, sind die Blaualgen, Eugleniden, Heterokonten und die planktischen Mycophyten.

Die Zellzahlen pro Liter schwanken zwischen 10^3 und 10^5, die entsprechenden Totalvolumina zwischen < 1 und maximal $40 \cdot 10^6 \mu^3$ im Durchschnitt für die ganze Wassersäule. Der Jahresmittelwert liegt bei etwa $5 \cdot 10^6 \mu^3$. In der Regel ist gegen Ende des Winters ein schwaches und im Spätsommer ein mehr markantes Maximum festzustellen. Das erste besteht hauptsächlich aus *Peridinium* und *Chlorella,* das zweite aus Chrysomonaden sowie gegen Herbst auch aus *Peridinum* und verschiedenen Grünalgen. Es kommt aber auch vor, dass die Planktonwerte des Sommers nicht höher liegen als die des Winters.

Auffällig ist, dass die Algen, und zwar Gruppen und Arten, häufig in zwei Maxima geschichtet sind. Besonders im Sommer, d.h. während der eisfreien Zeit sind meistens ein schwächeres Oberflächen- und ein stärkeres Tiefenmaximum festzustellen. Die Schichtung ist jedoch selten sehr stark ausgeprägt.

Eine gewisse Zonierung der verschiedenen Gruppen ist ebenfalls häufig zu beobachten: Chrysomonaden und Grünalgen halten sich im Durchschnitt weiter oben auf als Panzerflagellaten und Cryptomonadinen. Kieselalgen pflegen, aufgewirbelt vom Sediment, in den tieferen Schichten des freien Wassers aufzutreten. Ein Zusammenhang zwischen ihrer Verteilung und der Bodenbeschaffenheit lässt sich nachweisen.

Horizontale Verschiedenheiten in der Verteilung des Phytoplanktons sind sonst kaum bemerkbar. Lediglich in Ufernähe und im Bereich von Zuflüssen findet man einen verhältnismässig grossen Anteil tychoplanktischer Desmidiaceen und Kieselalgen, die überrieselten Felsen, sumpfigen Wiesen und anderen feuchten Biotopen aus der Umgebung des Sees entstammen.

Zooplankton

Diesem Abschnitt zugrunde liegen eigene Untersuchungen sowie die Arbeiten von PEJLER (1957) und TAUBE (1966).

Das Crustaceenplankton des Sees setzt sich zusammen aus *Cyclops scutifer, Bosmina coregoni, Chydorus sphaericus, Daphnia rosea* und *Cyclops gigas,* ferner *Eudiaptomus graciloides* und *Daphnia longispina hyalina.* Die beiden letzten Arten sind sehr selten. Die Rotatorien sind in erster Linie repräsentiert durch *Kellicottia longispina, Keratella hiemalis* und *Polyarthra vulgaris.* Die von PEJLER ausserdem verzeichneten Arten *Keratella cochlearis* und *Filinia terminalis* scheinen selten zu sein; sie konnten seither nicht wieder gefunden werden.

Die wichtigste Art des Zooplanktons ist *Cyclops scutifer. Cyclops scutifer* hat seine Fortpflanzungsperiode in den ersten beiden Wochen des August und bleibt normalerweise monozyklisch. In warmen Jahren kann eine zweite Periode der Eiablage im Herbst beobachtet werden. Die Nauplien erreichen im selben Jahr nur Copepoditenstadium; starke Indizien sprechen dafür, dass das adulte Stadium mitunter erst im dritten Jahr erreicht wird.

Cyclops scutifer hält sich hauptsächlich in grösserer Tiefe auf. Sein Maximum, durchschnittlich 20—30 Individuen pro Liter, alle Stadien zusammengenommen, ist in Bodennähe in 25—30 m Tiefe zu finden. In noch grösserer Tiefe nimmt die Individuenzahl wieder ab. Der Jahresmittelwert aller Tiefen ist allerdings kaum grösser als 2 Individuen pro Liter.

Die Horizontalverteilung der Art im See ist ziemlich heterogen. Flachere Ufergebiete werden gemieden. Im westlichen Teil des Sees ist eine deutliche Verdünnung der Polulation festzustellen, die keine Entsprechung im Phytoplankton findet. Zum Teil mag diese Verteilung mit Bodenbeschaffenheit und Seetiefe zusammenhängen. Moosbewachsene Gebiete und Gebiete mit Gyttja bieten lokal bessere Nahrungsverhältnisse. Möglicherweise kann auch das Phänomen der „Uferflucht" eine Rolle spielen. Das Verdünnungsgebiet fällt nämlich hauptsächlich mit dem Beschattungsbereich des Påketjårro zusammen. Aber auch im kleinen ist Heterogenität der Verteilung, Wolken- oder Schwarmbildung, gewöhnlich.

Megacyclops gigas ist vorwiegend im Litoral anzutreffen, besonders um den Eisbruch, wo die hauptsächliche Eiablage eintrifft. Eiertragende Individuen sind aber vereinzelt den ganzen Sommer zu finden, zu dieser Zeit jedoch mehr in der Tiefe. Die Nähe moosbewachsener Bodenzonen wird dabei bevorzugt. Die Absolutzahlen der Art sind zu gering als dass sich gegenwärtig sichere Aussagen über ihre Entwicklung machen liessen. Es scheint jedoch, dass die jüngeren Stadien von *Megacyclops gigas* eine mehr planktische Lebensweise haben als die Adulten.

Während das Auftreten der *Cyclops*-Arten von Jahr zu Jahr ziemlich gleich bleibt, erscheinen die Cladoceren mehr periodenweise. *Daphnia rosea*

und *Bosmina coregoni* können im Ablauf einiger Jahre förmlich alternieren. Die Ursachen dafür sind allerdings eher in Schwankungen des Milieus als in einer direkten Konkurrenz zu suchen.

Daphnia rosea entwickelt sich spät im Jahr und besonders in relativ warmen Herbsten. Ist der Frühsommer zu kalt, so kann sie praktisch ganz ausbleiben. Laboratorienzuchten erwiesen *Daphnia rosea* als echt kaltstenotherme Art, die über 15°C schlecht gedeiht und ihr Optimum bei 8—10°C haben dürfte. Andererseits sind Temperaturen unter 5°C ebenfalls ungünstig, sodass der Lebensbereich der Art temperaturmässig sehr eingeschränkt ist. Gleichwohl bestehen Indizien dafür, dass *Daphnia rosea* vereinzelt in erwachsenem Zustand überwintert. Eigentümlicherweise sind Ephippien ausserordentlich selten. Sie konnten bisher nur zweimal in Sedimentproben nachgewiesen aber weder im Plankton beobachtet noch in den Zuchten provoziert werden.

Die Cladoceren leben im Gegensatz zu den Cyclopiden hauptsächlich in den oberen Wasserschichten, d.h. bis in etwa 10—20 m Tiefe. Die obersten Meter werden allerdings auch von ihnen gemieden. Die Individuendichte beträgt maximal etwa 1 pro Liter für *Daphnia rosea* und bis zu 10 pro Liter für *Bosmina* und *Chydorus*. Die Jahresmittelwerte sind aber denen von *Cyclops scutifer* nicht annähernd zu vergleichen. Sie liegen in der Regel weit unter 0,1 Individuen pro Liter.

Unter den Rotatorien nimmt *Kellicottia* die bedeutendste Stellung ein. Ihre Verteilung ist ausgesprochen heterogen mit Anhäufungen vor allem in mittleren und grösseren Tiefen. Die absoluten Maxima (um 10 Individuen pro Liter) finden sich meistens in Bodennähe. Der Jahresdurchschnitt ist knapp 1 Individuum pro Liter. *Kellicottia* ist während des ganzen Jahres zu finden und fehlt nur gelegentlich in den obersten Wasserschichten. Ihre Haupt-Fortpflanzungsperiode liegt im Spätsommer.

Mit Jahresmittelwerten von weniger als 0,5 bzw. weniger als 0,1 Individuen pro Liter und Maximalwerten von etwa 5 bzw. 2 Individuen pro Liter folgen *Keratella hiemalis* und *Polyarthra vulgaris*. Beide ereichen ihre absoluten Maxima im Herbst und beide finden sich im Herbst hauptsächlich in tieferen Schichten, bilden aber im Winter, im Gegensatz zu *Kellicottia,* ihr Maximum direkt unter dem Eis.

Temporalvariation sowohl als auch Lokalvariation (in verschiedenen Tiefen) sind bei *Kellicottia* festzustellen, dagegen so gut wie gar nicht bei *Keratella hiemalis*. *Kellicottia* erreicht ihre grössten Dimensionen Ende des Winters sowie in grösserer Tiefe.

f) Bodenflora und Bodenfauna

Bodenflora

Diesem Abschnitt zugrunde liegen die Arbeiten von BODIN (1966), Beobachtungen von N. QUENNERSTEDT und mir selbst sowie Bestimmungen von O. MÅRTENSSON (Moose).

Das auffälligste Merkmal des Sees ist seine Bodenflora. Rund 40 % des Seebodens sind bedeckt von einem Lebermoos, *Marsupella aquatica*. Die Moosdecke erstreckt sich von etwa 2 m Tiefe bis etwa 35 m Tiefe. Ungeeignet als Unterlage erscheinen die Strandzone, wo das Eis die Steine abhobelt, die Steilufer unterhalb des Påketjårro, wo Erdrütsche und Steinschläge das Moos nicht Fuss fassen lassen, das Deltagebiet, wo loses Material das Sediment bedeckt, das Eisenockergebiet, wo Ausfällung von $Fe(OH)_3$ das Moos erstickt, sowie Gebiete mit Tiefen von mehr als 35 m, wo das Licht begrenzender Faktor werden dürfte.

Ausser *Marsupella* sind einige andere Moose in Spuren fast überall anzutreffen. Es sind dies *Scapania uliginosa, Blepharostoma trichophyllum* und *Cephalozia* cfr. *bicuspidata,* ferner *Drepanocladus exannulatus* mit v. *purpurascens, Philonotis fontana, Polytrichum gracile, Calliergon sarmentosum* sowie *Hygrohypnum styriacum.*

Seine grösste Ausbreitung hat das Moos in 25—30 m Tiefe. Die maximale Bestandsdichte, entsprechend einem Trockengewicht von 557 g/m², wurde in 27 m Tiefe gefunden, der durchschnittliche Bestand im moosbedeckten Gebiet ist rund 106 g/m².

Das Moos seinerseits bietet die Unterlage für Epiphyten. Hier ist eine Zonierung sowohl an den einzelnen Moospflanzen als auch in verschiedenen Tiefen festzustellen. Auf Moospflanzen von 5—10 m Tiefe dominieren Grünalgen, *Bulbochaete* am oberen, *Oedogonium* am unteren Teil der Pflanze; Kieselalgen sind ebenfalls reichlich vertreten, am wichtigsten sind *Amonoeoneis* und *Eunotia*; Blaualgen finden sich nur in geringen Mengen, meist *Lyngbya*; die Absolutmenge an Epiphyten ist relativ gross. In 10—20 m Tiefe nehmen die Grünalgen ab, *Bulbochaete* verschwindet; bei den Kieselalgen dominiert nun *Peronia*; die Blaualgen machen quantitativ und qualitativ die wichtigste Gruppe aus, neben *Lyngbya* finden sich nun *Chamaesiphon* und *Clastidium* sowie auch *Chroococcus* und *Aphanothece*; die Absolutmenge der Epiphyten wird geringer. In etwa 30 m schliesslich sind die Grünalgen ganz verschwunden. Bei den Kieselalgen dominiert *Peronia* vollständig, die Blaualgen bestehen praktisch nur noch aus *Lyngbya.* Eine scharfe Schichtung besteht längs der Pflanze: die Kieselalgen befinden sich nur noch an deren oberen Teilen, während *Lyngbya* ihr Maximum etwa in der Mitte der Pflanze aufweist. Quantitativ halten sich die beiden Gruppen etwa die Waage. Die absolute Bedeutung der Epiphyten ist in dieser Tiefe am geringsten.

Neben den eigentlichen Epiphyten, d.h. den festsitzenden Formen, finden sich auf und zwischen dem Moos ebenso wie auf dem nackten Sediment verschiedene andere Mikroorganismen, deren wichtigste unter den Pflanzen die Kieselalgen ausmachen. Tatsächlich bestehen die feineren Sedimente zum grossen Teil aus Kieselalgengyttja. Als Leitformen für den See können gelten: *Melosira distans* mit Varietäten, *Eunotia monodon* mit Varietäten, *E. robusta*

v. *diadema, E. pseudopectinalis, E. praerupta, Fragilaria construens, Surirella linearis, Pinnularia microstauron, P. gibba, P. interrupta, Achnanthes minutissima, Anomoeoneis* exilis sowie *Peronia Héribaudii.* Die Dominanten in den verschiedenen Tiefen sind in 5 m *Eunotia,* in 10—20 m *Surirella* und in grösseren Tiefen *Melosira distans* mit Varietäten sowie *Fragilaria construens.*

In der Strandzone, besonders in der Nähe der kleineren Zuflüsse, findet man hier und da auf den Steinen Überzüge oder Büschel von *Zygnema, Spirogyra, Ulothrix moniliforme, Binuclearia tatrana, Tabellaria flocculosa* und selten *Tetraspora cylindrica.*

Bodenfauna

Diesem Abschnitt zugrunde liegen in erster Linie Untersuchungen von G. LITHNER, ferner die Arbeiten von J. KARLSSON (1967) und Bestimmungen von W. SCHÖNBORN (Thecamöben) und C. MEIER-BROOK (Mollusken).

Betreffend die Makro-Bodenfauna kann generell festgestellt werden, dass der See als „Litoralsee" zu bezeichnen ist. Die meisten Arten finden sich in allen Gebieten des Sees und bis hinab in die grössten Tiefen. Eine gewisse Schichtung ist jedoch deutlich, ebenso sind verschiedene Bodengebiete verschieden dicht und unter Dominanz verschiedener Arten besiedelt.

Die wichtigste Gruppe sind die Chironomiden. Von ihnen nehmen Tanytarsinen mit Larven der *Tanytarsus gregarius*-Gruppe in flacheren Gebieten bis etwa 10 m Tiefe die wichtigste Stellung ein. In grösserer Tiefe überwiegen die Orthocladinen mit *Heterotrissocladius subpilosus* und mit *Pseudodiamesa.* Die letztere hat indessen ihr absolutes Maximum in geringeren Tiefen. Die Orthocladinen stellen auch den grössten Anteil der bisher festgestellten rund 20 Arten der Insektenfauna des Sees. Unter den Chironominen ist *Sergentia* der einzige Repräsentant. Die Gattung, die teilweise als Mesotrophie-Indikator gilt, ist hauptsächlich im Bereich des Einflussdeltas verbreitet.

Überwiegend in flacheren Zonen sowie allgemein im Moos findet sich *Pisidium conventus.* Ebenso wie die vereinzelt festgestellten Nematoden und Hydracariden dürfte *Pisidium* mit der üblichen Methode jedoch quantitativ nicht vollständig erfasst worden sein.

Oligochaeten sind vor allem im organogenen Material des Einflussdeltas anzutreffen. Trichopteren finden sich hauptsächlich nahe am Ufer und in den Moosgebieten der flacheren Zonen. *Dytiscus*-larven bevölkern etwa die gleichen Gebiete, ihre Adulten halten sich in unmittelbarer Ufernähe auf. Vereinzelt kommen Plecopteren und *Dicranota* vor.

Die Absolutzahlen der mit der Siebmaschenweite 0,6 mm zu erbeutenden Tiere variieren zwischen etwa 500 und 2500 Individuen/m² (ca. 10—50 Tiere pro EKMAN-Bodengreifer-Probe). Den weitaus grössten Teil davon stellen die Chironomiden. Die Pisidien liegen in der Grössenordnung 200—500 Indi-

viduen/m², die Oligochaeten in der Grössenordnung 50—500 Individuen/m², die Trichopteren in der Grössenordning 10—20 Individuen/m².

Die höchsten Zahlen sind zu Beginn des Sommers in flacheren Gebieten anzutreffen, im Spätjahr in grösserer Tiefe. Dies wird durch verschiedene Schlüpfzeiten bedingt. Erst unterhalb 30 m Tiefe ist eine allgemeine Abnahme der Individuendichte signifikant. Allgemein scheint die Bodenfauna auf moosbewachsenen Gebieten um das 2—3-fache reichlicher als auf nacktem Boden. Ärmer als der Durchschnitt scheint das Limonitgebiet, reicher speziell das Gebiet des Einflussdeltas. Allerdings ist die Verteilung auch innerhalb gleichartiger Gebiete bisweilen ziemlich heterogen.

Die hauptsächliche Schlüpfzeit ist die Zeit um den Eisbruch. In dieser Zeit schlüpfen *Pseudodiamesa* und *Heterotrissocladius*. Zumindest die letztere scheint zwei Generationen zu bilden mit einem zweiten Schlüpfmaximum im Herbst. Ebenfalls bis spät im Herbst schlüpfen die Trichopteren.

Die Fauna der Zufluss- und Abflussbäche ist artenarm aber stellenweise sehr individuenreich. Sie besteht in erster Linie aus *Simulium,* in zweiter Linie aus Chironomiden der *Diamesinae*-Gruppe.

Unter der Mikro-Bodenfauna nehmen die Thecamöben einen hervorragenden Platz ein. SCHÖNBORNS Liste umfasst nicht weniger als 48 Arten und Varietäten, darunter zwei neue Arten und drei neue Varietäten. Die wichtigsten Repräsentanten sind *Difflugia elegans* mit der *Varietät teres, D. oblonga, D. globulosa, Centropyxis aerophila, C. aculeata, Euglypha acanthophora, E. rotunda, Phryganella acropodia, Trinema euchelys, Pontigulasia spectabilis* sowie *Cyphoderia ampulla* v. *major.*

Die Verteilung der Arten ist ausgesprochen heterogen, sie kommen praktisch in allen Tiefen und gleichermassen auf Moos und auf nacktem Boden vor. Lediglich das Limonitgebiet ist deutlich artenärmer als jedes andere Gebiet. Die grösste Artenanzahl weisen flache Zonen mit Moosbewuchs auf.

g) Primärproduktion

Diesem Abschnitt liegen zugrunde eigene Messungen sowie Einzelangaben von RODHE (1962, 1963, 1967) und J. HOBBIE betreffend das Phytoplankton und die Arbeiten BODINS (1966) und meiner selbst betreffend Epiphyton, Bodendiatomeen und Moos. Alle Messungen bauen auf der C_{14}-Methode und alle Vorbehalte gegen diese Methode sind zu berücksichtigen.

Die Primärproduktion des Phytoplanktons folgt im grossen und ganzen ziemlich gut der Biomasse des Phytoplanktons. Die Jahresmittelwerte pro m² über 30 m Tiefe liegen zwischen 15 und 30 mg $C_{ass.}$ pro Tag. Entsprechend dem Spätwintermaximum des Phytoplanktons im Juni ist auch in der Primärproduktion ein schwaches Maximum zu verzeichnen, das, ebenso wie das des Phytoplanktons von einem absoluten Minimum unmittelbar nach dem Eisbruch und einem Sommermaximum Ende August/Anfang September

abgelöst wird. Das Sommermaximum kann bis über 80 mg $C_{ass.}/m^2 \cdot$ Tag betragen, übersteigt aber in normalen Jahren kaum 60 mg. Das Minimum nach dem Eisbruch kann unter 10 mg liegen. Ebenso wie beim Phytoplankton sind auch grosse Unterschiede von Jahr zu Jahr zu verzeichnen, und z.B. 1965 sind die Sommerwerte nicht höher als die des Winters.

Auch was die Tiefenverteilung betrifft zeigt die Primärproduktion leidliche Übereinstimmung mit dem Phytoplankton. Bei Vorherrschen grosser Sichttiefen reicht auch die trophogene Schicht bis weit hinunter und bis 30 m Tiefe ist keine oder nur schwache Abnahme der Primärproduktion festzustellen. Häufig findet man dagegen Unregelmässigkeiten in den Assimilationswerten von verschiedenen Tiefen. Besonders während der eisfreien Periode sind meistens zwei Maxima vorhanden, die entweder an der Oberfläche und in mittlerer Tiefe, oder in mittlerer Tiefe und nahe dem Boden liegen. Meistens folgen auch diese Unregelmässigkeiten einer charakteristischen Planktonverteilung und dürften im Sinne von optimalen Schichten zu deuten sein.

Ein auffälliger Zusammenhang besteht insbesondere zwischen zwei Gruppen des Phytoplanktons und der Primärproduktion. Die Assimilation der Chrysomonaden scheint am stärksten und am unmittelbarsten veränderten Lichtverhältnissen gleichsinnig zu folgen, während die Panzerflagellaten umgekehrt überhaupt keine Reaktion zeigen, d.h. Schwankungen in der absoluten und relativen Biomasse der Panzerflagellaten stehen keine entsprechenden Schwankungen der Assimilation gegenüber.

Marsupella scheint ebenfalls gegenüber Lichtveränderungen in weiten Grenzen unempfindlich. Ihre Produktion schwankt nur wenig mit den sehr verschiedenen Lichtverhältnissen verschiedener Tage und Jahreszeiten und in verschiedenen Tiefen. Eine Lichthemmung in den oberen Schichten konnte nicht festgestellt werden (tatsächlich ist das „normale" Verbreitungsgebiet der Art der Latnjajåkk) und erst unterhalb 30 m Tiefe ist eine deutliche, offenbar durch Lichtmangel bedingte Abnahme der Produktionsgrösse festzustellen.

Die Primärproduktion der Bodendiatomeen und des Epiphytons konnten bisher nur grössenordnungsmässig und bei einzelnen Gelegenheiten gemessen werden. Eine präliminäre Berechnung der totalen jährlichen Primärproduktion des Sees ergab für das Jahr 1965 ca. 2650 kg $C_{ass.}$, die sich folgendermassen auf die verschiedenen Komponenten unter den Primärproduzenten verteilen: Phytoplankton 60 %, Moos 20 %, Bodendiatomeen 15 %, Epiphyton 5 %. Diese Ziffern gelten indessen für ein ausgesprochen schlechtes Jahr und dürften sich in Normaljahren verdoppeln bis verdreifachen, in guten Jahren bis verfünffachen.

Zusammenfassung

Die Einwirkung des Einsatzes von Fisch auf das Ökosystem eines extrem oligotrophen Hochgebirgssees sollen am Beispiel des Sees Latnjajaure im

nördlichen Schwedisch-Lappland studiert werden. Der See ist bisher von Natur aus fischfrei. Zunächst sollen während mehrerer Jahre die chemisch-physikalischen sowie die Produktionsverhältnisse kartiert werden. Eine limnologische Feldstation ist am See errichtet und in Gebrauch genommen worden. Die bisherigen Ergebnisse des Projekts sowie diejenigen früherer Einzeluntersuchungen werden zu einer allgemeinen Charakterisierung des Sees zusammengefasst.

Summary

The effects of the inplantation of fish on the ecosystem of an extremely oligotrophic high mountain lake will be studied in Lake Latnjajaure in Northern Swedish Lappland. The lake is naturally fishfree. In the beginning its chemical-physical and biological environmental factors, together with the production will be categorized. A limnological field station has been built at the lake and brought into use. The existing results of the project, together with earlier individual results, are summarised in a general characterization of the lake.

Verzeichnis der im Texte erwähnten specics und genera

Algen:

Achnanthes minutissima KÜTZ.
Ankistrodesmus falcatus (CORDA) RALFS
Anomoeoneis exilis (KÜTZ.) CLEVE
Aphanothece
Binuclearia tatrana WITTR.
Bulbochaete
Chamaesiphon
Chlamydomonas arctoalpina SKUJA
— *lapponica* SKUJA
Chlorella
Chroococcus
Chrysolykos Skujai (NAUWERCK) BOURELLY
Clastidium
Cryptomonas Marssonii SKUJA
— *obovata* SKUJA
Dinobryon acuminatum RUTTNER
— *sociale* v. *americanum* (BRUNNTH.) BACHM.
Eunotia monodon EHRNB.
— *praerupta* EHRNB.
— *pseudopectinalis* HUST.
— *robusta* v. *diadema* (EHRNB.) RALFS
Fragilaria construens (EHRNB.) GRUN.
Gloeococcus Schroeteri (CHOD.) LEMM.
Gymnodinium lacustre SCHILLER
Kephyrion boreale SKUJA
Lyngbya
Melosira distans (EHRNB.) KÜTZ.
— v. *alpigena* GRUN.
— *ambigua* (GRUN.) O. MÜLL.
Mougeotia
Oedogonium
Oocystis submarina v. *variabilis* SKUJA
Peridinium aciculiferum LEMM.
— *inconspicuum* LEMM.
— *pusillum* (PENARD) STEIN
Peronia Héribaudi BRUN et HÉR.
Pinnularia gibba EHRNB.
— *interrupta* W. SM.
— *microstauron* (EHRNB.) CLEVE
Rhodomonas minuta SKUJA
Sennia parvula SKUJA
Spirogyra
Surirella linearis W. SM.
Synedra ulna (NITZSCH) EHRNB.
Tabellaria flocculosa (ROTH) KÜTZ.
Tetraspora cylindrica (WAHLENB.) C. A. AG.
Ulothrix moniliforme KÜTZ.
Zygnema

Moose

Blepharostoma trichophyllum (L.) DU MORTIER
Calliergon sarmentosum (WG.) KINDB.

Cephalozia cf. *cuspidata* (L.) DU MORTIER
Drepanocladus exannulatus (GÜMB.) WARNST.
— v. *purpurascens* SCHIMP., LOESKE) MÅRTENSSON
Hygrohypnum
Marsupella aquatica (SCHRAD.) SCHIFFNER
Philonotis fontana (L.) BRID.
Polytrichum gracile MENZ.
Scapania uliginosa (SW.) DU MORTIER

Protozooen

Centropyxis aerophila DEFL.
— *aculeata* (EHRNB.) PEN.
Cyphoderia ampulla v. *major* PEN.
Difflugia elegans PEN.
— v. *teres* PEN.
Difflugia globulosa DUJ.
— *oblonga* EHRNB.
Euglypha acanthophora (EHRNB.) PERTY
— *rotunda* WAILES et PEN.
Phryganella acropodia (HERTWIG et LESSER) HOPKINSON
Pontigulasia spectabilis PEN.
Trinema enchelis (EHRNB.) LEIDY

Rotatorien

Filinia terminalis (PLATE)
Kellicottia longispina (KELLICOT)
Keratella cochlearis (GOSSE)
— *hiemalis* CARLIN
Polyarthra vulgaris CARLIN

Crustaceen

Bosmina coregoni (BAIRD)
Chydorus sphaericus O. F. MÜLLER
Cyclops scutifer SARS
Daphnia longispina hyalina LEYDIG
— *rosea* RICHARD
Eudiaptomus graciloides (LILLJEBORG)
Megacyclops gigas (CLAUS)

Dipteren

Dicranota
Heterotrissocladius subpilosus (KIEFF.) EDW.
Tanytarsus gregarius (KIEFF.) EDW.
Pseudodiamesa
Sergentia

Lamellibranchiaten

Pisidium conventus CLESSIN

Verzeichnis lappischer Namen und Geländebezeichnungen

(Nach B. COLLINDER (1964): Ordbok till Sveriges Lapska Ortnamn. — Kungl. Ortnamnskommissionen. Almqvist & Wiksell, Uppsala)

Abisko (ápe-skov'vú) = Meer-Wald (gemeint ist der von SW gerechnet bei Abisko beginnende Birkenwald, der sich bis zur norwegischen Küste erstreckt)
Åjve (oai've) = Kopf, abgerundeter Berg
Jaure (jau're, jáv'ri) = See
Jåkk (johko) = Fluss, grosser Bach
Kuobla (koub'la) = Schneewächte oder überhängende Felswand
Kåppas (kohpas) = Kuppe (Lehnwort)
Kårsa (kors'a, kurs'sjú) = schmales Fluss- oder Bachtal umgeben von steilen Bergwänden, Schlucht
Latnja (ladnjá) = Attr., reich an Terassen oder Simsen, treppenartig zerklüftet (bezieht sich auf die Questa-Formen der westlichen und südlichen Abhänge des Latnjatjårro)
Låkta (lok'ta) = langgestreckte Bergterasse
Njira (njiráu, njirá) = zeitweise schutt- oder wasserführende Hangrinne, kleiner Sturz- oder Staubbach
Påke (pohke) = Einschnürung, Klamm, Engpass (hier: am Fusse einer Steilwand)
Tjåkko (tjohkko) = (Hochgebirgs-) Gipfel
Tjårro (tjorrú) = (schmaler) langgestreckter Bergrücken
Vagge (vágge) = grösseres, tiefes Tal zwischen hohen Bergen

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Zur Populationsdynamik von *Cyclops scutifer* Sars

I. Die Temperaturabhängigkeit der Embryonalentwicklung von *Cyclops scutifer* Sars im Vergleich zu *Mesocyclops leuckarti* (Claus)[1]

Von Inger Taube und Arnold Nauwerck

Im Rahmen des Latnjajaureprojektes (Nauwerck 1967) sollen die Produktionsverhältnisse des bisher fischfreien Sees Latnjajaure vor und nach dem Einsatz von Fisch studiert werden. *Cyclops scutifer* ist die wichtigste Zooplankton-Art des Sees. Die Kenntnis seiner Populationsdynamik ist die Voraussetzung für das Studium der Produktionsbiologie des Copepoden. Die vorliegende Arbeit gibt die ersten Ergebnisse unserer Studien über *Cyclops scutifer* in komprimierter Form. Eine ausführlichere Darstellung dieser Ergebnisse und besonders auch der Methodik findet sich bei Taube (1966).

Die Biologie von *Cyclos scutifer* ist in Scandinavien in jüngerer Zeit hauptsächlich von Lindström (1952, 1958) und Axelson (1961) untersucht worden. Nach Auffassung dieser Autoren sind bei der Art zwei „Fraktionen" zu unterscheiden, die durch gewisse morphologische Eigenarten und durch zeitlich getrennte Fortpflanzungszyklen gekennzeichnet sind.

Auch im Latnjajaure glaubten wir in manchen Jahren die Fraktionen zu beobachten. Ausführliche statistische Messungen zeigten jedoch, dass es sich nur um Extremformen ein und derselben Population handelte. Die Beobachtungen Lindströms und Axelsons legen indessen den Verdacht nahe, dass die Lebensdauer des *Cyclops scutifer,* die ihrerseits von Milieufaktoren wie Temperatur und Nahrungsangebot reguliert wird, über morphologische Veränderungen und Verschiebung von Fortpflanzungsperioden entscheidet. Unsere Arbeiten sollen auch zur Klärung dieser Frage beitragen.

Material und Methode

Das Material für die Versuche mit *Cyclops scutifer* entstammt dem Latnjajaure, das Vergleichsmaterial von *Mesocyclops leuckarti* dem Erken (siehe auch Nauwerck 1963). Zur Zeit der Probeentnahmen im Sommer 1965 herrschte im Latnjajaure eine Temperatur von 4—5°C, im Erken von etwa 15—17°C. Diese Temperaturen gelten für die Wasserschichten, in denen die Versuchstiere mit dem Planktonnetz gefangen wurden. Der Latnjajaure war immer homotherm, der Erken zeitweise schwach geschichtet. Das Material

[1] Mitteilung II des Latnjajaureprojektes.

wurde in Kühlverpackung nach Uppsala geschafft und die Versuche in den Konstanträumen des Limnologischen Instituts ausgeführt.

Zur Feststellung der Abhängigkeit der Dauer der Embryonalentwicklung von der Temperatur oder genau gesagt, der Zeit von der Eiablage bis zum Schlüpfen, sind zwei Methoden gebräuchlich. Die erste (1) wurde hauptsächlich von ELSTER (1954), EICHHORN (1957) und ECKSTEIN (1964) für verschiedene calanoide Copepoden verwandt. Sie geht davon aus, dass man frisch gelegte Eier oder Weibchen mit frisch gelegten Eiern isoliert und bis zum Schlüpfen in konstanter Temperatur unter Beobachtung hält.

Der Vorteil dieser Methode ist, dass man die Entwicklungs*dauer* des einzelnen Eies beziehungsweise das Zeitinterwall zwischen dem zuerst und dem zuletzt geschlüpften Ei eines Eipakets sehr genau bestimmen kann. Auch braucht man die Eier nicht von den Muttertieren zu trennen und kann so weitgehend natürliche Bedingungen beibehalten. Der Nachteil der Methode ist, dass man mit zahlreichen Parallelversuchen arbeiten muss, um individuelle Abweichungen zu erfassen und um sich gegen Verluste zu sichern. Man muss eine grössere Anzahl reifer Weibchen unter ständiger Kontrolle haben, um sie zu isolieren sobald die Eier ausgetreten sind, und da es schwer ist, gleichzeitig eine grössere Anzahl genau gleich alter beziehungsweise gleich frischer Eier zu erhalten, müssen die Versuche zu verschiedenen Zeitpunkten gestartet werden.

Die zweite Methode (2) ist von EDMONDSON (1965) vorgeschlagen worden, der sie selbst für Planktonrotatorien benutzt hat. Diese Methode geht davon aus, dass eine in Vermehrung befindliche Population Eier aller Entwicklungsstadien enthält und dass kontinuierlich neue Eier produziert werden. Eine grosse Anzahl Eier beziehungsweise Eipakete werden — unabhängig vom Entwicklungszustand — von den Weibchen isoliert und in konstanter Temperatur gehalten. Die Anzahl geschlüpfter Eier wird mit kurzen Zeitintervallen festgestellt. Auf diese Weise kann die Entwicklungs*geschwindigkeit* der Eier in einem gemischten Material ungeachtet das Alter der einzelnen Eier festgestellt werden. Die Entwicklungsdauer lässt sich dann am einfachsten graphisch ermitteln indem man die Anzahl ungeschlüpfter Eier zu verschiedenen Zeitpunkten gegen die Zeit aufträgt. Wo die durch diese Punkte gelegte Mittellinie die Zeitachse schneidet ist der Schlüpfzeitpunkt für das Ei, das theoretisch gerade bei Versuchsbeginn gelegt worden war. Die Methode erlaubt also ein Arbeiten mit einem aus Versuchsgesichtspunkt einheitlichen Material und verlangt weder lange Vorbereitungen noch weitläufige Versuchsanordningen. Ausserdem sind statistisch gut gesicherte Mittelwerte zu erwarten. Der Nachteil ist hauptsächlich, dass die Kontrollzählungen sehr zeitraubend werden können, besonders wenn, wie im Falle der Cyclopoiden, zwei Eipaketen nur der Wert einer statistischen Einheit zukommt und also die Anzahl der beim Versuch verwandten Eier sehr gross sein muss. Ausserdem werden in einer sehr konzentrierten Probe leichter

ungünstige Kulturbedingungen geschaffen und das Risiko für Verluste wird grösser als bei Methode (1).

In der Hauptsache wurde hier Methode (2) verwandt, weil sie einfacher in der Ausführung ist. Es zeigte sich aber bald, dass bei *Cyclops scutifer* die Voraussetzung kontinuierlicher Eiproduktion nicht befriedigend erfüllt war, weshalb ergänzende Versuche nach Methode (1) notwendig waren. Bei 14° wurde mit dieser Art ausschliesslich nach Methode (1), bei 20° nach beiden Methoden gearbeitet. Die Versuche nach Methode (2) wurden in folgender Weise ausgeführt. Eier von ca. 80 Weibchen, d.h. 800—1400 Stück, wurden in zwei Zählkammern verteilt, die etwa zur Hälfte mit membranfiltriertem Wasser (Membranfilter Millipor HA 0,45 μ) gefüllt waren. Die Kammern bestanden aus Glasröhren von 36 mm Diameter und 100 mm Höhe und waren mit einem Boden aus Deckglas versehen. Sie waren oben mit Glasbechern abgedeckt, die Luftzirkulation zuliessen. Die Kontrollzählungen wurden mit dem UTERMÖHL-Mikroskop durchgeführt.

Versuchstemperaturen und Kontrolldichte pro Tag geht aus folgender Tabelle hervor:

Temp. °C	25	20	14	8	5	4,5	2
Mesocyclops leuckarti	6	2	2	2	—	$1-\frac{1}{2}$	$1-\frac{1}{3}$
Cyclops scutifer	—	1—5	1	1—2	1—2	—	$\frac{1}{2}-\frac{1}{3}$

Die notwendige Kontrolldichte wurde anhand einiger orientierenden Versuche ermittelt. Bei Methode (1) können die Intervalle zu Versuchsbeginn natürlich länger sein und müssen kürzer werden, wenn das Schlüpfen einsetzt.

Bei jeder Kontrolle wurden die Anzahlen geschlüpfter, ungeschlüpfter und eindeutig abgestorbener Eier festgestellt. Auch tote Nauplien und Nauplienhäute wurden gezählt, soweit sie auftraten.

Bei den Versuchen nach Methode (1) wurden eilose Tiere in Aquarien mit Naturwasser und Zusatz verschiedener Algennahrung gehalten und sobald Eier gebildet wurden, wurden diese isoliert und weiter behandelt wie oben beschrieben. Um die Eignung verschiedener Algen als Nahrung zu testen, wurden ausser den Aquarien eine Anzahl Proberöhrchen mit membranfiltriertem Seewasser mit je ca. 30 Tieren bestückt. Die Tiere wurden mit *Chlamydomonas, Cryptomonas* oder *Chromulina* aus Reinkulturen gefüttert. Ausserdem wurden Tiere in Naturwasser mit reichlichem Chrysomonadenplankton und in membranfiltriertem Wasser ohne Futterzusatz gehalten. Alle diese Versuche beziehen sich nur auf *Cyclops scutifer*.

In den meisten Versuchsröhrchen begann die Eiproduktion nach ungefähr einer Woche, wurde aber nirgends besonders gross. Deutliche Unterschiede waren indessen festzustellen. Die beste Nahrung war offenbar das natürliche Chrysomonadenplankton. Die nächstbeste Eiproduktion erzielte *Cryptomo-*

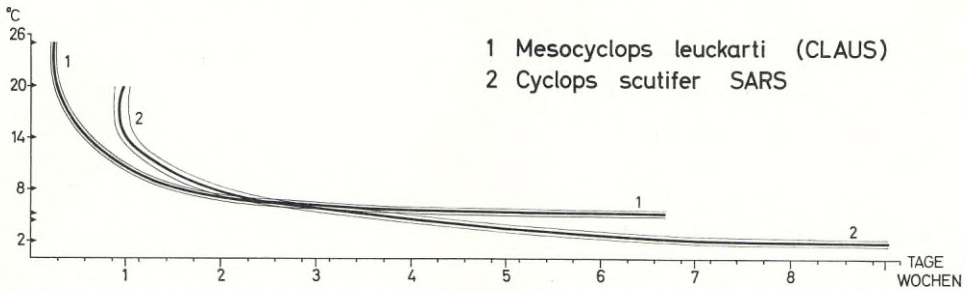

Abb. 1. Die Geschwindigkeit der Embryonalentwicklung von *Cyclops scutifer* SARS und *Mesocyclops leuckarti* (CLAUS) in Abhängigkeit von der Temperatur.

nas, jedoch starben hier die Tiere am schnellsten. Als schlechteste Nahrung erwies sich *Chlamydomonas.* In membranfiltriertem Wasser wurden nur in Einzelfällen kümmerliche Eipakete gebildet. Die Sterblichkeit der im Labor gelegten Eier war höher als die der in der Natur produzierten.

Resultate

a) Die Entwicklungsgeschwindigkeit der Eier

In Abb. 1 sind die Versuchsresultate zusammengeführt zu Kurven, die die Entwicklungsgeschwindigkeit der Eier der beiden untersuchten *Cyclops*-Arten in Abhängigkeit von der Temperatur erkennen lassen.

Am auffälligsten ist, dass *Mesocyclops leuckarti* bei höheren Temperaturen eine viel schnellere Embryonalentwicklung zeigt als *Cyclops scutifer,* dessen Entwicklung zwischen 15° und 20° zwei- bis viermal länger dauert, aber dass sich die Kurven der beiden Arten bei etwa 6° überschneiden, worunter sich die Eier von *Cyclops scutifer* schneller entwickeln als die von *Mesocyclops leuckarti.* In der Nähe von 5° geht die Kurve für *Mesocyclops leuckarti* asymptotisch nach unendlich, und die Entwicklung hört praktisch auf, während dasselbe für *Cyclops scutifer* erst unter 2° eintritt.

Tatsächlich handelt es sich jedenfalls bei *Mesocyclops leuckarti* nicht nur um eine Verzögerung der Entwicklungszeit. Rücksetzversuche zeigten, dass einmal auf unter 5° abgekühlten Eier in höheren Temperaturen nicht mehr entwicklungsfähig sondern abgetötet waren.

Nachdem die Kurven in Abb. 1 keine Exponentialfunktionen sein können (wenn auch ihre mittleren Abschnitte annährend solchen folgen mögen), sondern Optimumkurven sein müssen, ist eine Verlangsamung der Entwicklungsgeschwindigkeit auch oberhalb einer optimalen Temperatur bis zu einem für die Art noch erträglichen Temperaturmaximum zu erwarten. In der Praxis scheint die mit höheren Temperaturen stark ansteigende Mortalität der Eier die Grenze der Entwicklungsmöglichkeit in der Regel bereits im Bereich des Temperaturoptimums zu setzen, das heisst, die Entwicklungs-

geschwindigkeit nimmt zu solange noch lebende Eier vorhanden sind. Nur für *Arctodiaptomus salinus* (DADEY) ist bisher einer erneute Verminderung der Entwicklungsgeschwindigkeit bei hohen Temperaturen nachgewiesen worden (ELSTER et al. 1961). Die für *Cyclops scutifer* bei 14° und 20° praktisch identischen Entwicklungszeiten entsprechen auf jeden Fall einer relativen Verlangsamung der Entwicklung im Verhältnis zur höheren Temperatur. Die Form der Kurve macht aber ein Optimum bei etwa 17°—18° wahrscheinlich.

Unsere Resultate bestätigen also *Mesocyclops leuckarti* als Warmwasserform: Die Eier der Art entwickeln sich noch gut bei Temperaturen, die in europäischen Naturwässern nicht mehr vorkommen, sondern typisch werden für subtropsche und tropische Verhältnisse, unten denen *Mesocyclops leuckarti* ja auch überall anzutreffen ist. Das Optimum für die Eientwicklung dürfte über 25° liegen und das Maximum kann sehr wohl noch über 30° liegen. Dagegen können die Eier sich auch bei nur mässig niederen Temperaturen nicht mehr entwickeln, auch dies ein Umstand der *Mesocyclops leuckarti* in wärmere Milieus zwingt. (In temperierten Seen wird die kalte Jahreszeit bekanntlich mit Hilfe der Diapause überbrückt.)

Unsicherer wird man jedoch über die allgemein übliche Charakterisierung von *Cyclops scutifer* als typische Kaltwasserform. Zwar hat die Art die Fähigkeit, sich noch bei sehr niederen Temperaturen zu entwickeln und kann sich deshalb in kalten Gewässern halten. Auch liegt das Temperaturoptimum für die Eier eindeutig niederer als bei *Mesocyclops leuckarti,* aber es liegt doch weit höher als die Durchschnittemperatur, ja sogar höher als die Maximaltemperatur in vielen Biotopen, wo *Cyclops scutifer* anzutreffen ist.

Man muss den Schluss ziehen, dass *Cyclops scutifer* in wärmeren Biotopen einfach auf die Dauer nicht mit Arten konkurrieren kann, die die Fähigkeit schnellerer Entwicklung haben. Durchschnittstemperatur und Nahrungsstandard pflegen im grossen und ganzen parallel zu gehen: je wärmer das Wasser, desto nahrungsreicher ist es in der Regel, und steigende Temperatur bedeutet fast immer auch steigendes Nahrungsangebot. Die Art, die ein kommendes Nahrungsangebot ausnutzen kann, indem sie bei steigender Temperatur schnell eine grosse Population bildet, hat also die beste Chance, warme (und damit normalerweise nahrungsreiche, eutrophe) Biotope zu besiedeln und langsamere Arten auszukonkurrieren solange keine anderen Faktoren begrenzend werden. Umgekehrt ist diejenige Art im kalten (und damit praktisch immer nahrungsarmen, oligotrophen) Wasser besser daran, die sich nicht von kurzfristigen Temperaturanstiegen zu Massenentwicklungen „verleiten" lässt, weil diesen Temperaturanstiegen keine nennenswerte Steigerung des Nahrungsangebotes zu folgen pflegt. Eine Art, die unter diesen Verhältnissen unmittelbar mit Massenreproduktion reagierte, würde bald stark verschlechterte Lebensbedingungen gegenüberstehen und müsste verhungern aufgrund der Konkurrenz die sie sich selbst geschaffen hat.

Wiederholt sich dieser Vorgang ein paarmal, so muss die Art ganz aus dem Biotop verschwinden, weil keine Tiere mehr erwachsenes Stadium erreichen können.

Cyclops scutifer muss also nicht deshalb als Kaltwasserart betrachtet werden, weil er kalte Biotope vorzöge, sondern weil er aufgrund seiner langsamen Entwicklung in wärmeren und auch für ihn günstigeren Milieus nicht konkurrieren kann. Aber gerade die langsame Entwicklung wird in den kalten Biotopen zum Vorteil.

b) Die Entwicklungsdauer des ersten Naupliusstadiums

Es ist leicht, bei den Versuchen die auftretenden Nauplienhäute zu zählen, ebenso die gestorbenen Nauplien. Der Abstand zwischen den zuerst geschlüpften Eiern und dem ersten Auftreten von Nauplienhäuten kann als zuverlässiges Mass für die Lebenslänge des ersten Naupliusstadium in der betreffenden Temperatur gelten. Die Anzahl der toten Nauplien im Verhältnis zu den geschlüpften Eiern kann als Mass für das Wohlbefinden der Art unter den Versuchsbedingungen im allgemeinen und bei der betreffenden Temperatur im besonderen betrachtet werden.

Die folgende Tabelle gibt die Abstände zwischen Schlüpfen und erstem Wechsel der Nauplienhaut in Stunden.

	Mesocyclops leuckarti	*Cyclops scutifer*
25°C	34—39	—
20°C	49—53	(60—97)
14°C	83—91	72—73
8°C	> 290	195
5°C	—	?
2°C	—	?

Bei *Mesocyclops leuckarti* traten bei 8° während der Versuchszeit keine Nauplienhäute mehr auf, obwohl die Nauplien reichlich und die Mortalität gering waren. Die Dauer des ersten Nauplienstadiums muss also die Versuchszeit von 290 Stunden überschreiten. Ebenso waren bei *Cyclops scutifer* bei 5° und 2° die Versuchszeiten, die nur bis zum Schlüpfen der letzten Eier liefen, offenbar viel zu kurz als dass das zweite Nauplienstadium hätte erreicht werden können.

Bei *Cyclops scutifer* war es bei 20° aufgrund hoher Nauplliensterblichkeit schwer, exakt zu beurteilen, welche Eierschalen mit welchen Nauplienhäuten zusammengehörten. Man darf jedoch annehmen, dass die gegenüber 14° verlängerte Zeit, ebenso wie im Falle der Eientwicklung, als Folge der verschlechterten Lebensbedingungen bei der höheren Temperatur für *Cyclops scutifer* bewertet werden muss.

Die höchste Schlüpffrequenz war für *Cyclops scutifer* bei 8°, für *Mesocy-*

clops leuckarti bei 20° festzustellen. Auffällig war die bei *Cyclops scutifer* durchweg höhere Nauplliensterblichkeit. Sie betrug im Durchschnitt ca. 70 % der geschlüpften Individen gegenüber nur ca. 30 % bei *Mesocyclops leuckarti,* was auf allgemein grössere Empfindlichkeit des *Cyclops scutifer* schliessen lässt.

Interessant ist schliesslich die Feststellung, dass die Entwicklung der Nauplien bei *Cyclops scutifer* bereits bei 14° schneller geht als bei *Mesocyclops leuckarti.* Der Quotient der Entwicklungsdauern Eier: Nauplien-I ist bei *Mesocyclops leuckarti* durchweg kleiner als bei *Cyclops scutifer,* wächst aber mit sinkender Temperatur, während er bei *Cyclops scutifer* kleiner wird. Diese Befunde sind einstweilen zu kompliziert um im Sinne oder im Gegensatz zu der oben ausgesprochenen Theorie gedeutet werden zu können. Es bleibt abzuwarten, was die Untersuchungen über die Entwicklung der späteren Stadien ergeben werden.

Diskussion

Die Abhängigkeit der Embryonalentwicklung von der Temperatur ist in jüngerer Zeit bei einer Anzahl calanoiden Copepoden untersucht worden, zum Beispiel bei *Eudiaptomus gracilis* SARS durch ELSTER (1954) und ECKSTEIN (1964), *Eudiaptomus graciloides* (LILLJ.) durch NAUWERCK (1963), *Acanthodiaptomus denticornis* WIERZ. und *Mixodiaptomus laciniatus* (LILLJ.) durch EICHHORN (1957) sowie *Arctodiaptomus salinus* (DADEY) durch ELSTER et al. (1961). Über cyclopide Copepoden liegen nur einige älteren Arbeiten vor, nämlich von WALTER (1922) betreffend *Megacyclops viridis* (JURINE) und von ZIEGELMAYER (1925) betreffend *Macrocyclops fuscus* (JURINE).

Vergleichen wir unsere Resultate mit Resultaten betreffend andere Cyclopiden, so ist der auffälligste Unterschied die kürzere Entwicklungszeit bei niederen Temperaturen bei den früher untersuchten, freilich nicht-planktischen Cyclops-Arten. Die vollständigsten Angaben macht WALTER, in ihrem Fall soll die Entwicklungsdauer der Eier von *Megacyclops viridis* bei 1°C nur 15 Tage betragen. Auch ZIEGELMAYERS Ergebnisse deuten ähnlich kurze Zeiten bei niederen Temperaturen an. Nachdem keiner der genannten Verfasser nähere Angaben über seine Methode macht, insbesondere nicht darüber, wie die Temperaturen verwirklicht und beibehalten wurden (das Wort Thermostat wird nicht genannt), und nachdem die Temperaturen ausserdem als „Durchschnitt" angegeben werden, kann man sich fragen, ob die schnelle Entwicklung nicht zum Teil auf Temperaturänderungen während der Versuchszeit beruht. Da die Kurven keine Exponentialfunktionen sind, wird die Entwicklung auch nicht proportional der Temperatur beeinflusst. Zudem ist es möglich, dass schon die Änderungen selbst einen anderen Effekt erzeugen als die Summe der Effekte jeder einzelnen durchlaufenen Temperatur.

Will man indessen den Werten der älteren Verfasser Glauben schenken,

so können diese ein interessantes Beispiel darstellen für die Anpassung der Teicharten an ihr spezielles Milieu im Gegensatz zu pelagischen Arten. In Teichen pflegt das Nahrungsangebot auch unter der kalten Jahreszeit reichlich zu sein, umso mehr als diese Teicharten sich gerne am Boden oder im Litoral aufhalten, sodass eine schnelle Entwicklung hier immer ein Vorteil ist.

Bessere Übereinstimmung finden wir zwischen unseren pelagischen Cyclopiden und den pelagischen calanoiden Copepoden. Die Eier unserer Cyclopiden zeigen jedoch entschieden langsamere Entwicklungsgeschwindigkeit bei niederen Temperaturen als die der calanoiden Arten. Bei den hohen Temperaturen dagegen liegen überhaupt alle untersuchten Arten einander sehr nahe, bei 20° ist die Zeit für alle ausser Cyclops scutifer etwa 2 Tage.

Acanthodiaptomus denticornis und *Mixodiaptomus laciniatus* entsprechen in ihren Milieuansprüchen etwas besser *Cyclops scutifer,* sie sind monozyklisch und bewohnen hauptsächlich oligotrophe und kalte Gewässer. *Eudiaptomus gracilis* und *Eudiaptomus graciloides* entsprechen mehr *Mesocyclops leuckarti,* sie sind polyzyklisch und kommen in mehr eutrophen Gewässern vor. Auch die Embryonalentwicklung der jeweiligen Arten zeigt Entsprechungen: sie verläuft bei niederen Temperaturen verhältnismässig schneller bei den Kaltwasserformen als bei den Warmwasserformen.

NAUWERCK (1963 p. 65) nennt *Mesocyclops leuckarti* im See Erken monozyklisch. In seiner Abb. 34 findet man mindesten zwei ausgeprägte Maxima für eitragende Weibchen. Vergleicht man mit den aktuellen Temperaturen und rechnet mit den zugehörigen Entwicklungszeiten der Eier, so scheint es sehr wahrscheinlich, dass die Art mehr als einen Zyklus pro Sommer vollenden kann.

Was schliesslich *Cyclops scutifer* im Latnjajaure betrifft, so erneuert sich die Population sicher weniger als einmal im Jahr. Der See ist während 2—3 Monaten eisfrei und seine Maximaltemperatur überstieg im Sommer 1965 kaum 5°C. Die Eiproduktion im See fiel in die Zeit vom 10—20. August und die Nauplien schlüpften also Anfang September. Es ist ganz unwahrscheinlich, dass sie noch im gleichen Jahr über das Copepoditenstadium hinaus kamen und es ist nicht ausgeschlossen, dass die zuletzt geschlüpften Nauplien es nicht einmal im folgenden Jahr taten, womit die Voraussetzungen für eine „Fraktionierung" bereits gegeben wären. Tatsächlich hat ELGMORK (1965) mehrjährige Zyklen bei *Cyclops scutifer* bereits festgestellt.

Zusammenfassung

1. Die Abhängigkeit der Geschwindigkeit der Embryonalentwicklung von der Temperatur wurde untersucht bei *Cyclops scutifer* SARS aus dem See Latnjajaure in Schwedisch-Lappland und bei *Mesocyclops leuckarti* (CLAUS) aus dem See Erken in Roslagen, Mittelschweden.

2. Zwei Methoden wurden verwendet. Bei Methode (1) werden frisch gelegte Eier bis zum Schlüpfen unter Kontrolle gehalten, bei Methode (2) wird bei einer grossen Anzahl Eier verschiedenen Alters mit kurzen Zeitabständen der Schlüpfprozent kontrolliert. Mit Methode (1) erhält man die Entwicklungszeit direkt, mit Methode (2) erhält man die Entwicklungsgeschwindigkeit, mit deren Hilfe die Entwicklungszeit ermittelt werden kann. Methode (1) ist sicherer aber mehr langwierig, Methode (2) ist einfacher aber setzt voraus, dass das Eimaterial aus einer gleichmässigen Mischung aller Entwicklungsstadien besteht.

3. Die Versuche wurden bei konstanter Temperatur durchgeführt und zwar mit *Cyclops scutifer* bei 2°, 5°, 8°, 14° und 20°, wovon bei 14° ausschliesslich und bei 20° teilweise nach Methode (1), im übrigen nach Methode (2) mit *Mesocyclops leuckarti* bei 2°, 4,5°, 8°, 14°, 20° und 25° und ausschliesslich nach Methode (2).

4. Der Temperaturbereich für die höchste Schlüpffrequenz lag für *Cyclops scutifer* bei 8°, für *Mesocyclops leuckarti* bei 20°. Die Minimumtemperatur für die Embryonalentwicklung lag für *Cyclops scutifer* unter 2°, für *Mesocyclops leuckarti* über 4,5°. Die Optimaltemperatur für die Entwicklungsgeschwindigkeit lag für *Cyclops scutifer* zwischen 14° und 20°, für *Mesocyclops leuckarti* über 25°. Die Maximumtemperatur konnte für keine der beiden Arten festgestellt werden. Von den geschlüpften Nauplien starben durchschnittlich während der Versuche bei *Cyclops scutifer* ca. 70 %, bei *Mesocyclops leuckarti* ca. 30 %.

5. Oberhalb ca. 6° ist die Entwicklungsgeschwindigkeit zunehmend grösser bei *Mesocyclops leuckarti,* unterhalb dieser Temperatur bei *Cyclops scutifer.* Dieses Resultat wird als Konkurrenzvorteil für *Cyclops scutifer* in kalten und nahrungsarmen und für *Mesocyclops leuckarti* in warmen und nahrungsreichen Gewässern gedeutet.

6. Ein Literaturvergleich zeigt, dass die Temperaturabhängigkeit der Embryonalentwicklung bei *Cyclops scutifer* und *Mesocyclops leuckarti* in besserer Übereinstimmung mit derjenigen von pelagischen Calanoiden als mit cyclopiden Teich- und Litoralformen steht.

Summary

1. The speed of the embryonic development in relation to temperature was studied in *Cyclops scutifer* SARS from Lake Latnjajaure in Swedish Lappland and *Mesocyclops leuckarti* (CLAUS) from Lake Erken in Central Sweden.

2. Two methods were used. In method (1) new laid eggs are kept under observation until hatching, in method (2) the hatching percent of a large number of eggs of different ages is recorded with short intervals. Method (1) gives the development time direct, method (2) gives the development speed with the help of which the development time can be calculated. Me-

thod (1) is more reliable but also more time-consuming, method (2) is more simple but presupposes a homogenous material of eggs at all stages of development.

3. The experiments were made at constant temperatures, for *Cyclops scutifer* at 2°C, 5°C, 8°C, 14°C and 20°C; at 14°C exclusively with method (1), at 20°C with both methods and at the other temperatures with method (2). With *Mesocyclops leuckarti* the experiments were made at 2°C, 4.5°C, 8°C, 14°C, 20°C and 25°C and all with method (2).

4. The highest hatching frequency was recorded for *Cyclops scutifer* at 8°C and for *Mesocyclops leuckarti* at 20°C. Minimum temperature for possible development must be less than 2°C for *Cyclops scutifer* and more than 4.5°C for *Mesocyclops leuckarti*. The optimal temperature (at which development was most rapid) was between 14°C and 20°C for *Cyclops scutifer* and more than 25°C for *Mesocyclops leuckarti*. The maximum temperature for possible development could not be confirmed. The nauplius mortality under the experimental conditions was on the average about 70 per cent for *Cyclops scutifer* and about 30 per cent for *Mesocyclops leuckarti*.

5. Above 6°C development speed progressively becomes higher for *Mesocyclops leuckarti* and below this temperature for *Cyclops scutifer*. This result is interpreted as a competitive advantage for *Cyclops scutifer* in cold and oligotrophic waters and for *Mesocyclops leuckarti* in warm and eutrophic waters.

6. A comparison with the literature shows that temperature dependency of the embryonic development of *Cyclops scutifer* and *Mesocyclops leuckarti* is in better agreement with that of pelagic calanoids than with that of small-water or litoral cyclopoids.

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On the fauna in the lower reaches of River Viskan, southern Sweden

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The River Viskan is situated in the south-western part of Sweden and discharges its water into the Kattegatt. The drainage area covers about 2,200 km^2. Over a period of 55 years (1909—1963) the normal high water flow has been calculated to be 150 m^3/sec, normal medium water flow to be 33 m^3/sec, and normal low water flow to be 4 · 6m^3/sec. (Reports from SMHI, Stockholm).

Physico-chemical data for the river water are given in Table 1. The influence of sewage and other waste products from communities and industries is, amongst others, reflected in the high and variable values for biochemical oxygen demand, B.O.D., and for the content of suspended substances and bacteria in the water.

Periodically there occurs an inflow of sea-water giving the lower part of the river the character of an estuarine habitat (Stations 105—108) (Table 2). Above station 109 there is no influence from seawater because of the waterfall. Station 110 is thus only under the influence of fresh water.

The bottoms at the river-mouth are relatively rich in organogenic material, including coarse detritus. In the remaining portions of the region fairly thick deposits of fine sediment occur, mainly along the shores. The bottom of the river cutting is flat and is dominated by sand and stones embedded in more finegrained sediments. The comparatively restricted distribution of the aquatic vegetation can be ascribed to several factors such as the low transparency of the water, the steep slope of the shore, and the unstable conditions in the surface layer of the bottoms within the central parts of the river bed.

The examination of the bottom, carried out in June 1965, yielded, in addition to qualitative samples, 42 quantitative bottom samples distributed over the five stations 105, 106, 107, 108 and 110. The bottom sampler was of the Ekman-Birge type, the mesh of the sieve being 0.6 mm.

The bottom fauna

Quantity. The average abundance of bottom animals can be calculated to be 5,558 ind/m^2, and the average weight to be 14 · 3 g/m^2.

Table 1. River Viskan. Physico-chemical data at station 110. (Analyses by VATTENBYGGNADSBYRÅN, Stockholm.)

	13.6.61—15.2.62			8.9—15.9.65			21.4—28.4.66		
Temperature, °C				13			7		
Water flow, m^3/sec				15			38		
	4 samples			85 samples			85 samples		
	max.	med.	min.	max.	med.	min.	max.	med.	min.
Transparency, cm.	120	95	85						
pH				7.3	7.1	6.8	6.5	6.2	5.7
Conductivity, $\varkappa \cdot 10^6$	176	125	93	188	136	92	110	101	89
Turbidity, ZP	650	410	260	354	255	116	300	197	144
$KMnO_4$, mg/l	57	50	40	77	46	32	59	41	27
O_2, mg/l	13.9	10.8	8.3	9.2	8.7	8.1	12.2	11.5	11.0
O_2, %	101	92	81	91	83	76	101	95	90
B.O.D., mg/l	6.4	3.9	3.0	6.1	3.5	1.7	6.0	3.0	1.8
Coli, 37° ind/ml	30.000	3.700	200						
Coli, 45° ind/ml	20.000	1.200	40						

The distribution of the fauna differs both from one station to another, and within each station as a function of depth and type of sediment.

The quantitative differences between station 110 and the remaining stations (105—108) suggest that the examined part of the river may be clearly divided into two portions, viz. above and below the waterfall at Ås (Table 3). Apart from the periodical occurrence of brackish water below the waterfall, the environment in the two portions does not differ decisively. The small quantity of bottom animals below the waterfall can thus be interpreted mainly as an estuarine feature.

Other variations in quantity can be attributed to the composition of the sediments.

With regard to the variation within the stations, regions close to the banks have a richer fauna than the flat central region at greater depth. Thus the density of the fauna increases with an increasing content of organogenic material in the sediments (Table 4).

Table 2. Salinity, per mille.

Station	depth, m	20/6	10/8	6/9	4/10	10/11
105	0	—	< 0.1	0.91	< 0.1	< 0.1
	1.5	—	< 0.1	2.54	< 0.1	< 0.1
	3	—	< 0.1	11.61	< 0.1	0.1
106	0	0.37	< 0.1	0.44	< 0.1	< 0.1
	2	11.32	< 0.1	1.13	< 0.1	< 0.1
	4	13.62	< 0.1	7.09	< 0.1	< 0.1
108	0	—	< 0.1	< 0.1	< 0.1	< 0.1
	2	—	< 0.1	< 0.1	< 0.1	< 0.1
	3.5	—	< 0.1	< 0.1	< 0.1	< 0.1

Table 3. The variation in abundance and biomass of bottom animals between the stations.

	105	106	107	108	105–108	110
Abundance, ind/m²						
maximum	—	—	—	—	17,644	27,896
medium	6,437	3,458	3,933	2,810	4,157	9,361
minimum	—	—	—	—	132	2,332
Biomass, g/m²						
maximum	—	—	—	—	13.4	143.7
medium	10.5	8.3	6.5	8.9	8.6	37.0
minimum	—	—	—	—	0.1	2.1

This tendency towards greater abundance and biomass in connection with higher contents of organogenic material in the sediments is obvious also from comparisons between different stations. Within the estaurine portion the region of the mouth is richer than the remaining areae (Table 3).

These greater quantities of bottom animals in the river mouth are, however, not exclusively due to the accumulation of detritus in the bottoms, but are also partly caused by an invasion of organisms from neighbouring areas of the mixohaline Klosterfjorden Bay. At the time of sampling the brackish water organisms made up 16 per cent of the fauna at station 105 and 25 per cent at station 106 (Table 5). This invasion is presumably mainly of a passive type, i.e. the proportion of the brackish water organisms may vary with the direction of the currents.

Quality. The qualitative composition of the fauna can be seen in Table 5 which gives the percentage of the total number of individuals for every main group.

The oligochaetes, forming 95 per cent of the annelids, are the most important group at all stations. The dominance of the oligochaetes is one of the reasons for the correlation which exists between quantity of fauna and type of sediment.

The majority of the remaining bottom animals are forms bound to the sediment. A pronounced rheophil fauna, living on the drift, is poorly

Table 4. The variation in abundance and biomass of bottom animals within the stations.

	Abundance, ind./m²		Biomass, g./m²	
	105–108	110	105–108	110
shore regions	5.265	11.681	10.3	48.8
central regions	1.848	2.389	2.7	2.3

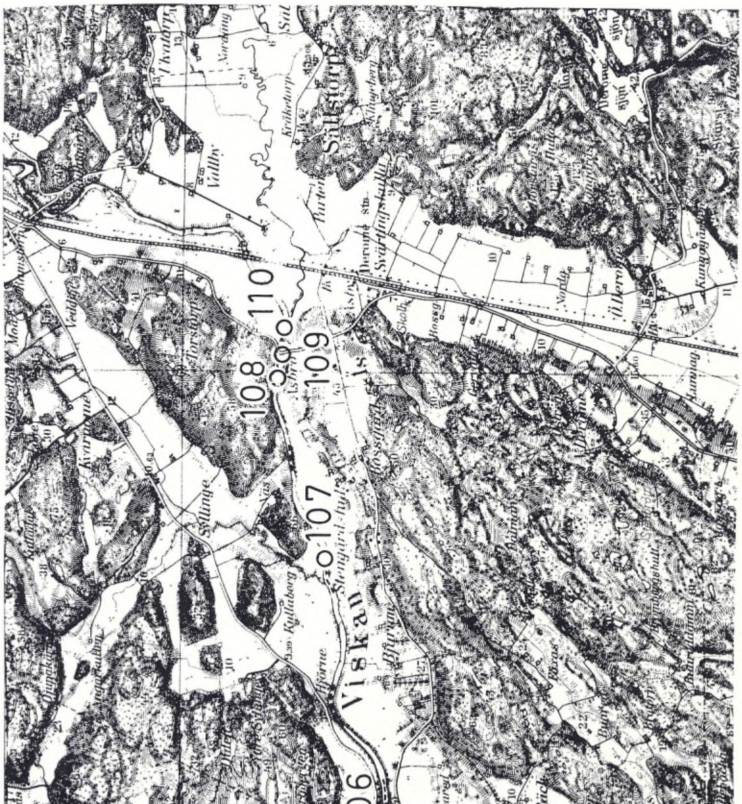
105
106
107
108
109
110
Viskan
Klosterfjorden
Värö
Sällstorp
Åsklosters st.
Väröbacka st.

Table 5. The relative abundance of various groups of bottom animals calculated as percentage of the total number of animals.

	105	106	107	108	110
Brackish water organisms:					
Crustacea	15	23	—	—	—
Polychaeta	1	2	—	—	—
Gastropoda	<1	—	—	—	—
Freshwater organisms:					
Crustacea	<1	7	5	15	17
Insecta	23	3	17	25	7
Mollusca	<1	—	3	5	4
Annelida	60	65	75	54	71
Remaining org.	<1	<1	—	<1	1

developed throughout the entire region, even in the stretch of rapids near Ås (Station 109).

The insect fauna is dominated by chironomids (98 per cent). The variations between stations are influenced by the periods for emergence and deposition of eggs of the different species; these are still unknown for the region in question. Nevertheless the small number of larger insect larvae is remarkable.

The results suggest a dominance of species within the *Chironomini,* mainly *Polypedilum nubeculosum* MEIG., in the region of the mouth; upstream these species decrease and are replaced mainly by the *Tanytarsini* above the waterfall. *Rheotanytarsus,* typical in localities with running water, has only been observed on rocks in the rapids at Ås (Station 109). Among larger insects *Leptocerus aterrimus* STEPH. (*Trichoptera*), *Ischnura* sp. and *Colymbetes* sp. can be mentioned.

The density of most of the other fresh-water organisms tends to decrease towards the river mouth (Tab. 6).

Among the hirudineans *Herpobdella octocullata* L. and *Helobdella stagnalis* L. are found at most of the stations, while *Glossosiphonia complanata* L. and *Pisicola geometra* L. were only encountered at station 110.

Table 6. The abundance of different groups of bottom animals at the various stations.

	105	106	107	108	110
Oligochaeta	3,834	2,218	2,856	1,455	5,676
Hirudinaea	—	17	50	63	902
Chironomidae	1,455	26	688	680	616
remain. *Insecta*	19	16	—	13	17
Pisidae	25	—	71	132	413
Gastropoda	22	—	44	19	22
Asellus aquat.	22	255	55	69	501
Cladoc.+Copepod.	9	18	160	358	1,133

The lamellibranchs, mainly pisids, become gradually rarer towards the river mouth. *Anodonta* occur only above the waterfall.

Gastropods are not numerous at any of the stations. *Bithynia tentaculata* L., *Bathyomphalus contortus* L., and *Acroloxus lacustris* L. occur as far down as the region of the mouth, where the material also contains an occasional specimen of the brackish water snail *Hydrobia ventrosa* MONT. *Lymnea peregra* MÜLL., *Planorbarius corneus* L., and *Hippeutis complanatus* L. seem to be restricted to the upper reaches of the river.

Crustaceans form an important element of the fauna, both in the mouth and in the uppermost portions of the river. *Gammarus oceanicus* SEGERSTRÅLE and *Neomysis vulgaris* THOMPS. are dominant brackish water organisms in the region of the mouth and are also numerous in Klosterfjorden. The remaining crustaceans belong to the fresh-water fauna. *Asellus aquaticus* L. occurs most abundantly at station 110 and appears with variable abundance in the other parts of the region. The cladoceres and copepodes are also most abundant above the waterfall and become gradually less numerous towards the mouth. Among important species *Eurycercus lamellatus* MÜLL., *Polyphemus pediculus* L., *Sida crystallina* MÜLL., and *Cyclops* sp. may be mentioned. Of these only *Eurycercus* and *Cyclops* occur below the waterfall.

Among the other components of the bottom fauna turbellarians, hydracarines, nematodes, hydras and bryozoans are represented only by isolated specimens, except above the waterfall at Ås.

The estuarine region forms an unstable transition area between brackish water and fresh water with the result that the fauna is impoverished both quantitatively and qualitatively.

Changes in the composition of the fauna are closely correlated with the quality of the water and its speed of flow. During times of strong discharge, detritus from the bottom of the river is transported into Klosterfjorden, leaving a minerogenic character in parts of the river bottom. Occasional inflows of brackish water occur during the remaining parts of the year, while at the same time some of the great amount of suspended material tends to sediment.

The composition of the fauna is thus principally influenced in three different ways:

1. The inflow of brackish water is accompanied by drifting in of brackish water organisms. These are free-swimming or otherwise mobile species which easily follow the currents and thus constitute an unstable element of the fauna.

2. All through the year a continuous down-drift of fresh water organisms takes place from the region above the waterfall at Ås. The composition of this living drift varies with the developmental rhythm of the different orga-

nisms; it gradually thins out towards the mouth since the facultative freshwater organisms cannot survive the periods when the water becomes brackish.

3. The typical characteristics of running water are modified by the turbidity of the water, by periods with increased sedimentation, and by the penetration of brackish water counteracting the establishment of a rheophile fauna and favouring the faunal elements that depend upon the sedimented material. This accounts for the correlation between the type of sediment and the quantity and quality of the fauna.

The variation in salinity from the mouth to the waterfall provides a transition region for migrating fish. This portion of the river presumably only constitutes a region for the dwelling and feeding of a stationary fish fauna, e.g. perch, to a minor extent.

Furthermore, the composition of the bottom fauna, which is of great importance for the production of fish, seems to be rather unfavourable in this region. The density of individuals is low. In the Hammarfors reservoir in the River Indalsälven the abundance within the comparable depth zone of 2—3 metres is between 16,412 and 45,056 ind/m^2 for soft sediments (GRIMÅS and NILSSON 1965). For the River Bråån in Scania, BADCOCK (1954) established during June and July a density between 4,340 and 11,584 ind/m^2. This value applies, however, only to hard bottoms. For the Danish River Susaa BERG (1948) obtained an average density of bottom animals varying between 8,500 and 32,000 ind/m^2.

In River Viskan these conditions of abundance are approached only at station 110 which is constantly under the influence of fresh water. The other stations show a low abundance and the scarcity of benthic organisms is similar to that at the mouths of other rivers with estuarine character (cf. CASPERS, 1958).

The same conditions exist with regard to the biomass of bottom animals. Investigations by ALBRECHT (1953) make it possible to compare River Viskan with rivers in Central Europe. On the basis of the biomass of bottom animals, among other factors, these rivers are classified into ten main groups with regard to their capacity for fish production. According to ALBRECHT's grouping the portion of the River Viskan between stations 105 and 108 can be considered to be poor in food, with a low potential production of fish while the region above the waterfall is moderately rich in food.

These comparisons between quantities ought, amongst others, to be supplemented by qualitative considerations, since the ability of the fish to utilize the bottom animals is connected with their exposure and availability (ALLEN 1942, GRIMÅS 1963). The tendency in River Viskan towards a dominance of organisms living in the sediment reduces their availability for predation by fish and, consequently, also reduces the yield of fish. It appears probable

that this tendency is applicable in the same measure to the regions both above and below Ås.

It also appears probable that the factors which influence the appearance of the bottom fauna, e.g. the turbidity of the water, the increased amount of silt upon the mineral bottoms, and the vegetation cover of the rapids, influence the specific composition of the fish fauna in River Viskan directly by affecting conditions for fish that spawn and live in running water.

The region of the river above station 110

An examination of the bottom sediments has been carried out with special regard to stretches of currents and rapids, in order to determine the degree of the covering of the bottoms by sediments and vegetation. This examination covers 30 kilometres upstream station 110 and was carried out in July 1966.

In the stretches of pronounced rapids the rock bottoms are strongly overgrown with vegetation. Water mosses, mainly *Fontinalis antipyretica* HEDW. occur over most of the rock surfaces. At all stations and at all speeds of the current the vegetation contains a mass of included fine sediments which at the slighest touch render the water turbid. These fine sediments also occur in the bed of the river and thereby enclose the other minerogenic surfaces. Pure gravel and sand bottoms are very scarce, and never cover large areas. Those gravel regions discovered occupy areas of only a few square decimetres and appear immediately below barriers of rocks at the edge of the rapids, where the turbulence of the water is at a maximum. In this way the surfaces of gravel form a narrow band, interrupted by bigger rocks with vegetation, across the bed of the river.

There was no well-developed rheophile fauna at any station. The fauna is dominated by hirudineans and gastropods, i.e. the fraction of the running water fauna which is not living directly on drifting organogenic material. There were few animals taking in their food by filtration, such as larvae of simulids and of *Rheotanytarsus*. Also larvae of *Trichoptera* were few in numbers, probably because of the high content in the water of suspended material which quickly clogs the catching nets of the filtering species.

This seems to restrict the possibilities for salmon production in the main channel of the river. The rinsing of gravel surfaces characteristic of typical spawning places is reduced by the inclusion of more fine-grained sediments. Furthermore, the environment does not seem to be suitable for the development of the fry. Among other things, this is connected with the composition of the drift.

The fry of roach and eel occur abundantly in the river and also in the

rapids. A juvenile specimen of *Pleuronectes flexus* L. was found about 10 metres above the waterfall at Åsbro, roughly 8 km from the mouth of the river.

The stomach contents of roach fry meassuring 25—40 mm consist to a large extent of chironomids, mostly larvae, but also pupae and imagines. Hydracarines, terrestrial insects, and algae can also be recognized. Characteristic food animals for roach fry, such as small crustaceans, were not found in any stomach examined. The stomach of *Pleuronectes* contained 6 larvae of *Rheotanytarsus*.

In order to elucidate the qualitative and quantitative composition of the fish fauna in River Viskan, test fishing has been carried out to a limited extent in the stretch between Ås (station 110) and Kullagård (EDMAN 1964) (Table 7). Certain comparisons can be made with the results from test fishing in River Mörrumsån (LINDROTH 1965, LINDROTH and PERSSON 1966). Most of the fishing was done during September.

The differences in the population density between the rivers can be explained to some extent by differences in the methods used for the electrofishing.

Of greater interest are the differences in the quality of the fish fauna in the rivers in spite of the fact that the material from River Viskan is relatively small. The composition of the fish fauna depends largely upon the appearance of the testing station, the velocity of the water, etc. The velocity of the water in River Viskan on the occasion of the sampling was, however, noted as being considerable. On comparison of the three most important species of fish in the rivers it is therefore remarkable that 1) roach and eel occupy such a dominant position in River Viskan, while they were almost absent in the results from the more extensive fishing in River Mörrumsån, and 2) minnow and brown trout are both important species in River Mörrumsån, but almost absent in River Viskan. The results suggest that those portions of River Viskan examined are not very suitable for fish favoured by running water. There thus exists an interesting parallel between the qualitative compositions of bottom fauna and fish fauna.

Investigations into the behaviour of the fry of salmon and brown trout (KALLEBERG 1958) and their choice of food in running water (NILSSON 1957, SÖDERGREN and ÖSTERDAL 1965) indicate that they feed mainly on living drift and that their main food consists of larvae of *Ephemeroptera, Trichoptera* and *Plecoptera*. The share of these larvae in the bottom fauna of River Viskan is remarkably small. Organisms living in the sediment such as oligochaetes, larvae of chironomids, and lamellibranchs which constitute the main part of the bottom fauna in River Viskan contribute very little to the living drift. In this way the appearance of the bottoms and the quality

Table 7. The quantity and quality of the fish fauna of River Viskan and River Mörrumsån, according to electrofishing. (EDMAN 1964, LINDROTH 1965, LINDROTH & PERSSON 1966).

Abundance, ind./100 m²	River		
	Viskan 1964	Mörrum 1964	Mörrum 1965
Salmon	10	39	37
Brown trout	1	14	24
Eel	16	1	1
Percentual share in the total catches	39 eel 29 roach 23 salmon 4 bleak 2 brown trout 1 ide < 1 perch < 1 minnow	47 minnow 35 salmon 12 brown trout 3 bleak 1 eel 1 bull-head 1 gudgeon < 1 burbot < 1 pike < 1 lamprey	43 salmon 30 brown trout 19 minnow 3 bleak 1 lamprey 1 eel 1 crayfish < 1 gudgeon < 1 roach < 1 pike < 1 bull-head < 1 burbot

of the food seem to be factors contributing to the composition of the fish fauna and explain the great share of bottom-living fish like roach and eel.

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Summary

River Viskan, southern Sweden, is influenced by periodical inflow of brackish water, which gives the lower reaches the charachter of an estuarine habitat. The river is also influenced by waste products from communities and industries. The effect upon the bottom animal community is discussed. The properties of the bottoms and their fauna seem to be factors contributing to the qualitative composition of the fish fauna.

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Mortality in hatchery-reared *Salmo salar* L. after exercise

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Introduction

Hard muscular work in fish cause an accumulation of lactate both in the muscle and in the blood (VON BUDDENBROCK, 1938; SECONDAT and DIAZ, 1942; BLACK, 1955, 1957 a, b, c, 1958; LEIVESTAD *et al.*, 1957; NAKATANI, 1957; PARKER and BLACK, 1959; PARKER *et al.*, 1959; MILLER *et al.*, 1959, 1962; BLACK *et al.*, 1959, 1960, 1962, 1966; HEATH and PRITCHARD, 1962; CAILLOUET, JR., 1964; DEAN and GOODNIGHT, 1964; WENDT, 1964 a, b, c, 1965, 1966; STEVENS and BLACK, 1966). At high water temperatures in the summer the rise in blood lactate is more pronounced than in the winter at low temperatures (WENDT, 1965). Several authors have reported significant mortality following muscular fatigue (VON BUDDENBROCK, 1938; SECONDAT and DIAZ, 1942; MILNE and BALL, 1956, 1958; BLACK, 1957 c; BATES and VINSONHALER, 1957; PARKER and BLACK, 1959; PARKER *et al.*, 1959; BEAMISH, 1966).

The present experiments are included in an investigation concerning the influences of different temperatures on carbohydrate metabolism in salmon and trout. In 1964 hatchery-reared salmon showed a significant mortality after hard muscular exercise. The experiments were repeated in 1965.

Material and Methods

The experiments were carried out at the Salmon Research Laboratory, Älvkarleö, Sweden on 1 1/2-year-old hatchery-reared salmon (*Salmo salar* L.) in August 1964 and in August 1965. In 1964 two groups were used, one was fed on a raw diet,[2] the other was given pellets.[3] Both batches were held in 11.5 m^2 throughs and were fed 4 times a day except on Saturdays (twice daily) and Sundays (once daily). In 1965 it was possible to use only one batch fed on the raw diet, as the pellet-fed one seemed to have got an intestinal catarrh.

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[2] 20 per cent liver, 30 per cent spleen, 24 per cent fish, 20 per cent prawns, 5 per cent yeast, and 1 per cent salt.

[3] 47.6 per cent protein, 4.9 per cent fat, 29.1 per cent nitrogen free extract, 1.5 per cent fibre, 10.4 per cent ash, and 6.5 per cent water.

Before testing, the fish were transferred to covered dark basins in which they were kept without feeding for 18—22 hours (WENDT, 1965). One at a time the fish were chased by hand in a hatchery trough (0.9 m^2), and left there to recover without feeding.

Ordinary hatchery water supplied the troughs and basins. The water temperature during August 1964 was 15°C, and the oxygen saturation ranged from 97 to 100 per cent. During August 1965 the temperature was 16°C, and the oxygen saturation ranged from 90 to 94 per cent.

Individual fishes were sampled before exercise, after 5, 10, and 15 min of exercise, and at different times during recovery. The moribund fishes were sampled when the gill movements ceased. The methods of sampling blood and tissues were the same as those described in WENDT (1965). Blood was analyzed for lactic acid according to SCHOLANDER and BRADSTREET (1962), and the glycogen of muscle and liver tissues was determined according to MONTGOMERY (1957).

Results

A. Behaviour during exercise

All the fish were considered to be in an unexercised condition before exercise. After 2—5 minutes of exercise the first sign of fatigue was seen. The stimulated fish seemed to disregard the stimulation. If left it would stop swimming and rest on the bottom. At the end of the exercise the fishes almost without exception were exhausted, and remained motionless in the trough until sampled. In August 1964 10 out of 24 exercised fishes from the pellet-fed group were moribund when sampled 115—360 minutes after the exercise. Those being moribund had turned their ventral side up, and their tails had become rigid. Their gill movements were weak, and had almost ceased in some of them. In the other group fed on the raw diet one out of 14 fishes was moribund 104 minutes after exercise. In August 1965 11 out of 35 fishes from the raw diet fed lot did not recover from the exercise but turned upside down and became rigid, a rigidity which spread from the tail forward, and finally extended the whole fish. When the gill movements ceased sampling occurred. Often their stomachs were filled with water. and the blood was in many cases "though".

B. Exercised in August 1964

Blood lactate. In the pellet-fed group 5 min of hard muscular work rose the blood lactate from an average level of 14.9 ± 5.7 mg per cent before exercise to 63.8 ± 8.7 mg per cent. After 15 minutes of exercise the average level was 94.3 ± 23.6 mg per cent. The highest average value or 163.8 ± 60.1 mg per cent for completely recovered fish appeared 2 hours after exercise (Tab. I; Fig. 1). Almost all of the moribund fishes had levels above 200 mg per cent,

Table I. Body weights and levels of liver and muscle glycogen and blood lactate after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1964. Pellets. $\left(SD = \pm \sqrt{\frac{s(x-\bar{x})^2}{n-1}}\right)$

		Unexercised	Exercised			Recovery from exercise		
			5 min	10 min	15 min	2 hours	4 hours	15 hours
Body Weight (grams)	Mean ± SD	27.5 ± 11.8	26.1 ± 7.7	7.7 ± 4.7	25.9 ± 10.9	26.0 ± 8.4	34.8 ± 7.9	32.5 ± 1.2
	(n)	(10)	(5)	(5)	(5)	(4)	(5)	(4)
	Range	16.0 — 56.0	19.5 — 38.0	22.0 — 33.5	20.5 — 45.5	20.0 — 39.0	21.0 — 40.0	21.5 — 41.5
Liver Glycogen (g %)	Mean ± SD	3.85 ± 1.11	4.55 ± 1.56	5.83 ± 1.88	3.57 ± 0.72	2.36 ± 0.73	3.84 ± 1.33	3.54 ± 0.85
	(n)	(10)	(4)	(5)	(5)	(4)	(5)	(4)
	Range	2.01 — 5.22	2.25 — 6.34	2.84 — 7.78	2.84 — 4.74	1.53 — 3.31	1.19 — 4.59	2.37 — 4.30
Muscle Glycogen (g %)	Mean ± SD	0.593 ± 0.148	0.625 ± 0.178	0.397 ± 0.289	0.285 ± 0.106	0.258 ± 0.134	0.316 ± 0.095	0.431 ± 0.279
	(n)	(10)	(4)	(5)	(4)	(4)	(5)	(4)
	Range	0.339 — 0.806	0.359 — 0.723	0.076 — 0.757	0.132 — 0.376	0.125 — 0.456	0.232 — 0.445	0.152 — 0.816
Blood Lactate (mg %)	Mean ± SD	14.6 ± 5.7	63.8 ± 8.7	75.8 ± 9.8	94.3 ± 23.6	163.8 ± 60.1	162.8 ± 55.0	22.5 ± 8.2
	(n)	(8)	(5)	(5)	(4)	(4)	(5)	(5)
	Range	7 — 24	51 — 74	62 — 87	72 — 123	159 — 238	92 — 239	11 — 30

Table II. Body weights and levels of liver and muscle glycogen and blood lactate after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1964. Raw diet. $\left(SD = \pm \sqrt{\frac{s(x-\bar{x})^2}{n-1}}\right)$

		Unexercised	Exercised			Recovery from exercise		
			5 min	10 min	15 min	2 hours	6 hours	15 hours
Body Weight (grams)	Mean ± SD	29.6 ± 6.6	26.4 ± 2.8	30.8 ± 3.0	33.0 ± 7.7	31.5 ± 6.5	38.8 ± 16.3	25.3 ± 1.7
	(n)	(10)	(8)	(5)	(8)	(5)	(4)	(4)
	Range	22.5 — 44.0	23.0 — 30.0	25.5 — 32.5	21.0 — 46.5	22.0 — 40.0	25.5 — 60.0	23.0 — 27.0
Liver Glycogen (g %)	Mean ± SD	4.31 ± 1.34	4.63 ± 1.42	3.90 ± 1.21	3.93 ± 1.73	2.66 ± 1.34	5.56 ± 3.35	4.11 ± 1.51
	(n)	(10)	(5)	(5)	(8)	(4)	(4)	(4)
	Range	2.79 — 6.64	2.88 — 6.02	2.36 — 5.42	0.72 — 6.11	1.46 — 3.99	1.23 — 9.16	3.14 — 6.39
Muscle Glycogen (g %)	Mean ± SD	0.657 ± 0.150	0.382 ± 0.026	0.239 ± 0.082	0.224 ± 0.095	0.282 ± 0.147	0.225 ± 0.148	0.305 ± 0.181
	(n)	(11)	(5)	(5)	(8)	(5)	(4)	(4)
	Range	0.521 — 0.985	0.045 — 0.638	0.164 — 0.362	0.026 — 0.304	0.133 — 0.487	0.086 — 0.385	0.055 — 0.463
Blood Lactate (mg %)	Mean ± SD	14.9 ± 7.8	70.8 ± 3.7	84.4 ± 14.1	96.0 ± 23.6	212·8 ± 23.9	54.5 ± 33.1	22.0 ± 10.3
	(n)	(9)	(5)	(5)	(8)	(5)	(4)	(4)
	Range	8 — 34	67 — 76	62 — 96	55 — 120	187 — 248	22 — 88	12 — 34

Table III. Body weights and levels of liver and muscle glycogen and blood lactate in hatchery-reared *Salmo salar* L. exercised by hand and sampled when moribund. August 1964.

Moribund after Ex. (min)	Body Weight (g)	Sex	Liver Glycogen (g %)	Muscle Glycogen (g %)	Blood Lactate (mg %)
115	31.0	♂	0.95	0.083	180
120	30.0	♂	2.63	0.114	235
120	40.5	♀	1.65	0.201	260
120	37.0	♀	0.05	0.033	193
120	20.5	♀	2.92	0.186	192
173	34.0	♀	2.79	0.111	269
185	44.0	♀	0.98	0.015	164
240	26.0	♂	—	—	—
345	30.0	♂	—	—	—
360	24.0	♀	—	—	—
	31.7 ± 7.5[1]		1.71 ± 1.99	0.106 ± 0.070	213 ± 13

[1] Mean ± SD.

which were among the highest obtained (Tab. III). In the group fed on the raw diet the same course occurred (Tab. II; Fig. 2). Somewhat higher average values were obtained in this group compared with the pellet-fed lot. The only moribund fish contained 260 mg per cent blood lactate. After 15 hours of recovery the level was still slightly above that of unexercised fish in both groups.

Muscle glycogen. 15 minutes of hard muscular exercise caused a decrease from an average level of 0.593 ± 0.148 g per cent before exercise to 0.285 ± 0.106 g per cent in the pellet-fed group (Tab. I), and from 0.657 ± 0.150 g per cent to 0.224 ± 0.095 g per cent in the other one (Tab. II). The pellet-fed batch showed the lowest average value after 2 hours of recovery. The moribund fishes showed even lower levels (Tab. III). During continued recovery there seemed to be no significant increase. In the pellet-fed lot there was a tendency to a slight rebuilding of muscle glycogen.

Liver glycogen. The average level of 3.85 ± 1.11 g per cent before exercise in the pellet-fed group was not significantly lower than 4.31 ± 1.34 g per cent in the raw diet fed one (Tab. I; II). Exercise caused no significant decrease in either group. During recovery the lowest values appeared 2 hours after exercise. The pellet-fed lot had lost 61 per cent compared with 38 per cent for the group fed on the raw diet. Then the levels rose again. 15 hours after exercise the same level as before exercise was reached again. The moribund pellet-fed fish had lost 44 per cent (Tab. III).

C. Exercised in August 1965

Blood lactate. 5 minutes hard muscular work rose the blood lactate from an average level of 17.1 ± 7.7 mg per cent before exercise to 55.4 ± 5.4 mg

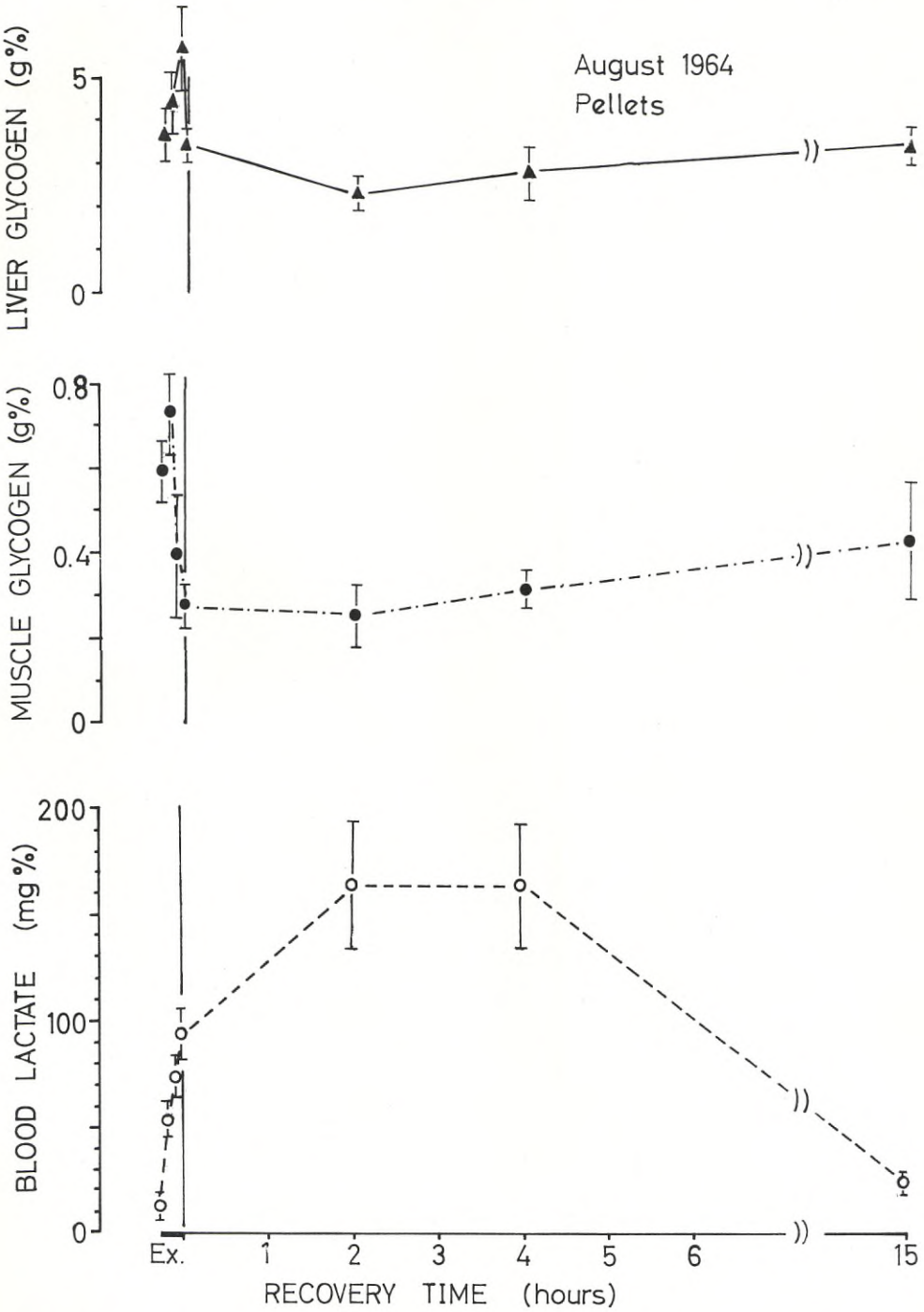

Fig. 1. Changes in liver and muscle glycogen and blood lactate after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1964. Pellets.

Table IV. Body weights and levels of liver and muscle glycogen and blood lactate after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1965. Raw diet. $\left(SD = \pm \sqrt{\frac{s(x-\bar{x})^2}{n-1}}\right)$

		Unexercised	Exercised		Recovery from exercise			
			5 min	15 min	2 hours	4 hours	6 hours	20 hours
Body Weight (grams)	Mean ± SD	26.5 ± 3.9	24.4 ± 2.9	26.8 ± 4.3	30.4 ± 2.5	33.3 ± 8.1	29.9 ± 4.9	28.2 ± 10.7
	(n)	(9)	(8)	(8)	(8)	(5)	(6)	(6)
	Range	21.5 — 34.5	20.0 — 29.0	20.0 ± 34.0	27.0 — 34.0	27.5 — 47.5	22.0 — 34.5	19.5 — 47.0
Liver Glycogen (g %)	Mean ± SD	3.31 ± 1.23	3.78 ± 0.92	3.96 ± 0.70	0.97 ± 0.62	2.32 ± 1.38	1.81 ± 0.67	3.10 ± 1.11
	(n)	(10)	(8)	(8)	(7)	(5)	(6)	(6)
	Range	1.71 — 4.84	2.62 — 5.38	3.19 — 5.16	0.34 — 1.77	0.88 — 3.69	0.94 — 2.45	2.08 — 5.18
Muscle Glycogen (g %)	Mean ± SD	0.318 ± 0.086	0.125 ± 0.107	0.106 ± 0.052	0.145 ± 0.084	0.235 ± 0.073	0.225 ± 0.080	0.193 ± 0.007
	(n)	(10)	(8)	(8)	(7)	(5)	(6)	(6)
	Range	0.185 — 0.458	0.026 — 0.359	0.035 — 0.187	0.067 — 0.280	0.163 — 0.315	0.137 — 0.318	0.110 — 0.291
Blood Lactate (mg %)	Mean ± SD	17.1 ± 7.7	55.4 ± 5.4	88.5 ± 30.7	153.5 ± 80.4	77.0 ± 64.0	31.5 ± 39.6	26.3 ± 13.8
	(n)	(8)	(8)	(8)	(6)	(5)	(6)	(6)
	Range	7 — 30	48 — 61	45 — 144	77 — 236	25 — 172	12 — 112	7 — 42

Table V. Body weights and levels of liver and muscle glycogen and blood lactate in hatchery-reared *Salmo salar* L. exercised by hand and sampled when moribund. August 1965.

Moribund after Ex. (min)	Body Weight (g)	Sex	Liver Glycogen (g %)	Muscle Glycogen (g %)	Blood Lactate (mg %)
60	38.8	♀	1.08	0.027	215
75	25.0	♂	—	—	225
85	27.5	♀	2.82	0.027	279
110	29.0	♀	1.09	0.059	281
120	27.0	♀	0.87	0.087	211
120	30.0	♀	0.44	0.098	240
148	29.0	♀	1.09	0.059	281
175	36.0	♀	0.11	0.015	219
240	27.0	♀	0.16	0.036	163
240	27.0	♀	0.28	0.101	190
300	55.0	♀	1.11	0.226	218
	31.9 ± 8.4[1]		0.91 ± 0.80	0.073 ± 0.062	229 ± 38

[1] Mean ± SD.

per cent. After 15 minutes of exercise the average level was 88.5 ± 30.7 mg per cent. After 2 hours of recovery the average level was 153.5 ± 80.4 mg per cent. Still 20 hours after exercise the average value 26.3 ± 13.8 was slightly above that of unexercised fish (Tab. IV; Fig. 3). The values were not significantly different from those obtained in 1964, and the moribund fishes showed an average level above 200 mg % (Tab. V).

Muscle glycogen. 15 min of hard muscular exercise caused an decrease from an average level of 0.318 ± 0.086 g % before exercise to 0.106 ± 0.052 g % after exercise (Tab. IV). The moribund fishes had an average value of 0.073 ± 0.062 g per cent (Tab. V). There was a tendency to increasing levels of muscle glycogen during the rest of the recovery period but no significant values were obtained. The levels before as well as after exercise were significantly lower than those obtained in 1964.

Liver glycogen. The average level before exercise was lower than the corresponding value of the raw diet group in 1964, 3.31 ± 1.23 g % and 4.31 ± 1.34 g per cent respectively (Tab. II; IV). The lowest values appeared 2 hours after exercise when the liver glycogen had decreased by 71 per cent. During the continued recovery the levels fluctuated. The decrease among the moribund fishes was of about the same range or 72 per cent.

Discussion

The described mortality appeared at high water temperatures (15—16°C) in August among fishes chased by hand but not among fishes exercised to fatigue in an exercising apparatus (WENDT, 1965). The levels of liver and

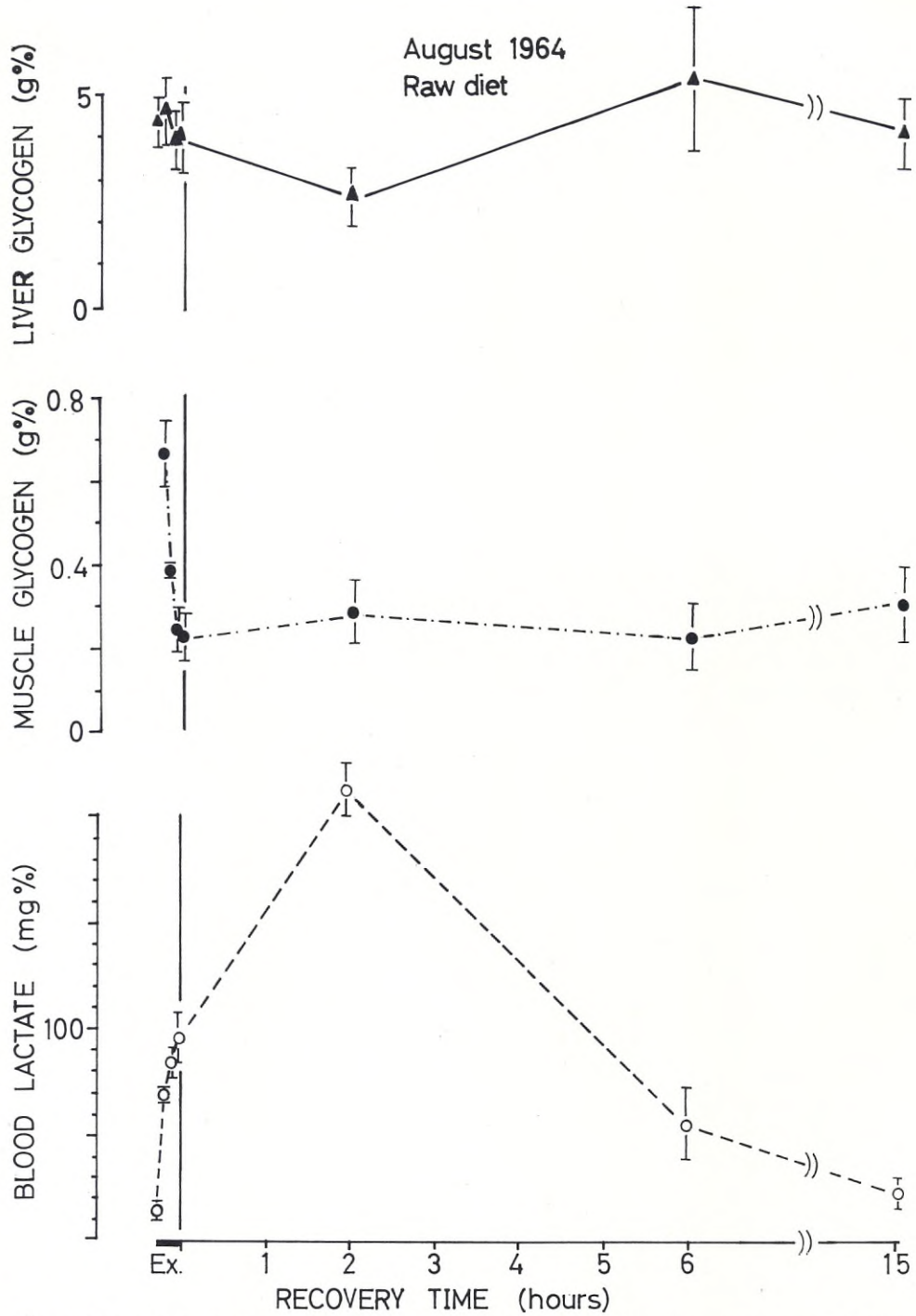

Fig. 2. Changes in liver and muscle glycogen and blood lactate after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1964. Raw diet.

muscle glycogen were high both in 1964 and in 1965. The level of muscle glycogen in unexercised fish was higher in August 1964 than that in August 1965, but both levels were higher than those reported for normally fed rainbow trout (MILLER *et al.*, 1959; HOCHACHKA and SINCLAIR, 1962; BLACK *et al.*, 1960, 1962). The ratio of liver to muscle glycogen was 7 : 1 in August 1964 and 10 : 1 in August 1965. The ratio in fish is thought to be 30 : 1 to 50 : 1 (BLACK *et al.*, 1960).

Exercise for 15 minutes caused a strong decrease but no depletion in muscle glycogen. In August 1964 there still remained 0.285 ± 0.106 g per cent or 48 per cent in the pellet-fed batch (42 % mortality), and 0.224 ± 0.095 g per cent or 34 per cent in the group fed on the raw diet (7 per cent mortality). Corresponding values for August 1965 were 0.106 ± 0.052 g per cent or 33 per cent (31 per cent mortality). The moribund fishes showed the lowest average values (Tab. III; V). MILLER *et al.* (1959) and BLACK *et al.* (1960) observed that 50 per cent of the muscle glycogen in rainbow trout was depleted during 2 minutes exercise, and 80 per cent was depleted during 15 minutes exercise. STEVENS and BLACK (1966) reported that 80 per cent of the muscle glycogen in rainbow trout was depleted during 5 minutes exercise. The difference between these values and the ones found by me seemed to be due to the higher initial levels of muscle glycogen in the salmon used for this study. All the summer the young salmon had been heavily fed.

Although no exhaustion of the muscle glycogen seemed to occur in the epaxial muscle used for sampling, the rigidity that spread from the tail forward might have been associated with *rigor mortis* and its concomitant chemical processes such as glycolysis, decomposition and depletion of adenine nucleotides and phospholipids. BLACK *et al.* (1962) found no indication that a greater muscular activity had taken place in the tail section than in other parts of the body.

Exercise for 15 minutes did not seem to cause any significant change in liver glycogen at any temperature (WENDT, 1966). After 2 hours of recovery, however, there was in August (15—16°C) but not in October (7°C), February (0.2°C) or April (6°C) a significant decrease this being most pronounced in the pellet-fed lot in 1964 (49 per cent) and in the group fed on the raw diet in 1965 (71 per cent). These two batches also showed the highest mortality. The moribund fishes also showed low liver glycogen levels at sampling (Tab. III; V).

The obtained blood lactate values were in accordance with BLACK's data for different salmonoid fishes after 15 minutes exercise (BLACK, 1957 a, b, c). There was a typical delayed response with the highest average levels of blood lactate occurring about 2 hours after exercise. Mortality seemed to be closely correlated with the blood lactate level. In August 1964 the highest mean value from 10 moribund fishes amounted to 213 ± 13 mg per cent. The corresponding average value from 4 fishes completely recovered was

163.8 ± 60.1 mg per cent. In August 1965 the average value from 11 moribund fishes amounted to 229 ± 38 mg per cent and 6 completely recovered fishes had an average level of 153.5 ± 80.4 mg per cent. BEAMISH (1966) suggested the critical threshold for lactic acid to be 100 mg per cent for otter-trawled haddock. PARKER *et. al.* (1959) considered levels above 125 mg per cent as a danger zone for three species of Pacific salmon. In this study the critical threshold of blood lactate is considered to be about 200 mg per cent.

SECONDAT and DIAZ (1942) found 20 per cent mortality in tench (*Tinca tinca*) after exercise, and BLACK (1957 c) observed 25 per cent mortality in sockeye (*Oncorhyncus nerka*) after chasing them by hand for 15 minutes. In other investigations by MILNE and BALL (1958), PARKER and BLACK (1959), and PARKER *et al.* (1959) on troll-caught chinook and coho salmon (*Oncorhyncus tshawytscha* and *O. kisutch*) the mortality ranged between 18 and 71 per cent. BEAMISH got between 7 and 78 per cent mortality in otter-trawled haddock (*Melanogrammus aeglefinus*). In this investigation the mortality rose to 41 per cent in August 1964 and to 31 per cent in August 1965.

The exact cause of death is still unknown. Depletion of energy reserves may play an important role. The observation that the blood in many cases was "tough" can be related to the phenomena discussed by BOUCK and BALL (1966). The high blood lactate level and a sluggish circulation supported their suggestion of *in vivo* coagulation and mortality from progressive shock. It is possible that the hand-chasing of fish may have caused sufficient stress to induce a shock. No mortality appeared among fishes exercised to fatigue in an exercising apparatus (WENDT, 1965).

As a matter of fact mortality was found only when the fish all the summer had been heavily fed on a diet rich in carbohydrates and exercised by hand at a high water temperature (15—16°C). At lower temperatures in October, November, February, March, April, and May no signs of mortality were seen (WENDT, 1966; unpubl.). As pointed out by PARKER *et al.* (1959) most fishes are chronically in oxygen distress because of the low solubility of oxygen in water. Especially at high water temperatures the effect may be disastrous if the fish has to perform a hard muscular work when at the same time carbohydrates as muscle and liver glycogen are quickly available as energy. Moreover BRETT (1964) found a sharp cut-off in active metabolic rate at 15°C, and suggested the presence of a limiting factor, suspected to be the oxygen concentration. The oxygen necessary for the digestion of a great amount of food may add further stress on the oxygen demand (BEAMISH, 1966). The results in my investigation support the hypothesis expressed by many authors (BLACK, 1958; BLACK *et al.*, 1959; PARKER *et al.*, 1959; WITTENBERGER and DIACIUC, 1965) that the death of fish after hard muscular work is the effect of an inadequate oxygenation.

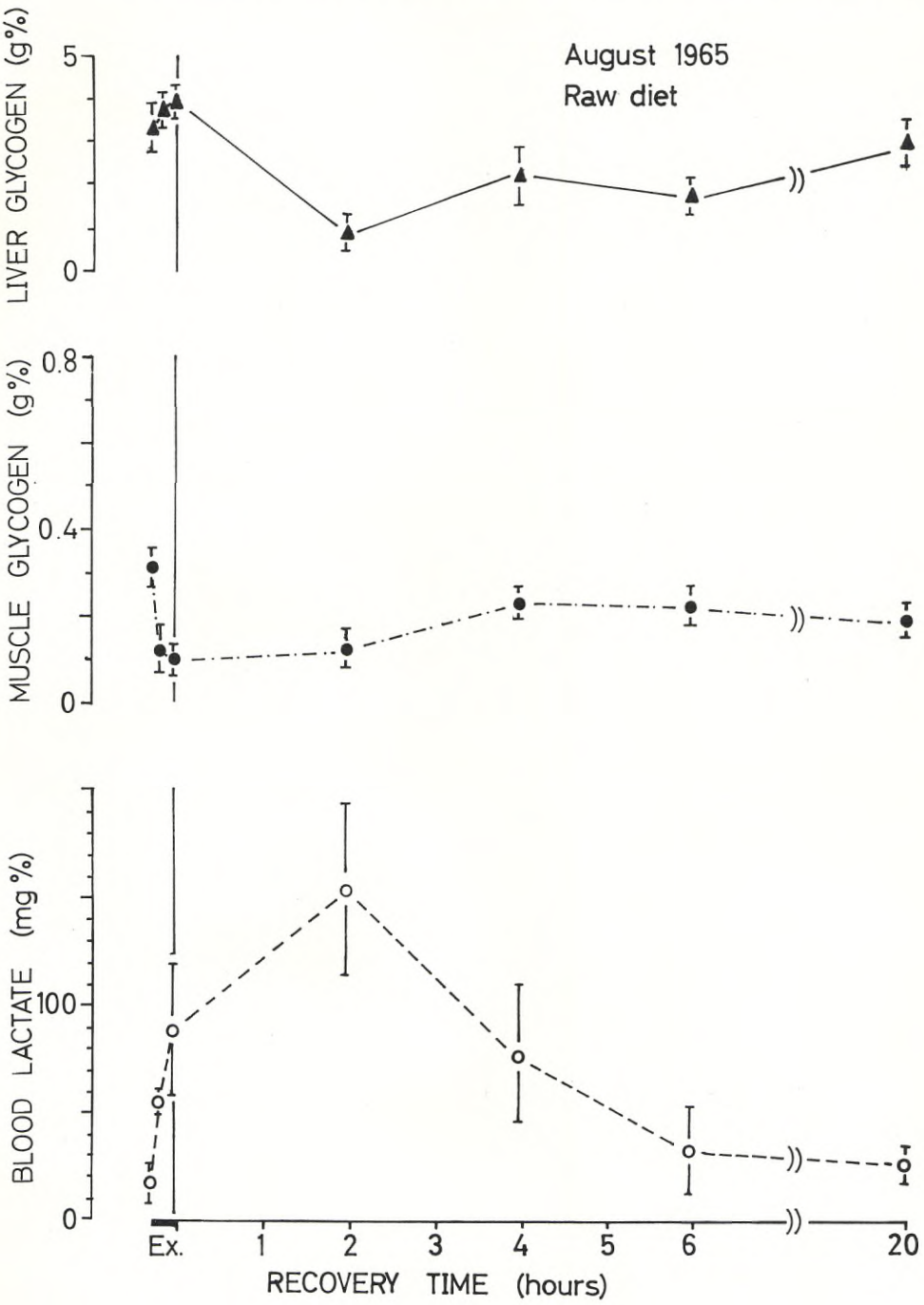

Fig. 3. Changes in liver and muscle glycogen and blood lactate after exercise and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1965. Raw diet.

Summary

In August 1964 42 per cent of a pellet-fed group of hatchery-reared salmon were moribund when sampled 115—360 minutes after exercise. In August 1965 31 per cent of a group fed on a raw diet were moribund when sampled as the gill movements ceased after 60—300 minutes. Mortality rate seemed to be closely related to the blood lactate level. The critical threshold for blood lactate in 1 1/2-year-old hatchery-reared salmon is considered to be about 200 mg per cent.

The exercise caused a decrease in muscle glycogen varying between 52 and 67 per cent. There was no significant decrease in liver glycogen immediately after exercise, but after 2 hours of recovery the loss ranged between 49 and 71 per cent. The moribund fishes also showed low liver glycogen levels.

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Successful introductions of glacial relicts as argument in a discussion of postglacial history

By MAGNUS FÜRST

Introduction

The absence of localities for glacial relict[1] crustaceans in certain areas of Sweden has long seemed puzzling. Such an area is comprised by the South Swedish Highlands (Småland), which according to NILSSON (1953) were covered for a period by the Baltic Ice-Lake. Fig. 1 illustrates a characteristic phase. According to SEGERSTRÅLE (1957), among others, the Baltic Ice-Lake contained most of the glacial relicts; he writes (pp. 36—37):

"It is natural to ask why there are no records of the classical Arctic relicts from the highlands of southern Sweden. One would expect them to live there as well as do the vendace, and other aquatic animals, such as gastropods, which were above concluded to have immigrated by way of the Baltic Ice Lake. Ecological factors can hardly be thought of, as the relicts concerned are common in Finnish lakes which are of much the same limnological type as those of Småland. Prof. SVEN EKMAN, with whom the author (SEGERSTRÅLE) has discussed the matter, thinks it possible that the lack of records from the highland of southern Sweden is simply due to this area having been comparatively little investigated by hydrobiologists."

There has, however, been since 1927 a limnological field laboratory belonging to the University of Lund in the centre of the area and it might therefore be expected that finds of glacial relicts would be made in the neighbourhood. For decades zoologists have maintained that finds of glacial relicts in an area of water indicates that the latter lay below the highest postglacial shoreline or that water containing these animals was carried up to higher levels as a result of ice dams. On the other hand the fact that glacial relicts had not actually been found in certain lakes could not be regarded as conclusive so long as reliable equipment for catching them was lacking.

Author's Investigations

a. Inventories of lakes within the area

For some years special equipment has been used for catching the glacial relicts, *Mysis relicta* LOVÉN, *Pallasea quadrispinosa* SARS, *Gammaracanthus*

[1] The term glacial relict is still used at least for practical reasons. According to HOLMQUIST (1959, 1966) the term is not adequate nor the terms marine-glacial relict or even relict.

lacustris SARS, *Pontoporeia affinis* LINDSTRÖM and *Limnocalanus macrurus* SARS. The use of this equipment makes it possible to establish quickly whether glacial relicts exist or not.

With the aim of throwing light on the contradictions described, I have on repeated occasions made surveys with the new equipments of Lakes Bolmen (max. depth 27 metres, area 184 km^2) and Vidöstern (max. depth 35 metres, area 44.8 km^2) with respect to the occurrence of glacial relicts. The results have been entirely negative. (Fig. 1.)

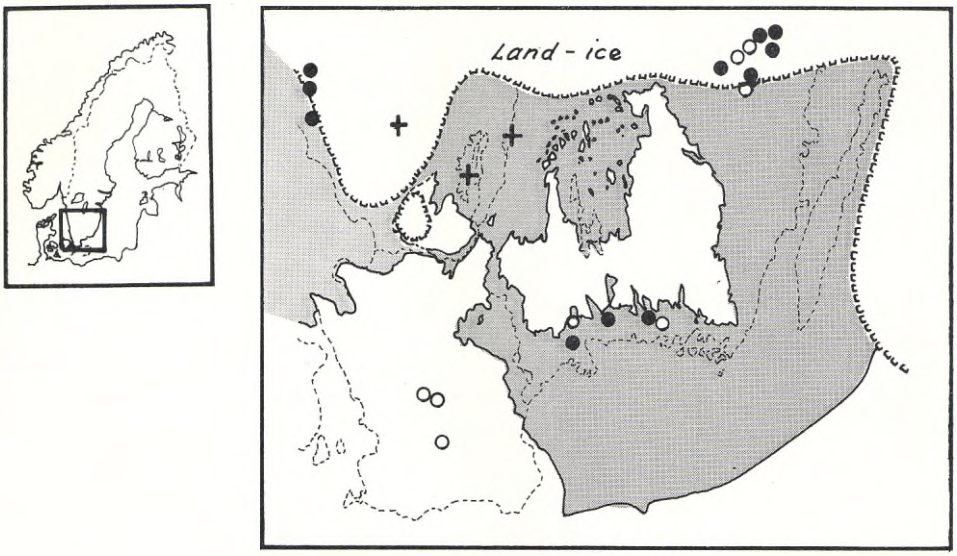
Another area which according to NILSSON was covered by the westward outlet of the Baltic Ice-Lake was the valleys of Rivers Ätran and Nissan (Fig. 2). Here, so far as is known, none of the glacial relicts occurs. A survey has been made of the following two lakes, with negative result in each case: Lakes Åsunden (max. depth 39.5 metres, area 33.9 km^2), Fegen (max. depth 25.5 metres, area 24.2 km^2).

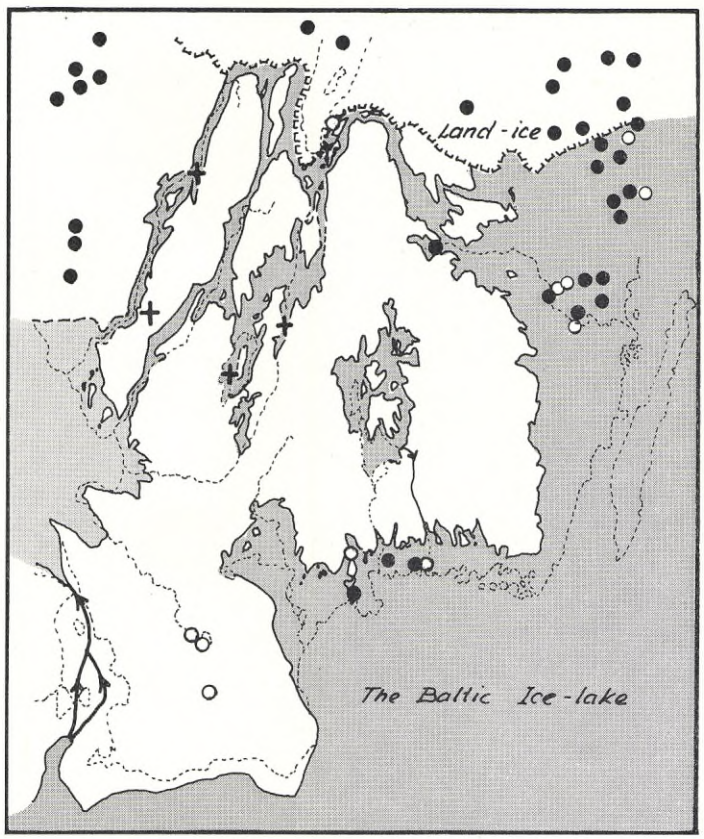
These lakes, which thus may once have been situated within the area of the Baltic Ice-Lake or within its outlets, were chosen as being particularly suitable, since their size and depth are more than sufficient and they cannot be said to deviate from normal relict lakes in any way. On the basis of experience so far gained it is further to be expected that some glacial relicts should be encountered in any lake below the highest postglacial shoreline, except in a few cases, e.g. lakes with pronounced oxygendepletion, or lakes near the coast formed during periods when the salt content of the surrounding water was so high that glacial relicts could not exist there. Several of the find localities in southern Sweden comprise very small and shallow lakes; thus, for example, *Mysis relicta* has been found in very small lakes, one of them, 6 1/2 metres deep, in eastern Småland (LETTEVALL 1962). Any possibility that the relicts were exterminated during some particularly warm later period precisely in Bolmen and Vidöstern or Åsunden and Fegen seems to be precluded in view of the many find localities at varying levels above the sea that exist around the area in question (Figs. 2 and 3).

b. Successful attempts to introduce glacial relicts above the highest shore line

The attempts which have been made in Sweden to introduce glacial relict crustaceans in lake reservoirs above the highest shoreline have been described earlier (FÜRST 1965).

During August 1966 it was established that *Mysis relicta* had formed a stock in Lake Blåsjön, where about 1.65 million specimens had been introduced in October and November 1964. The animals which were caught belonged to the second generation born in the lake. In Lake Torrön, where *Mysis relicta* was introduced in 1957, a dense stock has been formed. This introduction had previously been regarded as unsuccessful in view of the





Figs. 1 and 2. Redrawings of maps representing two phases in the history of the Baltic Ice-Lake (NILSSON 1953). Localities of glacial relicts are added. Unfilled circles represent lakes where only *Pallasea quadrispinosa* is found. Crosses indicate that no relicts occur. According to NILSSON the Baltic Ice-Lake covered parts of the south-Swedish highlands with alternating outlets through some western river valleys. In Fig. 2 the Baltic Ice-Lake had just changed its outlet from these valleys to Öresund (Arrows).

large mortality observed at the introductions. This mortality was attributed to a particularly high sensitivity of the species to differences in the electrolyte content between different lakes (FÜRST 1965). Cage experiments with fewer than 50 animals in each cage showed total mortality if carried out parallel with transplantations between such lakes. Of the approximately 20,000 specimens introduced in Lake Torrön only a very small number possessed sufficient tolerance to survive and to build up a stock. In Lake Anjan nearby, *Mysis* was introduced during three years beginning in 1959, but here on the other hand no survival has so far been established. From Lake Torrön *Mysis relicta* has *spread downstream to Lake Juveln and further still to Lake Kallsjön.* In the first lake the stock is dense but in the second it is at yet rather sparse. All recoveries were made with trawl. The consequences for the fishery of the successful introductions are under investigation.

In this connection the importance of the successful experiments consists in the demonstration that *Mysis relicta* (one of the most commonly occurring glacial relict) can live in water above the highest shoreline (cf. SPARROW et al. 1964 and SCHUMACHER 1966) and that it spreads downstream. There is no reason to suppose that the same thing does not apply to the other species.

Discussion

The surveys of Lakes Bolmen, Vidöstern, Fegen and Åsunden indicate that the absence of glacial relicts is real and significant. That glacial relicts actually existed in the early Baltic Ice-Lake seems to be beyond all doubt (SEGERSTRÅLE 1957); it is sufficient to refer to their present occurrence in the southern Baltic countries (THIENEMANN 1925).

As, through experiments in nature, it has been established that glacial relicts (*Mysis relicta*) spread downstream, one would expect to find these or other relicts in the lakes mentioned.

Since this is not the case, the interpretation of the quaternary geological shorelines must be affected. NILSSON's theory that the Baltic Ice-Lake drained away over Småland towards the west or down through the valleys of the Ätran or the Nissan does not accord with these results. It appears more probable that the highlands of South-Sweden were covered by a separate large ice lake draining towards the west and perhaps also to the south and east at different phases.

In any future alternative interpretations of the significance of the shoreline the occurrence of glacial relicts should be taken into account. It may be supposed that an exact mapping of the distribution of the various species may give a sharper contour to the biological data in the interpretation of quaternary geological problems. This would constitute an extension of the

biological significance which, for example, *Ancylus* or *Littorina* have already possessed and which has led to the designation of the various stages of the Baltic.

Summary

After artificial introductions, *Mysis relicta* has formed stocks in lakes far above the highest postglacial shorelines and has spread downstream. From this fact, as well as new evidence for the non-existence of *Mysis* and other glacial relicts in the southern highlands it follows that the Baltic Ice-Lake has probably never drained over the highlands as suggested (NILSSON 1953). The significance of relicts in interpreting glacial shorelines is stressed.

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Food and growth of an allopatric brown trout in northern Sweden

By NILS-ARVID NILSSON and GÖTE ANDERSSON

1. Introduction

In the northern Scandinavian highlands there are many lakes that are inhabited by brown trout (*Salmo trutta* L.) only. The history of the post-glacial immigration of this species, leading in some cases to allopatric populations but in most cases to coexistence with, for instance, arctic char (*Salvelinus alpinus* L.) or whitefish (*Coregonus* sp.) is in its details obscure. One — but by no means the only — explanation that in some cases brown trout, in other cases arctic char, occur as the sole species in some high-altitude lakes in Scandinavia was pointed out by EKMAN (1910) and HUITFELDT-KAAS (1918), who explained the distribution of several fish species as being the results of early human transplantations. For instance, there is an inscription on a Norwegian 12th-century runestone[1] indicating the introduction of brown trout into a lake, and many Lappish traditions confirm that it was customary to carry fish from one lake to another. It is easy to imagine that lakes originally empty of fish would be tempting objects for such actions.

The present example of an allopatric trout population is that of Lake Sippmikken (also called Semmingsjön). This lake is situated in the northernmost part of the province of Jämtland, 689 m above sea level. It discharges to Lake Blåsjön (434 metres above sea level), which like several other lakes in that region contains both brown trout and char, and has been the subject of numerous investigations (summaries by GRIMÅS 1965 and NILSSON 1965). It is about 4 km^2 in area and situated at the borderline between the subalpine birch-forest and the lower alpine belt. The greatest depth measured is 42 metres. A general description of the limnology and preimpoundment bottom fauna of the lake was given by BRUNDIN (1949). In 1953 a dam was built at the outlet and therafter the water-level was subjected to artificial fluctuations; every summer the level is dammed up 5.5 metres above the normal high-water level. Each year during the period 1953—61 1,000 one-summer-old fingerlings were released into the lake.

The present material consists of 195 trout, fished in the years 1946 and 1962. The fish were caught by standard sets of gill-nets (cf. NILSSON 1965). In 1962 a special test fishing with nets with small meshes (20—30 mm

[1] "Ailifr algr bar fiska i Raudsio"=Ailifr carried fish into Lake Rausjø (HUITFELDT-KAAS, 1918).

Fig. 1. The northern shore of Lake Sippmikken in September 1962 obviously exposed to erosion.

stretched mesh) was carried out in order to obtain material of fingerling trout.

2. General effects of the impoundment

The establishment of the dam at the outlet meant that one of the most important areas of trout reproduction was destroyed. The damming up and yearly water-level fluctuations resulted in erosion that was still obvious in 1962, 10 years after impoundment had commenced. (Fig. 1). Although no investigations of the bottom fauna or zooplankton were carried out after impoundment, it could be concluded that the occurrences in Sippmikken should be approximately parallel with what happened about the same time in Blåsjön. It is, however, noteworthy that in Sippmikken the impoundment does not mean a lowering of the water level below the original low-water level.

No spawning was observed in the lake itself. After the impoundment mature trout were caught in the vicinity of the inlet streams, and the abundance of young trout along the shores indicated a good recruitment of naturally reproduced fish. It is noteworthy that even one- and two-year old fish were caught in the lake itself. It thus seems that the trout in this lake stay in the streams for a relatively short time.

Table 1. Food of trout in July—August before and after impoundment. Figures represent mean percentage of stomach volume.

	1946	1962		1946	1962
Bythotrephes	—	22.3	*Tipulidae* l	1.4	6.7
Bosmina	—	0.1	*Trichoptera* l	23.4	10.5
Daphnia	—	8.6	*Chironomidae* p	3.5	6.4
Eurycercus	7.5	8.6	*Trichoptera* p	5.5	5.0
Gammarus	1.0	6.5	*Chironomidae* i	7.7	0.1
Lymnaea	9.9	2.8	*Trichoptera* i	6.6	0.1
Planorbis	1.1	2.8	*Tipulidae* i	—	2.9
Pisidium	—	0.3	*Empididae* i	—	0.2
Oligochaeta	—	5.7	*Plecoptera* i	—	0.2
Chironomidae l	1.3	4.7	Terr. insects	22.0	2.3
Dytiscidae l	—	0.8	Inorganic material	0.3	0.7
Ephemeroptera l	2.0	+	Plants	—	0.9
Plecoptera l	6.8	0.8	Number of fish	25	56

3. Food habits and flesh colour

Table 1 gives an expression of the difference between the food of the trout before (1946) and after the start of impoundment (1962). Although the well-known disposition of brown trout to prefer *Trichoptera* larvae (in this case

Table 2. Food of trout of different sizes in June—September 1962.

	<150	150–200	200–300	300–400	>400
Bythotrephes	—	1.5	13.9	13.7	—
Bosmina	—	—	0.1	—	—
Daphnia	—	—	8.6	16.5	—
Eurycercus	42.5	16.7	9.4	7.2	—
Gammarus	—	6.2	16.2	1.7	49.0
Lymnaea	—	0.1	6.6	9.4	44.0
Planorbis	—	0.6	4.1	—	—
Pisidium	—	—	0.2	—	—
Oligochaeta	—	6.5	2.0	—	2.5
Trichoptera l	14.0	35.5	15.6	13.2	0.5
Ephemeroptera l	—	—	—	0.1	—
Plecoptera l	—	—	0.4	1.9	—
Dytiscidae l	—	0.1	1.1	6.4	—
Chironomidae l	1.0	3.7	3.3	6.3	1.0
Tipulidae l	—	23.6	7.0	1.2	3.0
Diptera l	—	0.5	—	—	—
Trichoptera p	—	0.7	1.1	7.1	—
Chironomidae p	—	0.3	2.1	11.1	—
Trichoptera i	—	—	—	0.1	—
Plecoptera i	—	—	0.1	0.1	—
Coleoptera i	—	—	0.2	—	—
Chironomidae i	—	—	—	0.3	—
Tipulidae i	42.5	—	2.6	3.4	—
Empididae i	—	0.1	0.1	0.1	—
Diptera i	—	0.2	1.2	0.2	—
Terr. insects	—	—	3.1	—	—
Inorganic material	—	0.8	0.5	—	—
Plants	—	2.8	0.5	—	—
Number of fish	2	36	96	23	2

Table 3. The food of trout in 1962. Seasonal variation.

	June	July	Aug.	Sept.
Bythotrephes	—	—	32.9	4.2
Bosmina	—	—	0.1	—
Daphnia	26.5	—	11.7	3.8
Eurycercus	—	5.3	10.1	14.6
Gammarus	18.0	8.9	5.9	14.6
Lymnaea	15.6	6.0	1.1	6.5
Planorbis	—	1.9	3.3	2.8
Pisidium	—	0.1	0.4	—
Oligochaeta	0.3	17.6	—	1.2
Trichoptera l	21.5	26.8	2.8	25.7
Ephemeroptera l	0.1	—	—	—
Plecoptera l	2.4	—	1.1	0.1
Dytiscidae l	—	2.3	2.5	1.2
Coleoptera l	0.3	—	—	—
Chironomidae l	9.3	1.3	6.0	2.3
Tipulidae l	0.9	0.6	9.0	13.8
Diptera l	—	—	—	0.2
Trichoptera p	—	14.7	0.8	—
Chironomidae p	4.8	—	8.6	0.5
Trichoptera i	—	—	0.1	—
Plecoptera i	—	0.7	—	—
Coleoptera i	—	0.8	—	0.1
Chironomidae i	—	—	0.1	0.1
Tipulidae i	0.3	9.0	—	2.8
Empididae i	—	—	0.3	—
Diptera i	—	3.5	1.1	0.3
Dytiscidae i	—	—	—	0.1
Terr. insects	—	0.1	0.1	3.4
Inorganic material ...	—	—	1.1	0.5
Plants	—	0.4	0.9	1.3
Number of fish	15	18	41	85

mainly of the genus *Apatania*) is obvious both before and after impoundment, it is still more striking that the consumption of the small crustaceans *Bythotrephes, Eurycercus* and *Daphnia* had been extraordinarily substantial in July—August 1962. This is in agreement with what has been observed in several other impounded lakes inhabited by trout as sole or dominating species (DAHL 1932, HUITFELDT-KAAS 1935). It has also been demonstrated that there is regularly an increase in the abundance of small *Crustacea* (especially those that are semibenthic) in impounded lakes during the first few years after the start of the water-level fluctuations and the resulting erosion (DAHL 1932, HUITFELDT-KAAS 1935, GRIMÅS 1962). In lakes inhabited by both trout and char this surplus is mainly exploited by char (NILSSON 1955, 1965). Table 2 shows that not only the very smallest specimen had consumed small *Crustacea* in 1962. Of trout over 300 mm in length nearly 14 per cent had eaten *Bythotrephes* and 16.5 per cent had eaten *Daphnia*. One peak of *Daphnia* consumption was in June, one in August (Table 3). *Bythotrephes* and *Eurycercus* were mainly consumed in August and September. It is characteristic that it was mainly the big fish that had consumed

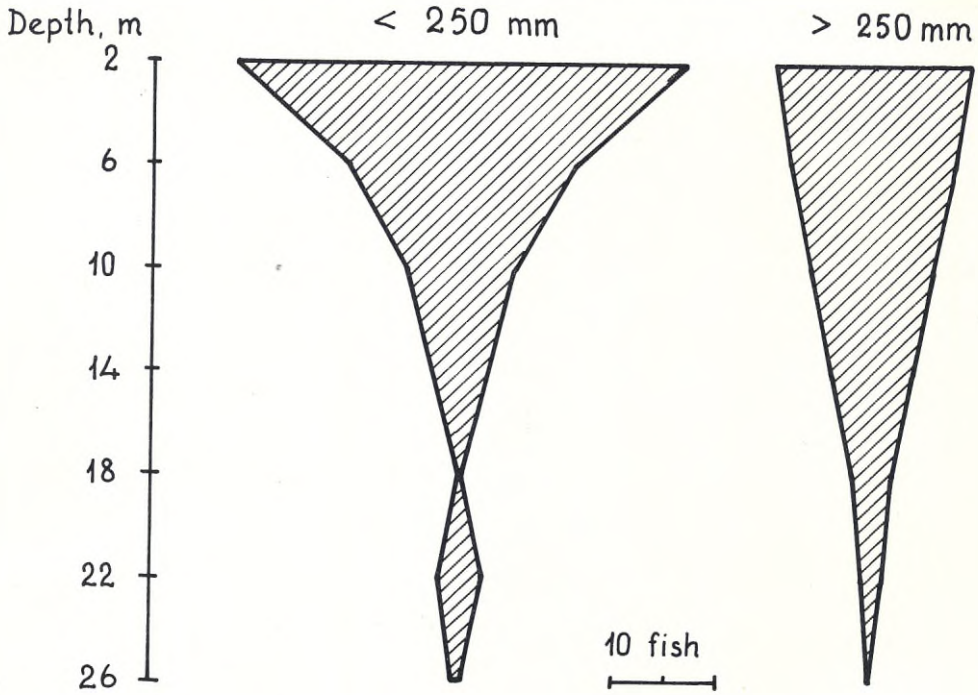

Fig. 2. Bathymetrical distribution of the catch of trout in Lake Sippmikken, June—September 1962.

Gammarus lacustris and *Lymnaea,* and these food items, as well as *Trichoptera* larvae, were important during the whole ice-free season. The diagram, Fig. 2, shows that most of the trout — especially the small ones — were caught in shallow water. This is in agreement with what is known from other investigations (NILSSON 1955).

In 1962 a special investigations of the flesh coloration was carried out. This simply involved the classifying of all trout caught as either "red" or "white". Flesh coloration is of great economic importance in salmon and trout fishery in Sweden, as only red or "salmon-coloured" specimens can be marketed with full profit. Red coloration originates from dietary fat-soluble carotenoids (in brown trout astaxanthin) (STEVEN 1948). It varies to a large extent with the size of the fish and with season. HACKER (1962), for instance, found that no lake trout (*Salvelinus namaycush* WALB.) in samples from Green Lake had coloured flesh except those between 11 and 22 inches. This was explained by reference to the consumption of crustaceans (*Mysis*), and it was noted that small trout (under 10.9 inches) appeared to be incapable of converting carotenoids as they had white flesh in spite of a crustacean diet, and fish-feeding trout lost their red coloration.

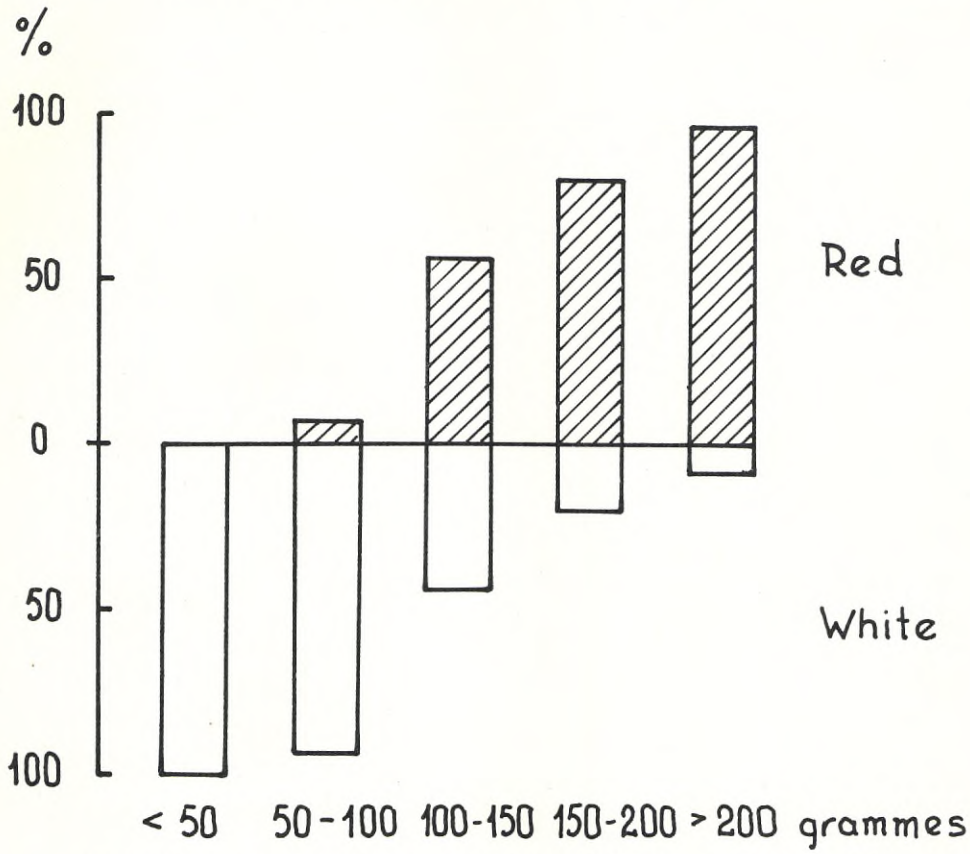

Fig. 3. Flesh coloration of trout of different weight. June—September 1962.

The diagram, Fig. 3, indicates that in Sippmikken nearly all trout weighing less than 100 grammes had white flesh, and nearly all those weighing more than 200 grammes had red flesh.

Table 4 shows that about half of the red-coloured trout had eaten crustaceans, while more than half of the white-coloured ones had eaten insects. These indications give very weak evidence, if any at all, for a correlation between diet and coloration. In this context it may be borne in mind that trout may easily change their feeding habits from one day to another. The

Table 4. Diet of trout with different flesh colour.

	Red	White
Crustacea	50.2	33.5
Mollusca	12.1	9.8
Insects	37.2	54.4

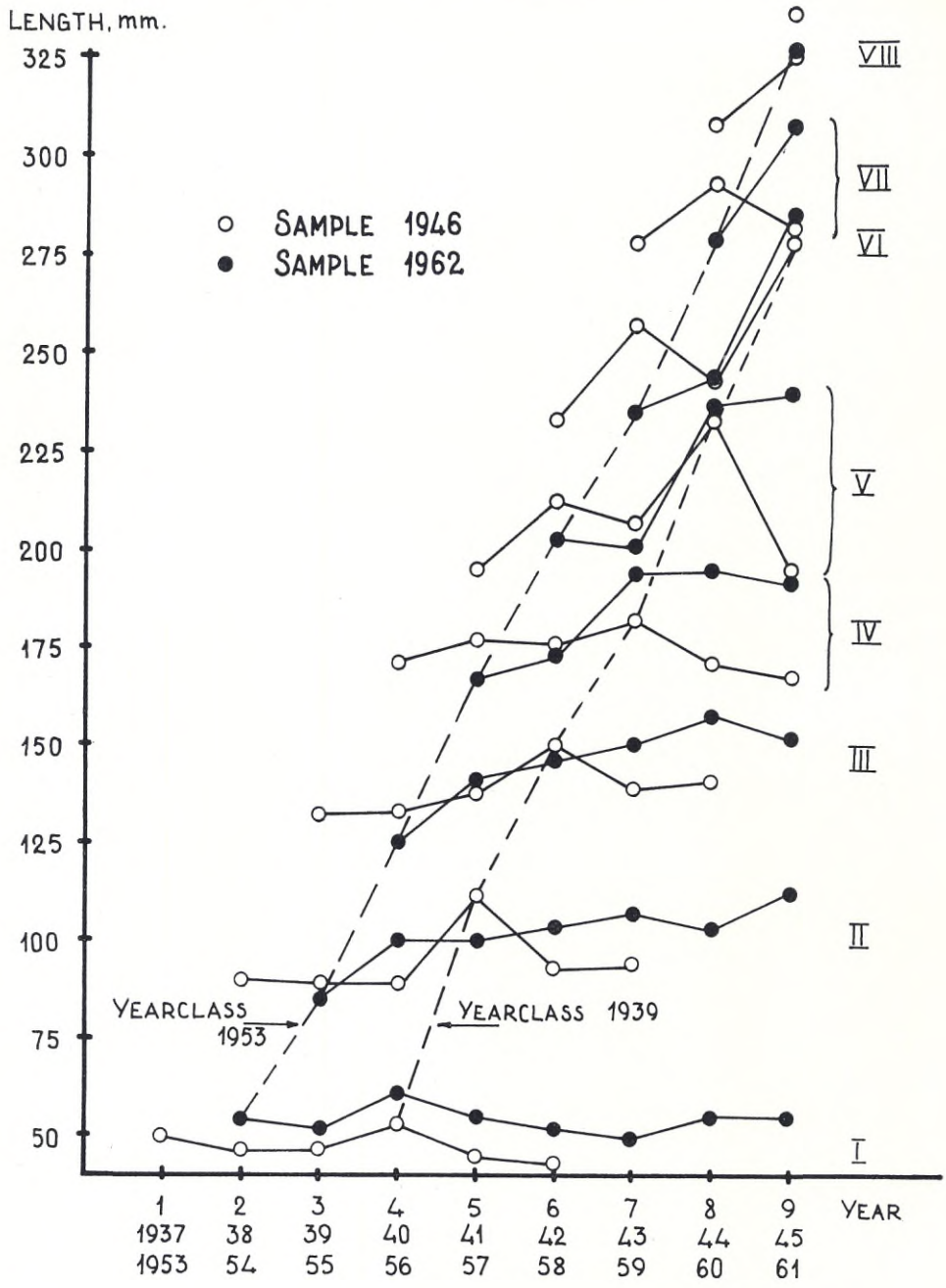

Fig. 4. Nine-year growth history of trout caught in 1946 (preimpoundment) and 1962. Solid lines connect points representing corresponding average lengths attained at ages indicated by Roman numerals. Broken lines indicate the growth of the year classes 1939 and 1953.

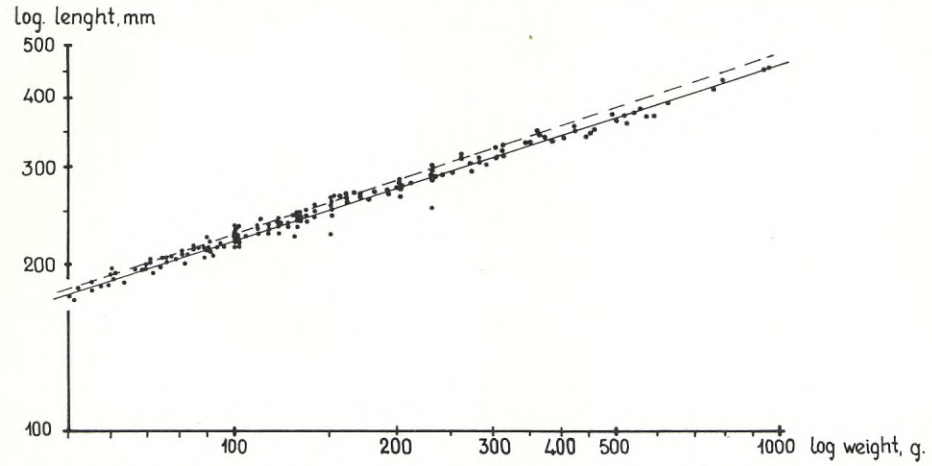

Fig. 5. Length-weight relationship of trout from Lake Sippmikken in 1962. Regression line of corresponding data from Lake Blåsjön (broken line) plotted for comparison.

possible inability of small trout to convert carotenoids (quoted above) may also be of importance.

4. Growth and condition

In order to compare the growth of the trout before and after impoundment the scales of all fish caught were aged and back-calculated. In the diagram, Fig. 4, the 1st—7th years of growth have been plotted with a view to comparing the sample from 1946 with that from 1962. As more nets with small mesh-sizes were used in 1962 the LEE phenomenon might be expected to have influenced the data of the first-, second- and third-year growth of the young fish in a higher degree that year.

A comparison of year classes suggests that two of them were exceptional. The class born in 1939 had an exceptionally good growth through all the years, while the class born in 1953 displays the opposite tendency. Disregarding these extremes, there is a tendency for all the post-impoundment year-classes to have better first- to third-year growth. There are at least three different possible ways of explaining this increase in growth rate after impoundment:

(1) a decrease in the area of reproduction,
(2) a high percentage of big hatchery-reared fingerlings in the catch,
(3) an increase in the supply of food suitable to small trout.

The last point presupposes a prolonged "damming-up effect" (NILSSON 1964, RUNNSTRÖM 1964), i.e. an increased food production during the first few years after the start of impoundment due to, among other things, erosion, redisposition of sediments, etc., and increased primary and secondary produc-

tion (AXELSON 1961, GRIMÅS 1961, RODHE 1964). CAMPBELL (1963) reported an increase in growth rate of brown trout in a Scottish reservoir that lasted at least 5 years after impoundment, and RUNNSTRÖM (1964) demonstrated a similar case from the north Swedish highlands. The fact that there was still considerable erosion along the shores of Sippmikken in 1962 supports the idea that there might still be a "damming-up effect", affecting for instance small crustaceans such as *Eurycercus* and *Bythotrephes*.

The length-weight relationship of the trout from Sippmikken in 1962 are plotted in the diagram, Fig. 5, and the regression line is compared with the corresponding line from the material of the nearby Lake Blåsjön in the same year. It is obvious that the Sippmikken trout are somewhat plumper. This is what might be expected, as the Blåsjön trout was seriously damaged by the impoundment of the lake (NILSSON 1961).

5. Discussion

One of the remarkable characteristics of the trout of Sippmikken is the post-impoundment diet, which to a great extent is dominated by small *Crustacea* (*Daphnia, Eurycercus* and *Bythotrephes*). "Plankton-feeding" brown trout have been reported from other lakes in Scandinavia. In 14 out of 22 Norwegian impounded lakes studied by PER AASS (personal communication) the principal food of brown trout consisted of *Cladocera* (*Eurycercus* in 6 cases, *Bythotrephes* in 6 cases and *Daphnia* in 2 cases). Similarly, in Lake Parkajaure, Swedish Lappland, 90.9 per cent of the food consisted of small *Crustacea* in August 1964 (NILSSON 1965) and the trout of Lake Jølstervann in Norway is known to consume plankton all the year around (*Bosmina obtusirostris* in summer, *Daphnia galeata* in autumn and winter and *Bythotrephes* in summer and autumn) (JENSEN and SENSTAD 1962, KLEMETSEN 1967). In that lake the trout also spawns on the bottom of the lake itself, like char. As mentioned above, post-impoundment consumption of more or less planktonic *Crustacea* has frequently been observed in Norway. It is of interest to note that in lakes inhabited by both brown trout and arctic char it is the char that exploits the planktonic *Crustacea*, and this habit is especially pronounced after impoundment (NILSSON, 1961, 1964). It is tempting to speculate that both the plankton-feeding and the lake-spawning habits in some allopatric trout populations may be due to the absence of competition from other fish species, such as char.

6. Summary

1. The food, growth, length-weight relationship and flesh coloration of brown trout in Lake Sippmikken, northern Sweden, were investigated.

2. The fish were found to feed to a great extent on small *Crustacea* after impoundment, and the first-, second- and third-year growth had improved.

The enhanced growth after impoundment may be due, among other things, to damming up and erosion.

3. The length-weight relationship was good as compared with the trout of the nearby Lake Blåsjön. The flesh coloration was white in trout weighing less than 100 grammes, and red in trout weighing more than 200 grammes.

4. The ecological characteristics of allopatric trout are discussed.

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On the importance of growth and spawning — site ecology of whitefish *(Coregonus)* for the survival of the young

By THOROLF LINDSTRÖM

Introduction

MAYR (1963) states as one aspect of the biological species concept that "Species are more unequivocally defined by their relation to non-conspecific populations ('isolation') than by the relation of conspecific individuals to each other. The decisive criterion is not fertility of individuals but the reproductive isolation of populations." According to the same author, sibling species may be defined as "morphologically similar or identical natural populations that are reproductively isolated". SVÄRDSON (1958, 1959, 1961) states that there are five sibling species in the *Coregonus lavaretus* group and that the populations of these species behave as subspecies in smaller lakes but as species in larger ones. He says that this stresses the dependence on ecology when no sterility barrier exists and that ecological isolation is responsible for the present isolation of the sibling species; they tend to live in different habitats, take different kinds of food, grow to different sizes, and so they select different spawning places and periods.

There is a considerable variation in the ecological features within each species as displayed, e.g., from the numerous transplantations to new environments, and the existing variation in nature between allopatric populations of a species is, according to SVÄRDSON, in the main environmentally induced, though the ecological differences between different species are positively selected for (1958, 1959, 1961).

From these statements it could be inferred that each species should display a species-characteristic way of restricting its ecology when living sympatrically with other whitefish species. When this seems not to be the case, the situation deserves special attention.

Terminology

The terms interactive and selective segregation are used in this paper *sensu* BRIAN (1956) and NILSSON (1966).

		Species				
		A	B	C	D	E
Lakes	1	+	+	+		+
	2	+	+			+
	3	+			+	+

Interspecific differences between sympatric populations (horizontal rows) depend either on selective or interactive segregation. Where each species can in appropriate circumstances cover the whole range of ecological variation of the species group and the populations restrict their ecology and move their optima when living sympatrically, the differences between sympatric populations are due to interactive segregation. If the segregation is wholly selective, the differences are manifest whether the species live sympatrically or not.

The present paper also deals with intraspecific genetical differentiation between allopatric populations, the vertical columns.

The whitefish populations in the Skellefte älv district

There are four whitefish species reported by SVÄRDSON from the Arjeplog district, i.e. from Lakes Hornavan, Uddjaur and Storavan and three of them are represented in Lake Storavan *Coregonus pidschian* (GMELIN), *lavaretus* (LINNAEUS) and *peled* (GMELIN). Their ecology is described by SVÄRDSON (1950, 1953, and 1957) and by LINDSTRÖM & NILSSON 1962.

An additional whitefish, the fifth in the district and the fourth in Lake Storavan, has been reported by the present author (1962 and a mimeographed paper in Swedish 1962). It is preliminarily called *älvsik,* the vernacular name for *C. nasus* (PALLAS). *Älvsik* are only caught in small numbers where they exist i.e. around the little islet off Gullön where the sample reported in Table 2 and Figs. 1 and 2 was taken on August 14, 1959. In unpublished notes from 1932 by the fishery officer OSSIAN OLOFSSON a whitefish is reported from the Bay Varras, not far from the *älvsik* locality. This Varras whitefish seems to be identical with *älvsik* (one specimen had 25 gillrakers). Another *älvsik* in the district inhabits Lake Gubbijaur, close to Lake Hornavan and five metres above the Hornavan lake level, as shown by Dr. OLOFSSON's notes (1933, 27 gillrakers) and Table 1. From Lake Gubbijaur *älvsik* can easily reach Lake Hornavan.

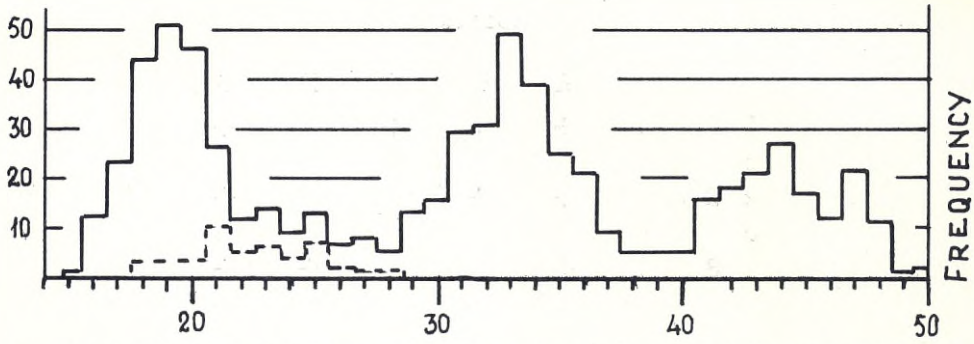


Fig. 1. Whitefish from Lake Storavan, number of gillrakers. Continuous line indicates all material, from left to right *Coregonus pidschian, älvsik, C. lavaretus* and *C. peled.* Broken line indicates sample of *älvsik* from Gullön, Storavan. A few *pidschian* are possibly included in this sample (the left wing).

Älvsik from Lake Storavan have an intermediate growth, similar to that of *C. pidschian* in these lakes, and a short life span, judging by the seine-caught sample, with most fish aged 4+ and 5+ years. 37 out of 44 should have spawned the following autumn. The spawning site is unknown and would probably be difficult to discover for this small population.

Age at maturity is also estimated for the fast-growing *C. peled* which spawns in running water and for the slow-growing *C. lavaretus* and for *C. pidschian* with intermediate growth. *Lavaretus* and *pidschian* spawn in the lake after the spawning of *peled* is over. The spawning circumstances of *pidschian* and of *lavaretus* are very close as regards both space and time. During summer and early autumn fishing in the years 1954—59 with seines of 6 and 12 cm perimeter mesh size, 36 *peled,* 55 *lavaretus* and 19 *pidschian* were caught and inspected for gonad development. Fairly often *lavaretus* specimens with an age of 3+ and sometimes 2+ years were encountered, showing convincing signs of ripening, but there was only one such specimen from the

Table 1. Gillrakers of a whitefish sample from Lake Gubbijaur, December 1965.

Number of gillrakers	20	21	22	23	24	25	26	27	28	29	30	31	35	36	40
Frequency	3	4	9	10	8	8	12	8	5	1	1	3	1	1	1

Table 2. Catch of *älvsik* at Gullön, Lake Storavan, on August 14, 1959, with a seine with 10 cm mesh perimeter. The gear should only catch the fast-growing fish of age 3+.

Age	3+	4+	5+	6+	7+	8+
Number of fish showing convincing signs of ripening	3	17	12	2	3	—
Number uncertain or juvenile	3	2	—	2	—	1

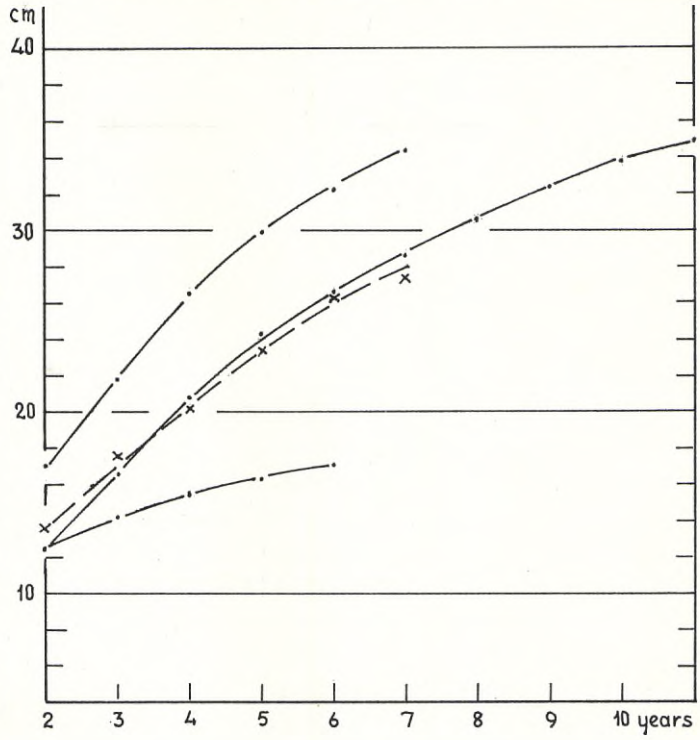


Fig. 2. Growth of whitefish, Lake Storavan. Catch year 1958 (*Älvsik* 1959). *Coregonus peled* at the top, *lavaretus* at the bottom, *pidschian* (dots, continuous line) and *älvsik* (crosses, broken line) in the middle. All growth curves in this paper are constructed with back-calculated material, means for the individual means.

other two species aged 3+ years and none younger. This material, however, is not quite conclusive, as it is difficult to evaluate the gonad development of fish without access to histological preparations (cf., e.g., BOWERS & HOLIDAY 1961), when the spawning time is remote: there is a risk that mature fish are classified as uncertain if they are not yet ripening. In 1958 and 1959 spawning *peled, pidschian* and *lavaretus* were sampled at spawning sites. The sets of gill nets had the following composition.

The sets are appropriate for catches of the small spawning specimen of the different species except the smallest 2+ *lavaretus*. To state an age at maturity requires an estimate of the fraction of the total age class that is

Table 3. Gill-net sets used in spawning place fishing, number of nets of different mesh sizes.

Year	Species	Knot — to — knot bar measure, cm						
		5.0	3.8	3.3	3.0	2.5	2.1	1.7
1959	*peled*	1	1	4	4	1	—	—
1958	*lavaretus*	3	4	3	1	—	—	1
1959	*pidschian* and *lavaretus*	2	2	4	4	2	2	2

Table 4. Number of spawning *C. peled, lavaretus* and *pidschian* in Lake Storavan in the gill nets specified in Table 3. Uncertain or juvenile fish in the catch are not tabulated.

Date	Species	Age									Total
		2+	3+	4+	5+	6+	7+	8+	9+	10+ and older	
1959, Oct. 27—Nov. 6	*peled*	—	—	—	3	13	10	18	22	18	84
1958, Nov. 11—Dec. 1	*lavaretus* ...	6	14	20	7	2	1	—	—	—	50
1959, Nov. 6—Dec. 5	*lavaretus* ...	48	96	42	12	2	—	—	—	—	200
1959, Nov. 6—Dec. 5	*pidschian* ..	—	3	10	11	17	10	6	10	8	75

mature, but this is difficult to arrive at. From the data in Table 4 an arbitrary age at maturity is estimated.

Length at maturity, Table 5, is the actual length at age of maturity in the autumn and the K and L_∞ are computed from back-calculated material in FORD-WALFORD growth regressions (RICKER 1958).

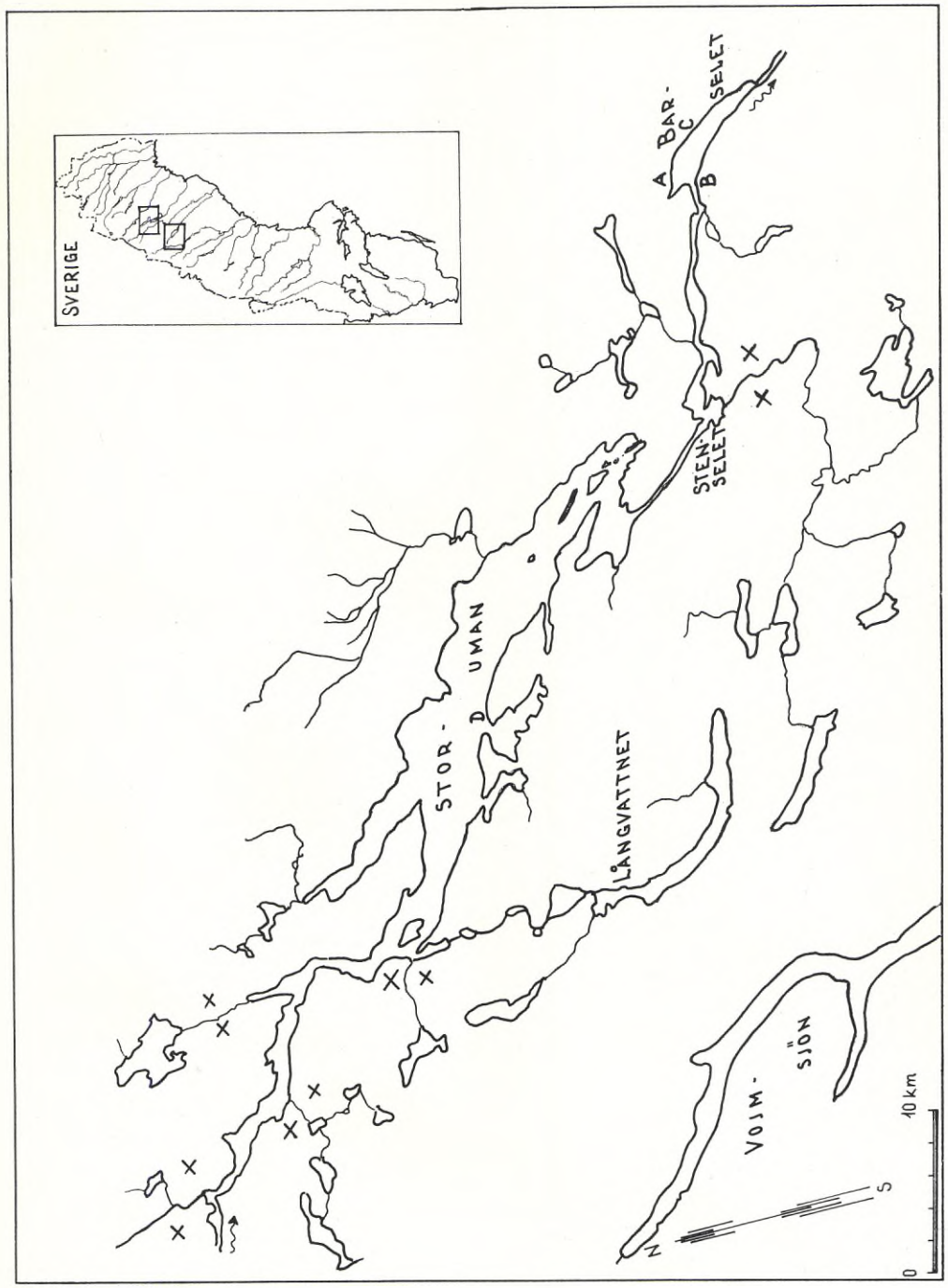
C. peled has a good growth in the lakes along the central course of the river. This whitefish also occurs in small adjacent lakes with free access for whitefish to and from the central lakes. Apart from these lakes there are a lot of small lakes in this district of the Skellefteälv river system, and many are discussed in the fishery regulation act and notebooks of Dr. OLOFSSON. *C. peled* or *asp* is reported only from Lakes Sebnesjaure, Gubbijaure and Jutis and from the Maskaure lakes and in no case is it the whitefish species

Table 5. Length and age at maturity, arbitrary estimates and growth parameters. A sample of *nasus*×*pidschian* from Storuman has K=0.12 and L_∞=50 and l_m is moderate.

Species Lake	*C. peled* Storavan	*C. lavaretus* Storavan	*Älvsik* (*nasus?*) Storavan	*C. pidschian* Storavan	*C. peled* Storuman	*C. peled* Barselet	*C. nasus*× *pidschian* Barselet
Length at maturity, cm	35	15 15	24 23	24	18	20	27
Age at maturity	6+	3+ 2+	4+ 3+	4+	2+	3+	6+
K	0.21	0.26	0.20	0.15	0.54	0.80	0.29
L_∞, cm	44	22	35	62	20	21	29

Fig. 3. Map of the Ume älv district. In the small tributaries, marked with two crosses, whitefish did not inhabit the lakes originally, according to the notebooks of DR OLOFSSON from the 1920s. Later, whitefish was introduced in some of these lakes in the small tributaries, but *peled* has not developed a population in any of the lakes, so far as is known. In the Långvattnet system, where whitefish is indigenous, no *peled* is found in the investigated samples (1965).

The upper square in the inserted map of Sweden indicates the Skellefte älv system. Map and further particulars in LINDSTRÖM 1962.


SVERIGE
A
BAR-
C
SELET
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STEN-
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STOR-
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VOJM-
SJÖN
10 km
N
S
0

Fig. 3.

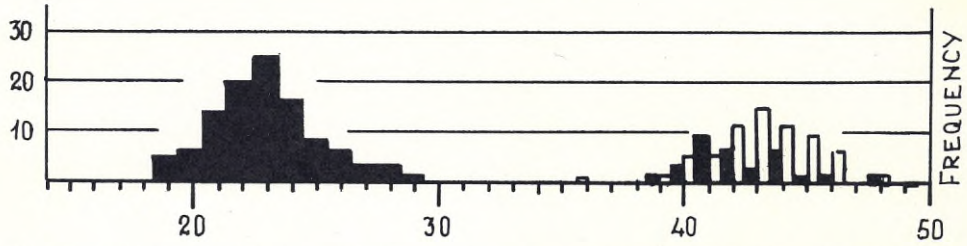

Fig. 4. Whitefish from Lakes Barselet and Storuman, number of gillrakers. Barselet black columns, Storuman white columns. Further material is presented in SVÄRDSON, 1957.

with the poorest growth (a recent sample of 33 whitefish from Maskaure only contained *C. lavaretus,* mean of gillrakers =33.2).

The whitefish populations in the Ume älv district

The whitefish species in the Ume älv river system is described by SVÄRDSON (1957) who states that *Coregonus nasus* and *pidschian* form a pattern of introgression and replacement within the whole river system and that the bimodality of the population is reflected by the gillraker cline 22.3—23.8—25.8 from the northernmost part of Lake Storuman (Fig. 3) downwards to Lake Stenselet just downstream from Lake Storuman. From Lake Storuman SVÄRDSON also reports a dwarfed population of *C. peled.* According to mimeographed memoranda both the *peled* population and the *nasus—pidschian* complex, denoted in the present paper as *nasus*×*pidschian,* have spawning places in still water in Lake Storuman, the latter also spawning in a current between two islets in the southern part of the lake. The *nasus*×*pidschian* population of Lake Stenselet has a spawning site in the river just above the entrance to the lake and this population has the best growth of all in these lakes of the Ume älv river, including Lake Barselet. In Lake Barselet the *nasus*×*pidschian* spawns e.g. some hundred metres off the river entrance. The spawning site of *peled* is not known in Lake Barselet.

Lake Barselet, Fig. 3, was a *sel* in the Ume älv River, i.e. the flow was — and is — great compared with the volume of the lake. The *sel* was influenced by dam constructions, channel digging and power plant construction in the river above Barselet, and the turbidity increased, particularly in 1958. The *sel* was transformed into a power plant reservoir ("river reservoir") in 1957 and this effect is discussed by the present author (1965). About one half of the yield consists of whitefish. Pike, perch, grayling, trout and burbot are also caught.

The gillrakers of whitefish from Lake Barselet are reported in Fig. 4. There are some indications of exchange between the whitefish populations in the three lakes discussed and a growth analysis from Lake Barselet suggests

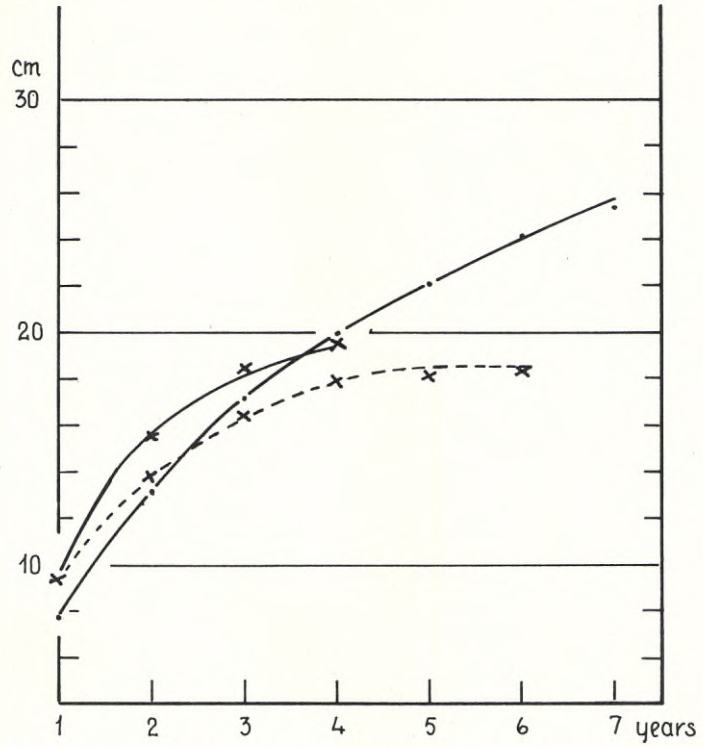

Fig. 5. Growth of whitefish, Lakes Barselet (1964) and Storuman (1965). Owing to the LEE effect, the length of *C. nasus*×*pidschian* in Barselet (dots and continuous line) still appears to be less than that of *C. peled* in Barselet (crosses and continuous line) at the age of three years, whereas the 2+ *C. nasus*×*pidschian* were actually a little longer than *peled* at the capture in September. Crosses and broken line=growth of *peled* in Lake Storuman.

that its population may have been fortified through migrations from the region higher up in the system during 1958, but there is no conclusive evidence. Lately the *peled* population of Lake Barselet has not been much observed as it is usually not caught in the gears but old people have talked about a dwarfed whitefish maturing in small size. Growth of the *peled* and *nasus*×*pidschian* populations is reported in Fig. 5. *Peled* was mainly caught in the vicinity of A on the map, Fig. 3, as shown by the following table.

Table 6. Occurrence of *C. peled* and *nasus*×*pidschian* in the catch September 1964, with four gill nets each night, 2.1 knot-to-knot bar measure.

Date	Station	*C. peled,* number	*C. nasus*×*pidschian,* number
Sept. 27	A	25	26
Sept. 28	B	4	29
Sept. 29	C	1	21

Table 7. A sample from Barselet September 26—29, 1964. The category "not ripening" may of course contain some mature fish, which will not spawn this autumn.

Age	*C. peled*		*C. nasus×pidschian*	
	Number ripening	Number not ripening	Number ripening	Number not ripening
1+	—	—	1	1
2+	1	1	—	21
3+	20	—	1	27
4+	9	—	2	21
5+	—	—	2	4
6+	—	—	8	3
7+	—	—	6	3
8+	—	—	4	1
9+	—	—	—	—
Older	—	—	1	—

At station A, dwarfed and mature whitefish are caught earlier in lake-survey fishing covering the whole lake. This therefore seems to be another example of a small local population, but in contrast to the situation in Lake Storavan it is formed by *C. peled* whereas the main population of the lake is *C. nasus×pidschian*. Only one *peled* but 22 *nasus×pidschian* were caught in four gill nets with 3.3—3.0 cm bar measure, set each night at the same stations. The life span of *peled* is short.

Age at maturity is estimated from Table 7, and both age at maturity, and growth parameters are introduced in Table 5.

In a *peled* sample from Lake Storuman (Fig. 3, D) all specimens were ripening, and the age at maturity is estimated to be 2+ (Table 8).

Number of gillrakers and a growth curve are presented in Figs. 4 and 5.

Whitefish from a number of adjacent lakes in the Ume älv river system are also studied (Fig. 3) but in no case is a *peled* population found or surmised to occur. The material studied includes Dr OLOFSSON's notebooks.

The exploitation of the whitefish stocks in Storavan and Barselet

The fact that back-calculated length values for some age groups are smaller the older the fish were at capture, i.e. the LEE effect, can at least partly be explained by selective fishing, taking fast-growing specimens of some age groups while the slow-growing specimens are not yet available to the fishing. This LEE effect is there studied by comparing fish of age 3+ at

Table 8. Age composition of a *peled* sample from Lake Storuman October 1, 1965, gill nets 2.1 and 1.7 cm knot-to-knot bar measure.

Age	2+	3+	4+	5+	6+
Frequency	18	27	16	6	1

Table 9. The LEE effect. Differences in mm between length values obtained from fish that were 3+ at capture and values obtained from older fish.

		Age of the compared fish at capture		
		3+ and 4+	3+ and 5+	3+ and 6+, 7+
"Älvsik", Storavan.	1 year	9	18	15
Seine, perimeter 10 cm	2 years	13	27	18
	3 years	23	38	34
	3+ and 4 years	> 34	> 48	> 41
C. peled, Storavan.	1 year	−3	−11	−4
Seine, gill nets and kakuami	2 years	5	−16	4
	3 years	14	1	14
	3+ and 4 years	all values negative, but growth of 3+ not finished		
C. nasus×pidschian,	1 year	3	8	27
Barselet.	2 years	7	11	39
Gill nets, 3.3, 3.0 and	3 years	14	9	30
2.1 cm bar measure	3+ and 4 years	> 18	> 15	> 30
C. peled, Barselet.	1 year	3	—	—
Gill nets, (3.3, 3.0 and)	2 years	11	—	—
2.1 cm bar measure	3 years	5	—	—
	3+ and 4 years	> 2	—	—
C. peled, Storuman.	1 year	−2	13	—
Gill nets, 2.1 and 1.7 cm	2 years	1	16	—
bar measure	3 years	7	19	—
	3+ and 4 years	> 2	> 11	—

capture and older age groups, and it is measured as the difference in mm between calculated length values at the end of the first, second and third years of life. The value obtained from older fish is subtracted from the value obtained from those fish that were 3+ at capture. The difference between the actual length of the 3+ fish at capture and the calculated length at the end of the fourth year of life is also introduced in Table 9, (last line in each species).[1]

As total yield figures for the different whitefish species can hardly be obtained, the LEE-effect analysis is introduced to give a hint about the fishing pressure on the different stocks, Table 9. Gill nets with 3.0 cm knot-to-knot bar measure or more are generally used in Lake Storavan for *peled* and *pidschian* and also in Lake Barselet for *nasus×pidschian*. In Storavan small-meshed seines are used for *lavaretus* and thus young fish of other species may be caught. It can be estimated that the gill nets should take fish of 25 cm total length with some efficiency and thus catch *pidschian*, *peled* and *älvsik* in Storavan and also *C. nasus×pidschian* in Lake Barselet while leaving the *peled* stock in Barselet almost untouched. The *peled* stock in Barselet no doubt shows a very small LEE effect but in the data from the exploited *peled* stock in Storavan there are even some negative values, indi-

[1] Back-calculation method: the graph movable round the intercept with the body-length axis.

Table 10. The LEE effect in some summer catches of *C. peled* in Lake Storavan with a bait seine, mesh perimeter 6 cm. The effect is measured as in Table 9.

	Age of the compared fish at capture	
	3+ and 4+	3+ and 5+, 6+, 7+
1 year	9	0
2 years	15	9
3 years	21	25

cating that the length calculated from 3+ fish is smaller than the length calculated from older fish. The *peled* sample in Storavan were caught with seine, kakuami and gill nets at several places. The results imply that the method can only be used to give information about fishing pressure for a less heterogeneous sample. Such material is presented in Table 10, a sample caught with a bait seine, mesh perimeter 6 cm, showing a higher LEE effect than the *peled* sample from Lake Barselet. If the method is relevant, the LEE effect analysis has thus confirmed that the exploitation of the Barselet *peled* stock is very slight. The *peled* in Lake Storuman is somewhat exploited.

References to some other whitefish populations

The ecology of the whitefish in Lake Vojmsjön has been described by FABRICIUS (1950). He discusses the interrelationships between temperature, bottom material and spawning time. *C. pidschian* spawns in the tributaries and outflows of the lakes in the district and also in the lakes and the depth is generally comparatively shallow. *C. peled* is smaller-sized and spawns in Lake Vojmsjön, where the bottom slopes more or less steeply down to greater depth. In the shallowest parts of the lake most of the *peled* spawning sites are situated on the slopes running down to a deep channel extending the length of the lake, where the current is recognizable. *C. oxyrhynchus* is extremely dwarfed and is likely to spawn at quite considerable depths. The systematics of the species are discussed by SVÄRDSON (1958) and growth curves for *pidschian* and *peled* are presented by LINDSTRÖM & NILSSON (1962). SVÄRDSON (1949) has published a photo giving an indication of the average size of the third species. Length at maturity is greater for *pidschian* than for *peled*.

LINDROTH has published an account of the whitefish of the Sundsvall Bay district in the Baltic (1957). There are two species, both with good growth, and according to SVÄRDSON (1957) they are *C. lavaretus* and *nasus*, with some introgression between the species. LINDROTH states that *lavaretus* spawns in the Indalsälven river and *nasus* on the stony grounds of secluded coastal bays. He gives a description of the life history of the first year for

lavaretus and discusses the katadromesis in whitefish. He states that the migratory behaviour quantitatively most important for the maintenance of the *lavaretus* stock is represented by the mass transportation of the newly hatched fry in the Indalsälven, down into the Sundsvall Bay.

This is a large-scale example of what is realized in some inland lakes: one whitefish species spawns in a tributary and the fry is rapidly transported down into the lake, while another species spawns in the lake below the inlet of the tributary.

SVÄRDSON presents a case (1957, p. 296) of *C. nasus* spawning in a tributary to Lake Nälden, followed by the spawning of *lavaretus* later in the autumn in the same river, with the spawning periods for the two species overlapping. Details of the spawning sites within the river are not yet published, but they are certainly not widely spaced. *C. pidschian* is also described from Lake Nälden, *op. cit.*

Discussion

In the preceding pages cases are presented where there is not only a change in ecology of allopatric populations of one whitefish species but also an apparent interchange in ecology between different species. To some extent such cases can be explained if we assume that the different species combinations and other environmental variations between lakes give enough variation in the premises to make a species respond, for example, with good growth in one lake and poor growth in another, apparently interchanging growth ecology with other species in the two lakes (LINDSTRÖM & NILSSON 1962, p. 335—337).

Longevity and size at maturity may depend on the growth, and so also, according to SVÄRDSON (1965), does the reproductive isolation. In that case, highly essential ecological features are controlled by a delicate interplay between the population and its environment. It could furthermore be maintained that the genetical differences between the ecology of the white-fish sibling species might mainly concern some basic reactions in the biology of the whitefish young, growth, longevity, size at maturity and reproductive isolation only being delayed consequences of the young fish biology. This model is, however, not very realistic.

According to the earlier interpretation, cited in the first paragraph, intraspecific genetical differences between allopatric populations and interspecific selective segregation are assumed to play subordinate roles for growth but they are not assumed to be altogether inactive, and further investigations and further data are needed in order to establish the importance of the different agents. An estimation of the importance of "heredity" and "environment" seems to be premature at present. More experimental work and more data from the whitefish ecology in nature is needed. The present paper is concerned with certain growth parameters, size at maturity

as well as with spawning-site choice, to which a kindred argumentation applies.

A. Spawning-site segregation

There are some cases where there would seem to be a very "narrow escape" for the reproductive isolation if ethological barriers or size differences were not working against hybridization. In some parts of Lake Vojmsjön the spawning time of *C. pidschian* and *peled* coincide but there is a difference in spawning bottoms (FABRICIUS 1950). In the Nästån River there is an overlap in spawning time for *lavaretus* and *nasus* (SVÄRDSON 1957), and in Lake Storavan the spawning of *C. pidschian* and of *lavaretus* in the lake are very close in space and time. In the last two cases there may exist a space segregation that could be revealed by a detailed analysis, and *lavaretus* seldom reach the size at which *pidschian* matures in Lake Storavan — a fact that supports the theory of reproductive isolation through size at spawning, presented by SVÄRDSON (1965).

If streams were the preferred spawning sites for one species only, this could contribute to the segregation. It has, however, been shown that different species spawn in running water in different lakes, a typical "interchange ecology". In the Storavan district, the Ume älv district and the Vojmsjö district, it is the species with the highest length at maturity, l_m, that occupies the streams for spawning. In some other rare cases there may even be more than one species using the same stream for spawning. It is well within the capacity of each whitefish species to spawn both in lake and stream, and there is reason to believe that this is also within the capacity of most whitefish populations, as has been conclusively shown for a char population by FABRICIUS (1950). According to FABRICIUS, a certain type of bottom is one of the most important factors for the release of the spawning activities in whitefish and the fact whether it is running or stagnant water is of less importance. It is also difficult to establish a clear-cut distinction between lake spawners and stream spawners in certain lakes. The stream-spawning *pidschian* in Vojmsjön also spawns in the lake, whereas the lake-spawning *peled* partly spawns on the slopes running down to a channel in the lake, with an indication of a noticeable current (*op. cit.*). In Lake Storuman the *pidschian*×*nasus* spawns both on the shores and in a current between two islets in the lake, whereas this introgressed species complex spawns in the main tributary to Lake Stenselet and in the lake just below the inflow of the main tributary to Lake Barselet, where the current is still appreciable, as well as further down in that lake.

Do all these facts show that the different whitefish species have much the same reactive pattern vis-à-vis streams and lakes, respectively, as spawning-sites and that the spawning-site segregation that actually exists only reflects interactive segregation? Probably not.

First, it could not be maintained that the spawning-site segregation between species should be less evident when population abundance is low in conformity with food segregation when food is superabundant (NILSSON 1965). As reproductive isolation ordinarily is *inter alia* dependent on spawning-site segregation, it ought not to be so easily modified. Homing is one mechanism by which spawning site segregation might be maintained even when the population number is low.

Secondly, there is, generally speaking, hardly a lack of bottom that might release spawning in an appropriate situation of heterogeneous stimulus summation as defined by FABRICIUS 1950, but there is a demand for 'habitat area for successful development of whitefish broods' in excess of immediate supply. This question concerns the interrelation between the parental generation and the progeny.

The parents' choice of spawning-site gives part of the premises with which the genetic set of the eggs and the fry in next generation has to cope, and the survival of the progeny depends *inter alia* on the habitat in which the early life is enacted. Selection has, of course, the best opportunity to act during this period of high mortality, but not only young with less appropriate feeding habits, habitat choice and reactions against predators but also the progeny of parents with bad spawning-site choice should be selected against. (Once an appropriate spawning-site is established, homing might reduce this selection pressure).

If more than one whitefish species inhabit a lake, the difference in spawning-site choice is thus one of the ecological differences that should be positively selected for if segregation of their young are to be established. The segregation has taken different directions in different districts as can be inferred from the fact that *peled* is the stream spawner in all important streams in the Storavan district, not only in the streams flowing into or out of this lake, whereas *pidschian*×*nasus* has the corresponding position in the Ume älv district referred to in this paper, and *pidschian* is the stream spawner, in all important streams in the Vojmsjö district of the Ångermanälven river, according to FABRICIUS (1950). It is not likely that only interactive segregation is the working agent, as this presupposes environmental differences between districts and similarities within each district, which are difficult to envisage. Some other component must be involved.

B. Growth Ecology

There are similarities between spawning-site ecology and growth ecology, viz. a possible importance of differences in growth of the parents for survival of the progeny, as there is some interrelation between size of spawning female and size of eggs and size of fry at hatching, summarized e.g. by BROWN (1957) and NIKOL'SKIĬ (1962). (Egg size should be of some importance, as the bottom material on the spawning-sites varies in grain size).

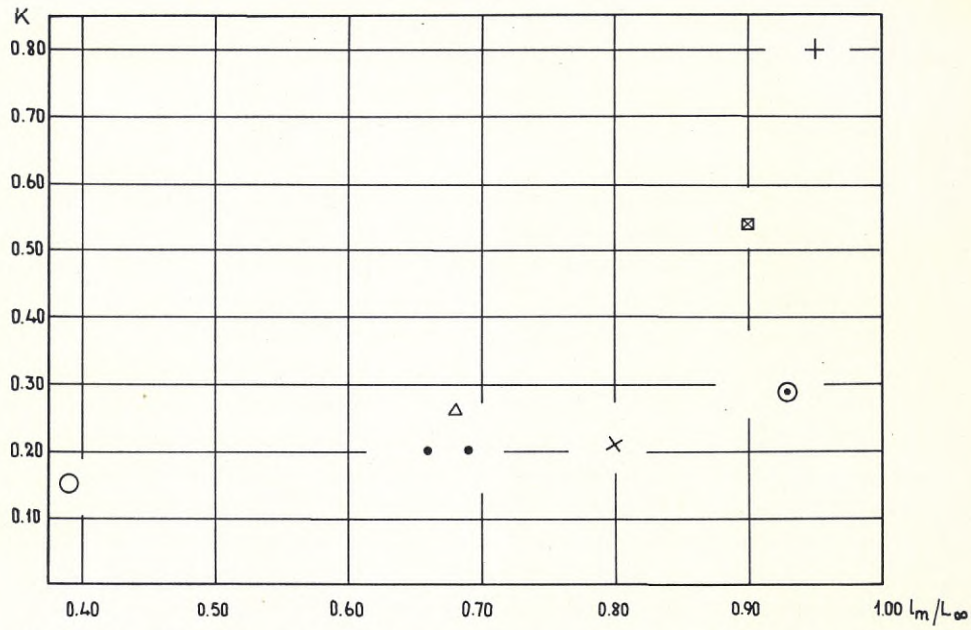

Fig. 6. Interrelationships between the growth parameter K, RICKER 1958 — high K-values for fish approaching their asymptotic size rapidly — and l_m/L_∞, i.e. length at maturity/asymptotic length. The relation is discussed by HOLT 1962.

Lake Storavan: *C. pidschian* ○, *Älvsik* •, *C. lavaretus* △, *C. peled* ×.
Lake Barselet: *C. nasus*×*pidschian* ⊙, *C. peled* +.
Lake Storuman: *C. peled* ⊠. (*C. nasus*×*pidschian* in Table 5.)

Selection can eliminate the progeny of parents with less appropriate growth, and growth differences between the whitefish species inhabiting a lake may thus contribute to the segregation of their young. If there is such a segregation between species, it has taken different directions in different districts also when growth ecology is concerned. There is, however, a good deal of controversy about the genetic control of growth. In growth analysis, the parameter K describes the relative rate of approach to the asymptotic length, and K increases with the temperature but is less modifiable by changes in food consumption than the asymptotic length itself (HOLT 1962). The size of spawning females is related to length at maturity, l_m. There is a broad range of variation within the species *C. peled* in Lakes Storavan, Storuman and Barselet. In a relation between the parameters K and l_m/L_∞ (HOLT, *op. cit.*) constructed for whitefish in Fig. 6, the *peled* populations occur over a wide range of the diagram.[1]

[1] The growth heterogeneity, discussed on p. 138 for a *peled* sample from Lake Storavan, is also observed for growth of *C. lavaretus* in this lake and affects the estimation of K and L_∞. The *lavaretus* and *peled* values in Table 5 for these two parameters are calculated with

Table 11. Mean water temperature in the outflow from Lake Storavan and the outflow from Lake Storuman according to the *Metereological and Hydrological Institute of Sweden.*

		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1953	Storavan	—	—	—	—	—	13.08	16.23	14.61	9.03	4.45	0.98	0.37
	Storuman	0.90	0.90	1.25	1.83	3.96	6.99	13.00	14.28	10.37	6.56	2.86	1.26
1954	Storavan	0.28	0.26	0.28	0.84	4.02	10.04	16.02	13.87	9.55	2.60	0.83	0.71
	Storuman	0.69	0.66	0.82	1.19	4.39	8.01	—	—	10.69	5.03	1.52	1.70
1955	Storavan	0.14	0.79	0.65	0.83	2.50	6.93	14.10	14.22	10.09	2.93	0.63	0.92
	Storuman	0.83	0.71	0.78	1.05	2.17	5.92	11.48	13.45	11.72	5.49	1.35	0.77
1956	Storavan	0.98	0.95	0.92	1.16	3.98	9.31	15.30	12.55	7.63	1.94	0.28	0.39
	Storuman	0.80	0.70	0.74	1.08	3.46	7.36	12.83	12.25	9.18	4.18	1.37	0.74

The *peled* of Lakes Storavan and Uddjaur is known to keep to the surface in summer and occurs frequently in shallow water. In the Skellefteälven river system, Lake Hornavan is deep but both Uddjaur and Storavan are shallow lakes. Lake Storuman in the Ume älv river system is deep but Lake Barselet is shallow, and the dwarfed *peled* in Lake Storuman occurs both pelagically in the main body of water and in a shallow bay. In Lake Barselet the dwarfed *peled* is only caught in a sheltered bay. Outflow temperatures from Lakes Storavan and Storuman are presented in Table 11.

These data and Fig. 6 are not quite consistent with a temperature effect on the K of *peled* and, besides, the K of the other species is much less variable. Some other factors must have obscured the temperature effect on the *peled* K. (Admittedly one cannot tell exactly what temperatures the *peled* of the different lakes have experienced; better data can only be obtained experimentally).

The Storavan *peled* stock is exploited, whereas the Barselet *peled* stock is hardly exploited at all. The differences in K and l_m/L_∞ are not affected through different fishing pressure in a way recalling how growth and maturity were altered after changes in fishing on a whitefish stock described by MILLER (1956). The exploited Storavan stock has certainly better growth but it has also a higher age at maturity. ALM (1959) and HOLT (1962) have recently discussed the relation between growth, maturity, fishing mortality and natural mortality, and HOLT — quoting an earlier paper by BEVERTON & HOLT — suggests, on the basis of that study, that within a particular taxonomic group the coefficient of natural mortality M and the growth parameter K were positively correlated. HOLT continues that the existence of a mechanism relating maturity size with K would ensure "that in a population subjected to a high extrinsically determined natural mortality, and containing individuals with a genetically determined range of K values, the

material from two different stations of the lake, catch year 1958. The *lavaretus* growth curve in Fig. 2 is constructed with only part of this material, and gives other values for K and L_∞.

fish with high K values, which mature earlier, would have a selective advantage over those with low K values, so that an adequate number would reach maturity in each generation to ensure its survival". This might apply to the *peled* stock in Lakes Storuman and Barselet, the high K and l_m/L_∞-values being concurrent with a high natural mortality.

C. Towards a selective model for the structures of the whitefish populations. Conclusions

The rigid relation between K and l_m/L_∞ — borne out also by the present investigation — is thus related to the extrinsically determined natural mortality above the young stages, and to this should be added a reference to the "similarity, or even identity, of physiological processes which determine the rates of natural mortality and growth" (HOLT 1962). In sections A and B is discussed a probable relation between growth of adults and survival of the young via l_m, egg and fry sizes and choice of spawning-site. It is thus possible to get some insight by growth studies into the age-specific birth rates and death rates and thus into actual rate of increase of the populations (ANDREWARTHA & BIRCH 1954, BIRCH 1960, MAYR 1963 e.g. page 422). The genetic control over the capacity of increase is discussed by BIRCH and by MAYR who on p. 64 concludes that there is a strong genetic component.

When a selective model for the whitefish populationstructure and its changes is attempted, the phenotypic flexibility and the complexity of the major components of fitness must be regarded. Transplantations have shown that the growth parameters of whitefish are modifiable within wide limits (SVÄRDSSON 1951, Table 13, Figs. 4 and 8; cf. also SVÄRDSSON 1965, hybrid whitefish). Whitefish show a high phenotypic flexibility, mainly behavioural flexibility as defined by THODAY 1955, in their ecological characters. This circumstance, repeatedly shown, inter alia, in several papers from the Drottningholm laboratory, reduces the selection pressure.

It is equally necessary to consider the cooperation of several components in the phenotype on which the selection acts (MAYR). Selection can hardly change whatever hereditary component there is in growth without there being simultaneous changes in food preferences (NILSSON 1960, 1965) and young biology (LINDSTRÖM & NILSSON 1962, LINDSTRÖM 1962, Ch. 12). Growth, food preferences and first year biology must cooperate to form the fitness of the phenotype, to mention only a few such relations. This does not mean that the simultaneous changes in food preferences and young biology must be changes in genotype (cf. MAYR Ch. 14).

How then can one account for the apparent interchange in ecology, mentioned in the introduction and on p. 139? A splitting e.g. of the *peled* species into one species for the Skellefte älv district and another for the Ume älv district could hardly be established without a test of the involved populations

in sympatrical condition, and might soon be followed by new splitting claims for other situations. At present it seems more likely, however, that the "interchange ecology" is explained by the following three points, and thus there is no need for a discussion of species splitting.

(1) Environmental differences can account for different ecology in different lakes but hardly for all the differences between the *peled* ecology in the two river systems as discussed on p. 141.

(2) A certain amount of intraspecific differences in the gene pools between the Skellefte älv and Ume älv *peled* populations may have evolved, possibly in some K genes, p. 143.

(3) *Peled* occurs to the right of other sympatric whitefish populations along the regression in Fig. 6, and this seems to be a character of this species. Length at maturity is governed for all species by the position in this regression, i.e. by K and the L_∞, where L_∞ is more sensitive to changes in food consumption. Thus K and L_∞ decide which species will be stream-spawning viz. the species with highest length at maturity. When species interact, their habitats and their food consumption are affected and so their asymptotic lengths may shift, but only when their K-values are established are their new l_m-values decided. The effects on K of temperature and extrinsically determined natural mortality have been discussed above. A continued investigation into the factors affecting the K-values should be rewarding.

The value of the length at maturity and the spawning-site choice partly decide some essential features in the ecology of the progeny and affect their survival (pp. 141—2).

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