Great plasticity in Arctic char populations. Populations have the ability to change their growth and spawning time (half-life), spawning depth (shallow water), growth rates, spawning age (size), and environment. These changes can occur in a few generations for a single family stock.

- Spawning a later in spring, a different location

- Distinctly different stocks traceable to specific locations during ice ages and lake dispersal (essentially 2 or 3 species)

Proceedings of the first SACF workshop on Arctic char, 1980
Proceedings of the first ISACF workshop on Arctic char, 1980

Proceedings of the first ISACF workshop on Arctic char, 1980

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PREFACE

This collection of papers reporting on the manifold aspects of Arctic char population research emanates from the first international workshop on the subject. The workshop was initiated and sponsored by ISACF, short for the International Society of Arctic Char Fanatics, an international body of selected scientists founded in 1979 and gradually expanding its coverage with the final aim of having members in all countries inhabited by Arctic char. The objective of ISACF is to further cooperation on an informal basis between specialists in this field.

The chief objective of the first workshop was to summarize the major aspects and problems of the ecology and taxonomy of Arctic char as seen by Fisheries Biologists working with char management.

It is then essential to study in detail the complicated systematics of the various char species lumped together under the name of *Salvelinus alpinus* (L.). Within this species complex great controversy still remains as to the taxonomic position of numerous allopatric taxa and the management problems arising from this confusion. The taxonomy and management of this group of fishes is also complicated by the occurrence of multiple sympatric taxa differing in ecological adaptations. Introgression between these taxa, selective fishing methods and other types of human interaction with the char populations do indeed stress the importance of gathering intimate knowledge of the various populations.

It was thus the intention of the workshop to try and gather and coordinate pertinent information on populations of Arctic char to obtain a dynamic picture of the various taxa of char throughout their geographical distribution. Special emphasis was on multiple approach methods for recognizing char taxa, viz. the combination of genetic and ecological parameters.

A further objective of this workshop was also to discuss and formalize the statutes of ISACF and no additions or deletions to the original proposals have yet been filed.
The papers presented are summaries of varying length of the papers presented at the workshop on the premises of the Askö Laboratory (University of Stockholm) from October 7–9, 1980. The kind and tolerant assistance of the staff of the Askö Laboratory, and Lars Westin and Kerstin Ernqvist in particular, was much appreciated and provided a fruitful basis for the safe progress of the workshop activities.
ELECTROPHORETIC ANALYSIS OF THE ARCTIC CHAR OF CUMBRIAN LAKES

A. R. Child

Cumbria is situated in the north-west of England. There are eleven major lakes and of these six contain populations of Arctic char, Salvelinus alpinus L. Electrophoretic studies have been carried out on populations from three of these lakes, Windermere, Coniston Water and Ennerdale Water. In contrast to the Arctic char of other European countries, the Cumbrian char have two distinct spawning times. In Windermere, two populations exist which spawn at different times, autumn and spring. In Coniston, char spawn in spring and in Ennerdale spawning occurs in autumn. The spring spawning char always spawn in deep water (15-20 m) whereas the autumn spawners are found in shallow water (1-3 m). The biology of the Cumbrian char has been extensively described by Frost (1965). The aim of my work was to analyse the serum of char from the three lakes and to study genetic variation at the esterase and transferrin loci.

For the majority of fish, blood was extracted under MS222 anaesthesia and the char subsequently released into their lakes. The electrophoretic methods were as described in Child (1977). Autumn spawning char were taken at two sites in Lake Windermere, Red Nab and Rawlinson Nab and in two years, 1976 and 1977. Spring char were taken at Holbeck Point. All fishing was with gill nets set on the bottom and only sexually mature char were analysed.

The char were polymorphic at the serum transferrin and esterase loci. The numbers of fish examined with the observed numbers of genotypes and the expected number of genotypes calculated from Hardy-Weinburg equilibrium are shown in Table 1, together with the gene frequency of the anodal allele at each locus and the estimated 95% confidence limits. Since no differences between site and year were noted for autumn spawning char in Windermere all data have been pooled.
(i) Transferrin

The spring spawning population from Coniston Water was significantly different from the other three populations. No variation was noted between autumn and spring char from Windermere.

(ii) Esterase

The autumn Windermere char consistently showed a heterozygote excess for esterase. This has been observed by L. Nyman (pers. comm.). The gene frequencies for spring and autumn Windermere char were different and displayed no overlap of the 95% confidence limits.

The Coniston char had a high Est F frequency, as with transferrin, different from all the other char populations. The autumn spawning Ennerdale char had gene frequencies for the Est alleles indistinguishable from the Windermere spring population.

The inference from the gene frequency data is that the Coniston char are quite distinct from the other Cumbrian char analysed at two loci. The Windermere spring and autumn char can be separated by the esterase gene frequencies and the Ennerdale (autumn spawning) char are similar to the Windermere spring char.

The results of tagging experiments by Frost (1965) suggests complete separation of the autumn and spring char, both of which have strong homing tendencies. However, breeding experiments revealed no barriers to cross-fertilization and no genetically-fixed spawning time.

The differences in spawning time and location of the spawning ground and the distinctive esterase gene frequency values indicate that there is no mixing of the genetic pools of these two groups of char, suggesting sympatric speciation. I am not convinced that these two populations should be considered as separate species, however. Large differences in the transferrin and esterase frequencies have been found in char from Welsh lakes (Child, 1977) but I am not prepared to accept that these
char represent different species. It is more likely that the gene frequency differences are due to genetic drift or founder effect in isolated populations.

The majority of char spawn in autumn, however, in three other Cumbrian lakes, Hawes Water, Crummock Water and Buttermere the char spawn in December/January (Frost, 1965).

It is suggested that the original colonizers of Cumbrian lakes were able to spawn over a wide range. The peaks of autumn and spring spawning occur when the day length is about 8 1/2 hours and it is possible that the late spawners (December) delayed ripening until the day length was more advantageous. The deep water spawning of spring char is probably an adaptation to overcome problems of the temperature conditions at the time of hatching. Spring spawned eggs which hatch in early summer would be unable to survive the higher temperatures found in shallow water.

The results do not suggest the existence of two ancestral populations of char with different breeding seasons but rather adaptation by the char to two ecological niches which optimize breeding success. Subsequent changes in gene frequencies are considered to be the result of either genetic drift or founder effect.

Further information from other gene loci might help to clarify the situation.

REFERENCES

Table 1

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PARASITISM BY Diphyllolbothrium spp. AND THE INHIBITION OF MIGRATORY BEHAVIOUR IN Salvelinus alpinus, THE ARCTIC CHAR, A PROGRESS REPORT

M. A. Curtis
J. G. Hunter

Abstract of a paper read at the ISACF Workshop on Arctic Char at the University of Stockholm's Askö Laboratory, October 8, 1980.

ABSTRACT

The viscera of non-migratory, lake-resident arctic char are often heavily parasitized by larval cestodes of the genus Diphyllobothrium, whereas anadromous char at most harbour light infections. To investigate the possibility that Diphyllobothrium may be implicated in blocking the migratory behaviour of normally anadromous char, scale and otolith samples acquired during several past surveys of char stocks in the Canadian Arctic that included parasitological observations were examined.

Strontium, which is differentially incorporated in otolith formation depending upon its presence in the environment, was measured from stored otolith samples in order to determine whether or not individual fish were anadromous.

Otoliths from char which had been physically landlocked had strontium concentrations in both parasitized and non parasitized fish at approximately 200 ppm. Otoliths from anadromous char contained amounts in excess of this up to 1700 ppm-strontium. In Nettling Lake, Baffin Island, the presence of heavily parasitized char exhibiting high strontium concentrations in their otoliths indicates that such fish were once anadromous. These heavily parasitized fish are never found in the sea-run component of the lake's char population, even though they are non-reproductive and thus could have been expected to migrate to sea during the summer. It appears most probable that anadromous
char may acquire *Diphyllobothrium* during years in which they remain in lakes to spawn and once becoming infected no longer migrate to the sea.
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- **Heavily Infected**
- **Lightly Infected or Uninfected**
In Ireland lacustrine populations of charr are widespread especially in the western part of the country and their present distribution has been extensively reviewed by Went (1945, 1971). Regan (1908, 1911) recognised six groups or "species" of charr in Ireland and nine in Great Britain. However, he acknowledged that all were forms of *Salvelinus alpinus* but thought it simpler "to keep the binomial nomenclature". This use of binomials rather than trinomial sub-specific names has led some workers to interpret Regan's "species" too literally.

Samples of charr have been obtained from seven Irish lakes and from Windermere in N.W. England, representing five of Regan's "species". Skeletal muscle, liver and heart samples were examined by starch gel electrophoresis and isoelectric focusing in polyacrylamide gels (pH 3.5 - 9.5). After starch gel electrophoresis the following enzymes were localised: adenylate kinase, alcohol dehydrogenase, enolase, esterase, glucose-6-phosphate dehydrogenase, glyceraldehyde-3-phosphate dehydrogenase, glycerol-3-phosphate dehydrogenase, lactate dehydrogenase, malate dehydrogenase, phosphoglucone isomerase, phosphoglucomutase, phosphomannose isomerase, sorbitol dehydrogenase, valyl-leucine peptidase and xanthine dehydrogenase.

All enzymes except esterase were found to be monomorphic in the 204 individuals examined. Esterase showed a diallelic polymorphism which is undoubtedly the same one as described by Nyman (1967, 1972) in Scandinavian and other Arctic charr populations and by Child (1977) in British populations. Significant heterogeneity was found among localities in the esterase allelic frequencies. No significant correlation of allelic frequencies with latitude was found when all populations were tested. However, when the two "dwarf" populations (sexually mature at < 18.0 cm) were excluded then a significant correlation was present.

Separations of muscle extracts by isoelectric focusing and staining for general proteins showed a maximum of 56 bands. Eye extracts similarly examined revealed 47 bands, brain 41, heart
31 and liver 25. A few minor bands varied among individuals from the same lake but there were no consistent inter-lake differences in the electrophoreograms of these tissues.

The high degree of similarity of the isoelectric focusing general protein electrophoregrams, representing in excess of 60 loci, and the identical mobility of the enzyme products of a putative 26 loci, suggests that the charr populations examined are very close genetically in spite of their divergence in morphological, meristic and ecological features. This would suggest that all the charr populations examined should be regarded as conspecific and have been derived from a common colonizing ancestor in the last glacial period.

Charr from one lake (Coomasaharn) showed a significantly higher number of gill rakers than the other populations examined and similar to that found in the Alpine European populations and those of the Kara Sea-Taimyr Peninsula (Behnke, 1972). This particular population is clearly worthy of further study.

Irrespective of whether it is chosen to regard the various populations of charr in Britain and Ireland as members of one or several species, these populations have persisted as glacial relicts for at least 10,000 years. As such they represent excellent models for the study of genetic changes in isolation and all possible measures should be taken to conserve as many as possible of these populations in their pristine state.

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PLASTICITY OF CHAR POPULATION STRUCTURES AND THE CHAR COMPLEX

P. Grotnes

ABSTRACT

Char populations of neighbouring lakes often appear to be strikingly different. Sympatric populations of char are also differing in important population parameters. Although it apparently would not explain the existence of sympatric chars, the differences have largely been ascribed to differences in environment. Mostly there has not been any attempt to qualify the ways environment interact with population processes. Especially for char there are large population variances in important parameters (i.e. growth and mortality rates, age/size of maturation). These variances imply that environmental differences give rise to large structural differences in populations even when they are derived from one founder population. Both mathematical analysis and empiry suggest that such differences may be established within a few generations. The analysis also demonstrates that sympatric speciation is possible. Three case studies, Ellasjøen (Bear Island), The Skjomen lakes (North Norway) and Takvåten (North Norway) demonstrate the principles involved.
ELECTROPHORETIC STUDIES ON ARCTIC CHAR IN THE COUNTY OF VÄSTERBOTTEKN, NORTHERN SWEDEN, AND ICELAND: A SURVEY OF THE DISTRIBUTION OF THE ARCTIC CHAR SPECIES

Rolf Gydemo

In 1976 a survey of Arctic char in the county of Västerbotten, northern Sweden, was started. It was based on electrophoretic analyses of serum esterases according to the method described by Nyman (1972) in Arctic char in order to obtain data relevant to further management of the populations.

In the period 1976 to 1979, more than 45 lakes of economic and/or management importance were investigated. The lakes in the area belongs to four watersheds, from the north to the south: River Vindelälven, River Umeälven, River Vapstälven and River Angermanälven. The rivers run to the Bothnian Sea except for River Vapstälven which runs through Norway into the Atlantic Ocean.

The results from the survey (Gydemo 1978, 1979, 1980) combined with data from other investigations show a pattern of distribution that coincides with the immigration theory proposed by Nyman et al. (1981). Generally spoken, the area is dominated by F-char (char with a high frequency of the fast (F-allele) with "normal" char (char with intermediate frequency of the F-allele) in the central areas and S (slow)-char (low frequency of the F-allele) in the low altitude areas.

River Vindelälven is dominated by F-char with two exceptions, one of which is known to be a man-made introduction of "normal" char from a lake in the River Umeälven system. The result has been introgression resulting in a dwarfed stock.

In the River Umeälven system, the smaller lakes usually contain F-char while in the larger lakes "normal" char occur in allopatric and/or sympatric populations together with F-char.
In the Vapstälven river system, as well as in the northernmost tributary to River Ångermanälven, River Vojmän, F- and S-char dominate, sympatrically in the larger lakes and either of them allopatrically in the smaller lakes. The populations in the main drainage of the River Ångermanälven are of all three types.

In high altitude lakes the populations are of F-type, thus supporting the theory that they are the first immigrants. The dominance of N-char in the big lakes indicates their competitive superiority. The S-char in Rivers Vapstälven and Vojmän could be an indication of immigration from the Atlantic in the west. The presence of them in four lakes outside their expected distribution could in two cases be due to transplantations by man and in the other two (the twin lakes Östra and Västra Marssjöarna) result from these being refuges.

During 1978 and 1979, 24 localities on Iceland were sampled. The analyses indicate the presence of all three species in Iceland as well. Among the landlocked populations the F-char is probably the most widespread one, dominating lakes in higher altitudes (the "plateau" of Iceland) appr. at altitudes above 75-100 m. The normal char occurs in lower altitudes while the presence of landlocked S-char still is somewhat unclear due to small sample sizes.

All three species are probably also anadromous. However, the sample sizes are in most cases too small to allow for a definite statement. The gene frequency including all anadromous populations ranges between 0.00 to 0.81. Most of the anadromous populations have gene frequencies between 0.67 and 0.79. There is, so far, no distinct pattern as to the geographical origin of the three species.

The landlocked Arctic char species show the same pattern of distribution as in Västerbotten, i.e. F-char dominate in high altitudes. The "normal" char dominate the larger lakes and is the most competitive one. Only one case of probable landlocked S-char has been registered so far, the extreme dwarfs, isolated in lava clefts close to lake Thingvallavatn.

More material are being collected to improve data.
REFERENCES


Several investigations concerning the Arctic char populations of lake reservoirs in Scandinavia have shown the great complexity and variety of impacts by regulations (Runnström 1946, 1951, 1955, Nilsson 1961, 1964, Aass 1964, 1965, 1970, Fürst, Boström and Hammar 1978, 1981 (in prep.)). The varying results have been explained by the plasticity of the Arctic char. A new approach to the problems of Arctic char biology where the taxonomic part of the complex was analysed, opened new aspects and possibilities for management (Nyman 1972, Filipsson and Svårdson 1976, Nyman, Hammar and Gydemo, in prep.).

The introductions of new fish food organisms in regulated lakes were designed with the emphasis on the population genetics and the dynamics of the Arctic char complex (Fürst et al. 1978, Hammar, in prep.).

In this paper I will present some aspects of the ecology of different sibling species within the Arctic char complex in some lake reservoirs in the north of Sweden.

DISTRIBUTION

The main target area of the "Mysis project" is in the northwestern part of the province of Jämtland (Lat. 63°-65° N.). The distribution of the three Arctic char species in the two major river systems is shown in Fig. 1. The patterns are similar, "F-char" allopatric in the headwater lakes and the "S-char" and "Normal char" often introgressed in lower lakes. The order of succession suggests that the "F-char" was the first immigrant after the Ice Age, followed by the "S-char" and then as number three the larger and most competitive "Normal char". Regulations, impoundments and fish stocking have changed the balance between the original char species.
Lake Ajaure and Lake Övre Björkvatnet, where Pallasea quadrispinosa Sars were introduced as a new fish food organism, are located on River Umeälven.

GROWTH

In Sweden several old dialect names are known of distinct Arctic char forms and are still in use. Names like "tita, gaka, blattjen and smulf" refer to "dwarfs" in sympatric populations. In Lake Blåsjön they were described in the last part of the 19th century (Johansson 1967) and could easily be distinguished in a growth diagram (Fürst et al. 1978). The genetic analyses show a dwarfed "S-char" and a highly introgressed "Normal char" (Nyman 1972, Hammar unpubl. data). This growth picture is the most common one seen on River Faxälven.

In Lake Ajaure, River Umeälven, the same pattern occurs but in this case with a big "Normal char" and a dwarfed "F-char" (Hammar unpubl. data).

All three species can be found in Lake Suorva, River St. Luleälven, where both "F-char" and "S-char" are dwarfed in relation to the "Normal char" (Hammar and Nyman, unpubl. data).

The combination "F-char" and "S-char" is rare and Henricson and Nyman (1976) describe the "S-char" as dominant over the "F-char" in Lake Fättjaure, River Vojmän.

The maximum sizes attained in allopatric populations of the three species reflect their "hereditary size capability". Both the "Normal char" and the "F-char" are known to reach close to 10 kg but there are so far no examples of "S-char" bigger than 1 kg. In Fig. 2 the growth and size relationships of the sympatric populations in Lake Blåsjön and Lake Ajaure are shown.
FOOD HABITS

Nilsson (1963) characterized the allopatric char as a fish inhabiting the same ecological niche as the brown trout. In sympathy they are split up with the trout close to the shore, feeding on benthic and terrestrial invertebrates and the char pelagic, feeding on plankton. Introductions of *Mysis relicta* Lovén in Lake Blåsjön and Lake Torrön show two different reactions of the Arctic char populations. The formerly plankton-feeding "Normal char" in Lake Blåsjön is today an efficient benthic *Mysis* predator all year around while the char in Lake Torrön, an "S-char", still feeds on plankton during the summer and spends part of its life cycle pelagically in spite of a dense *Mysis* population (Fürst et al. 1978, 1981 (in prep.)). The population of brown trout is denser in Lake Blåsjön than in Lake Torrön, a fact that would suggest the opposite reaction. In Lake Ajaure both char species ("Normal" and "F") feed on the introduced benthic amphipod *Pallasea*. In Lake Övre Björkvattnet, Nilsson and Filipsson (1971) found a benthic fish-eating dwarfed "F-char", called blattjen, and a plankton feeding "Normal char".

REPRODUCTION

The landlocked Arctic char in Sweden is known to spawn in general from September through November in both lakes and streams. In Lake Blåsjön the "Normal char" spawns around October 25 in shallow water and the dwarfed "S-char" between the end of October and the beginning of January in deeper water (H. Lundgren, pers. comm.). In Lake Torrön the "S-char" spawns a month earlier and in shallow water, but even earlier a probable remnant of a stream-spawning "F-char" of the lakes upstream migrates up into some of the tributaries to spawn (Hammar, in prep.). In several other lakes the "F-char" is known to spawn in streams and in some high altitude creeks Arctic char is completely streamliving (Lindström 1954, Curry-Lindahl 1957, Gydemo 1980, Hammar, in prep.).

We do not know when the eggs of Arctic char hatch in these lake reservoirs but there is a strong relation between years with a
minimum of water in early spring and poor year classes. In Fig. 3 the relative strength of year classes of char in Lake Torrön is compared with water levels in spring and the summer temperature (Hammar, in prep.). It is a possible characteristic of the "F-char" to spawn in streams and if so it is a valuable genetic resource to be used in the management of regulated lakes where the spawning grounds each spring are damaged by the low water level.

HABITAT

In some lakes a pelagic population of Arctic char is known to occur, and it was one of the theories behind the Mysis introduction that these populations would react positively on the new pelagic fish food organism.

In Lake Torrön a detailed analysis was made of the pelagic and benthic populations. There is an obvious difference in age distribution with young and old fish along the bottom, the young deep and the old ones close to the littoral zone. The pelagic Arctic char consists of a narrow age structure of middle-aged char with a mean length around 250 mm. This makes it likely to believe that there are still habitat changes during the life cycle of the landlocked Arctic char, like those reported in the anadromous char of the Arctic. In Lake Båtsvatn, Klemetsen and Grotnes (1980) found a similar pattern which they interpreted as an anadromous part of the life cycle of the now landlocked but formerly sea-running population. In Lake Torrön no genetic difference is found between the benthic and pelagic populations. In Lake Blåsjön, Lake Ajaure and Lake Övre Björkvatnet the benthic and pelagic populations on the other hand have different genetic origin. In Fig. 4 the distribution of Arctic char in different habitats of Lake Torrön is shown.

INTERACTIVE SEGREGATION BETWEEN BROWN TROUT AND THE THREE SIBLING SPECIES OF ARCTIC CHAR

In all lake reservoirs mentioned the brown trout is considered a valuable species for the management of Arctic char (Filipsson
and Svärdson 1976, Fürst et al. 1978). The relations between brown trout and Arctic char treated as a group were studied by Svärdson (1949) and Nilsson (1960, 1963, 1965). The distribution of brown trout and different sibling species of Arctic char shows an interesting pattern of different degrees of interactive competition. In Lake Blåsjön the "S-char" is deep living indeed and the "Normal char" pelagic with the existence of a benthic brown trout. In Lake Båtsvatn, Klemetsen et al. (1972), and Klemetsen and Grotnes (1972, 1975) described the dwarfed "S-char" as littoral. In this lake the brown trout is missing. In Lake St. Rösjön the dwarfed "F-char" is caught close to the shore (Andersson et al. 1971, Nyman 1972, Hammar unpubl. data) while the big "Normal char" is more "pelagic" and brown trout do not occur. In Lake Övre Björkvatnet, Nilsson and Filipsson (1971) found "blattjen" along the bottom from the shore down to almost 30 metres while the "ordinary char" was pelagic. According to Nyman (1972) the "blattjen" is an "F-char" and the other one a "Normal char". This suggests a certain similarity and probably competitive pressure between brown trout and "F-char" while the "S-char" seems to chose a more distant habitat. Finally, Henricsson and Nyman (1976) in their studies of the difference in parasite infestation of Arctic char in Lake Fättjaure found a pelagic "S-char" and a benthic and littoral "F-char" where the brown trout also is present.

The variety of ecological parameters characterizing the different taxa of the Arctic char complex supports the theory of three sibling species (Nyman et al. in prep.) and this knowledge must be considered in every case of management of natural or impounded lakes with Arctic char to avoid damage to original stocks and genetic resources adapted to the local environment, and also when considering the economic consequences.

REFERENCES


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Fig. 1 Map showing the distribution of three sibling species within the Arctic char complex in the province of Jämtland, north Sweden.
Fig. 2 Growth and size relationships of Arctic char in Lake Blåsjön and Lake Ajaure, two sympatric populations with dwarves. The gene frequencies of the different fractions are shown in the figure.
Fig. 3 The relations between relative strength of year classes of Arctic char, water levels in spring and summer temperatures in Lake Torrön.
Fig. 4  The relationship between length of fish and depth in benthic and pelagic test fishing for Arctic char in Lake Torrön.
INCREASED MORTALITY RATE IN CHAR SALVELINUS ALPINUS, CAUSED BY INFECTIONS OF DIPHYLLOBOTHRIUM DENDRITICUM

Jan Henricson

There are many reports on the adverse effects, including mortality, on salmonids caused by plerocercoids of *Diphyllobothrium dendriticum* (Cestoda: Pseudophyllidae). However, hitherto all reports have been directed towards the effects on the individual fish and no attempts have been made to express the mortality, directly or indirectly caused by the parasite, in quantitative terms at the population level.

Henricson (1977, 1978) studied a char population, infected with both *D. dendriticum* and *D. ditremum*, in a north Swedish lake (Lake Bjellojaure). Mortality, correlated with infection levels of *D. dendriticum*, was indicated by 1) a decrease in intensity of infection in the oldest age-groups of fish, 2) decreases in intensity of infection with long (and old) plerocercoids in the same year-class of char over a time period and 3) the occurrence of plerocercoids in vital organs such as liver, swimbladder and kidney.

The char population and the plerocercoids of *D. dendriticum* constitute an intermediate host-parasite system (Kennedy 1970), which is closed. This means that the only possibility for a parasite to escape from the system (outflow), is through the death of the parasite or its host fish. As char seems unable to destroy plerocercoids of *D. dendriticum*, the only possibility for an outflow of parasites from the system is through the death of infected hosts. The major factors controlling the inflow of plerocercoids to the system are the availability of infected copepods and the feeding habits of char. The intensity of infection is determined by the relation between inflow and outflow. Knowledge of copepod life-cycles and the food composition of char in different seasons combined with data on the variations in the length frequency distribution of plerocercoids with time make it possible to determine periods of infection (inflow to the system).
If mortality, correlated with intensity of infection, is in progress in the char population period or very low inflow is ideal to study this. During the winter (October-April) the inflow of plerocercoids to the char population in Lake Bjellojaure was negligible.

A host population may be compartmentalized according to parasite load. Hosts with 0, 1, ..., n parasites are treated as separate "populations" and the distribution of parasites in a certain year-class of fish are set up in a frequency distribution. During a defined time-period the changes in the shape of the distribution and its parameters (mean $\bar{x}$, median, overdispersion $s^2/x$) are studied.

If the probability of death is the same for every fish in an age-group, irrespective of the number of parasites it carries, the shape of the frequency distribution and the values of its parameters should not change with time during a period without inflow. The relative number of fish in each "population" should be the same in the beginning and end of that period. Henricson (1978) used log-probability paper to illustrate the changes in the frequency distribution and demonstrated an outflow of parasites, from the fish host-parasite system, caused by the death of heavily infected fish. The log-probability paper, in combination with a formula proposed by Lopukhina et al. (1973), makes it possible to quantify, in relative terms, the mortality rate associated with parasite numbers. In Fig. 1 the mortality rate of char infected with more than a certain number of plerocercoids of D. dendriticum is shown. A char infected with more than about 4 plerocercoids or more runs an increasingly greater risk of death.

Because of the overdispersed distribution of parasites, however, only a relatively small proportion of the char population reaches infection levels with a very high probability of death.

That the mortality was not only correlated with number of parasites but also with their location in the fish was shown from the seasonal variation in the proportion of plerocercoids in different organs.
REFERENCES

Fig. 1. The relative mortality of char *Salvelinus alpinus*, infected with more than a certain number of plerocercoids of *Diphyllobothrium dendriticum*, from October 1972 to May 1973, in Lake Bjellojaure. Year-classes 1964-66.
THE ARCTIC CHARR OF NORTH NORWAY, INCLUDING BEAR ISLAND

Anders Klemetsen

This synopsis reviews the main results of the charr studies carried out from the University of Tromsø up to 1979.

In the Båtsvatn reservoir (Skjomen mountains, co. Nordland) the existence of two sympatric populations of charr has been established. They conform to different serum esterase CHW equilibria. Typical F-frequencies for dwarf charr are 0.15 and for normal charr 0.51. Few dwarfs exceed 22 cm body length. Normal charr grow considerably larger. Spawning ages differed markedly between the two types. Also their spawning dresses are very distinct. Dwarfs are drab, and parr finger marks are frequently found.

Dwarf charr spend their whole lives at the lake bottom, preferring the shallow littoral. They even ascend small brooks in the summer. Young normal charr live together with the dwarfs along the bottom. Both eat the same food (benthos, pleuston). At lengths of some 16-18 cm the normal charr leave the littoral, shifting to a pelagic mode of life in the summer. Here they wander about in loose schools, feeding on plankton and pleuston. Schools often consist of fishes of the same size, probably of the same year class. Their dresses are silvery, with only a few spots and no finger marks. They very much resemble sea charr smolts. Larger normal charr may be found both pelagically and benthically in the summer.

This habitat and behaviour shift of the normal charr is interpreted as being part of a relict sea charr life cycle whereby the marine coastal waters are replaced by the reservoir's pelagic zone. Dwarf charr show no signs of a sea charr behaviour in Båtsvatn.

On this background we have suggested that these two populations are derived from different ancestors, one freshwater and one
anadromous. The hypothesis is that the dwarf is the freshwater species, immigrating to Fennoscandia via the Ancylus lake, and the normal charr the anadromous species, immigrating via the marine coasts of Sweden and Norway. The glacial refuge of the first may have been in or near the Great Siberian ice lake, and that of the second the region of the southern coasts of the British Isles and the Biscay Bay (perhaps this is where the Celtic word root of charr was attained!). The hypothesis implies that sea charr or its resident descendants near the sea gradually have been spread upstream by man. Especially among the Lap peoples fish carrying probably has been common practice. Given the time span of several centuries anthropogenic dispersal may well be a chief factor to account for the present distribution of normal charr in northern Fennoscandia. From the top of the westbound watercourses the distances to east-running rivers are short and the landscape at the water divides usually is of gentle relief. Once there, further dispersal transversally and especially downstream is therefore fairly easy.

In his cand.real. thesis Petter Nilsen undertook a study of charr populations in the Smørfjord area, Porsanger, Finnmark. The locality was chosen in order that west/north-bound freshwater immigrants very unlikely could have invaded. Three populations were compared: sea charr, resident charr which had shared habitat with the sea charr up to very recently, and landlocked charr which had been isolated for several thousands of years.

No double charrs were found. The landlocked population was nearly homozygous for the allele F. Only one heterozygote occurred in the material. The sea charr stock had a F-frequency of 0.45 and the resident charr stock value was 0.67. Similar esterase values were later found in samples from Kvalsund, W.Finnmark and Oksfjord, N.Troms. Therefore the situation on the coast of northernmost Norway may indicate that the S-allele is selected against when the charr turn to a resident mode of life. In landlocked populations it may nearly or completely disappear. Do these results signify that the S-esterase is best adapted to hydrolyzing marine lipids and the F-esterases limnic/terrestrial lipids? Do
they contradict Nyman's temperature hypothesis and his latitude cline? Obviously we need to know more about the biochemical and physiological characteristics of the two enzymes to be able to answer questions like this.

A similar "leakage" of S-alleles may have happened on Bear Island. Stevatn is a head lake in the Lakselva drainage system, which flows northwards and still may have sea-run charr in it. Here the F-frequency was 0.75. Ellasjøen in the southern part of the island is today closed for ascending anadromous fish. Here the F-frequency was 1.00 (out of more than 1 700 fish four were FS).

The Ellasjøen charr had other interesting attributes. A similar population split as in Båtsvåtn seemed to exist. The lake held two groups of fish which were non-overlappingly distinct in their spawning sizes. Also their spawning ages differed. However, their gill raker and pyloric caeca counts did not differ. Neither did their F-frequencies. The few heterozygotes occurred among both small and large fish. Apart from the different spawning ages (which may or may not be genetically based) the Ellasjøen charr therefore appeared to constitute one panmictic population. This is the conclusion of Halgeir Holthe in his cand.real. thesis (in prep.). His results are partly based on another thesis (in prep.) on age and growth by Knut Kristoffersen.

These results immediately raise the old, controversial question of the reason for split charr populations. Are they genotypically or phenotypically based? The Ellasjøen charr so far seem to indicate that phenotypical splitting is possible, and that the resulting forms may appear very similar to forms which belong to different gene pools. Northern islands most probably offer good opportunities for the study of these intriguing questions. We eagerly await further results from Iceland, Spitsbergen and the Canadian Arctic!

We also have some results from the southern part of Senja, a large island in S.Troms. No double resident charrs were recorded. In Storvatnet, above present sea charr range, the F-frequency
was 0.29. However, the results did not correspond to a CHW equilibrium (no F homozygotes). Resident charr from Avatn in another river system had 0.33 F. Sea charr pass Avatn on migration to and from Rödsandvatn, where they spawn and stay over the winter. Charr from this lake which were caught when the anadromous fish presumably were at sea, had a F-frequency of 0.52. These results are preliminary and difficult to interpret. On the face of it they seem to contradict the results from further north, and it is also puzzling that Avatn and Rödsandvatn charr should differ so much. The next step in this region will be to get samples from sea charr. We have a few already, and hope to get more in 1981.

A perhaps far-fetched but interesting question is raised in Nilsen's thesis. Did charr (possibly anadromous) have a refuge on the Siberian coast, east of the Weichselian ice cap? Recent discussions among geologists have brought up the possibility of open water in that region. If so, such charr may have spread westwards after the ice retreat and also may have reached Fennoscandia. Perhaps this is the fixed FF (or nearly so, mutations to S may certainly occur) of Bear Island, Finnmark and N. Troms? At least such an explanation fits both our immigration hypothesis for two species (above) and Nymans three species hypothesis:

1) "Normal" charr, glacial refuge SW Europe coasts, marine immigration, partly anthropogenic dispersal.

2) S-charr, glacial refuge Great Siberian ice lake, freshwater immigration (Ancylus lake).

3) F-charr, glacial refuge E. Siberian coasts, marine immigration, possibly some anthropogenic dispersal.

The idea being hereby raised for contradiction!
POPULATION DYNAMICS OF THE ARCTIC CHAR IN LAKE MÝVATN, ICELAND

Jón Kristjánsson

THE LAKE

Lake Mývatn is situated in North-East Iceland. Height above the sea level is 277 metres and the areal is 30 km². The lake is shallow (3-4 m) and highly eutrophic. The dominating fish species is Arctic char, but also brown trout and sticklebacks occur in the lake. The annual catch of char in recent years has been 10-30 thousand fish, with average weight 500-700 grams. Mesh size used has been 45 mm, knot to knot, and the fishing season is from February through September, when the spawning season begins. The lake was heavily overfished until in the spring of 1977. Up to 700 nets were used each day throughout the fishing season. In April 1977 the fishermen agreed upon not using more than about 100 nets each day. The Institute of Freshwater Fisheries used this opportunity to set up a plan in order to get reliable information on catch and effort. The results are presented in Table 1. Lamby’s study (Lamby 1941) in 1941 had shown that the char had linear growth (7cm/year) up to the age of 7+, fish of age 5+ and 6+ dominated the catch. In recent years 3+ and 4+ dominate the catch, 5+ fish being almost absent, supporting the theory of overfishing.

RESULTS

Basic data are shown in Table 1, where catch and effort (number of gill net nights) is shown for every month. From these data, Table 2 is constructed for the months February, March and April, in 1978. In these months the gill nets are set under the ice and conditions in the lake are thought to be stable (temperature, activity, minimal growth, minimal recruitment).
Table 1. Effort and catch of char in Mývatn 1977 and 1978

<table>
<thead>
<tr>
<th>Month</th>
<th>1977</th>
<th>1978</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>catch</td>
<td>effort</td>
</tr>
<tr>
<td>Febr.</td>
<td>2217</td>
<td>no</td>
</tr>
<tr>
<td>March</td>
<td>1457</td>
<td>2378</td>
</tr>
<tr>
<td>April</td>
<td>872</td>
<td>2,273</td>
</tr>
<tr>
<td>May</td>
<td>707</td>
<td>1,139</td>
</tr>
<tr>
<td>June</td>
<td>3973</td>
<td>1,637</td>
</tr>
<tr>
<td>July</td>
<td>7113</td>
<td>2,232</td>
</tr>
<tr>
<td>Aug.</td>
<td>12403</td>
<td>2,379</td>
</tr>
<tr>
<td>Sept.</td>
<td>4096</td>
<td>1,058</td>
</tr>
</tbody>
</table>

Table 2.

<table>
<thead>
<tr>
<th>Month</th>
<th>(C_t)</th>
<th>(K_t)</th>
<th>(f_t)</th>
<th>(C_t/f_t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Febr.</td>
<td>5407</td>
<td>2703,5</td>
<td>2378</td>
<td>2,273</td>
</tr>
<tr>
<td>March</td>
<td>3467</td>
<td>7140,5</td>
<td>2624</td>
<td>1,321</td>
</tr>
<tr>
<td>April</td>
<td>2239</td>
<td>9993,5</td>
<td>1965</td>
<td>1,139</td>
</tr>
</tbody>
</table>

\(C_t\) = catch (no fish taken during time interval \(t\) (one month)

\(K_t\) = cumulative catch to the start of interval \(t\) plus half of that taken plus half of that during the interval

\(f_t\) = fishing effort (gill net nights) during time interval \(t\)

\(C_t/f_t\) = catch per unit effort during the interval \(t\)

\(C_t/f_t\) is plotted against \(K_t\) (Leslie's method. Ricker 1975, p.150)

and this gives following estimates:

\(N_0\) = 16431 fish, prior to fishing season (stock catchable by 45 mm nets)

\(q = 1.61 \cdot 10^{-4}\) = catchability - the fraction of the population taken by one gill net night

\(r = 0.97\) (correlation coefficient)
F = (fishing mortality) for each month if \( f_t \cdot q \) and the same \( q \) is used throughout the year. It is not known how \( q \) changes throughout the year, one might expect that it would be greater in the summer due to increased activity of the fish, but in the summer there are other factors that would decrease the \( q \), such as cladophora and detritus blocking the nets and decreasing their catchability, a very pronounced fact in Lake Myvatn. Mean stock for each month is computed from Baranow's catch equation, \( C = F \cdot N \cdot F' \cdot a \).

\( M = \) (natural mortality) has not been computed, so a value estimated from other lakes, 0.32 pr annum is used, evenly spread throughout the year, with little more weight in the spawning season which is October.

The stock size prior to the fishing season is computed from the catch/effort in September the year before. It is interesting to see that the estimates for No 1978, one based on the catch/effort in 1978 (=16431) and the other based of that of 1977 (=17783) are identical, the only common factor used is the \( q \), found in 1978.

Fish caught by 19.5-26 mm nets in June 1978 were to be the recruits in 1979. Giving these nets lower \( q \) and taking natural mortality into account the recruitment in 1979 seemed to be very low, in the order of 3000 fish. The catch in 1979 was estimated to be about 9000 fish if the effort would be equal to that in 1978.

The catch in 1979 turned out to be 11300 char or a 50% reduction, from 1978. The effort was similar these two years, and the forecast therefore was some 25% conservative. Preliminary results from the catch in 1980 also support the validity of this method.

Mean stock each month is calculated from Baranow's equation:
\[ C_t = F_t \cdot \bar{N} \]
Table 3. Stock model for char (catchable stock) 1978, based on catch and effort in February, March and April. Natural mortality is not known, but a value of $m=0.32$ (annual basis) is used.

No 1978 = 16431

<table>
<thead>
<tr>
<th>t</th>
<th>Month</th>
<th>$N_t$</th>
<th>$C_t$</th>
<th>$f_t$</th>
<th>$F_t$</th>
<th>$M_t$</th>
<th>$Z_t$</th>
<th>$a_t$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Febr.</td>
<td>14229</td>
<td>5407</td>
<td>2378</td>
<td>0.32</td>
<td>0.015</td>
<td>0.379</td>
<td>0.33</td>
</tr>
<tr>
<td>2</td>
<td>March</td>
<td>8255</td>
<td>3467</td>
<td>2624</td>
<td>0.42</td>
<td>0.015</td>
<td>0.435</td>
<td>0.35</td>
</tr>
<tr>
<td>3</td>
<td>April</td>
<td>6997</td>
<td>2329</td>
<td>1965</td>
<td>0.32</td>
<td>0.015</td>
<td>0.335</td>
<td>0.28</td>
</tr>
<tr>
<td>4</td>
<td>May</td>
<td>10319</td>
<td>1651</td>
<td>1009</td>
<td>0.16</td>
<td>0.015</td>
<td>0.175</td>
<td>0.16</td>
</tr>
<tr>
<td>5</td>
<td>June</td>
<td>13900</td>
<td>3892</td>
<td>1744</td>
<td>0.28</td>
<td>0.015</td>
<td>0.295</td>
<td>0.26</td>
</tr>
<tr>
<td>6</td>
<td>July</td>
<td>14800</td>
<td>5180</td>
<td>2167</td>
<td>0.35</td>
<td>0.015</td>
<td>0.365</td>
<td>0.30</td>
</tr>
<tr>
<td>7</td>
<td>August</td>
<td>11368</td>
<td>432</td>
<td>238</td>
<td>0.038</td>
<td>0.015</td>
<td>0.071</td>
<td>0.068</td>
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<tr>
<td>8</td>
<td>Sept.</td>
<td>12033</td>
<td>361</td>
<td>194</td>
<td>0.03</td>
<td>0.015</td>
<td>0.045</td>
<td>0.044</td>
</tr>
<tr>
<td></td>
<td>Oct.</td>
<td>11764</td>
<td></td>
<td></td>
<td></td>
<td>0.2</td>
<td>0.2</td>
<td>0.18</td>
</tr>
</tbody>
</table>

No 1979 = 9631

$q = 16.1 \cdot 10^{-5}$

$C_t$ = catch

$f_t$ = no gill net nights

$F_t = f_t \cdot q$ = instantaneous rate of fishing mortality

$M_t$ = instantaneous rate of natural mortality

$a_t$ = monthly mortality rate

No = stock size prior to fishing season

REFERENCES


ARCTIC CHAR IN EAST FRIDMUNDA RVATN

Jón Kristjánsson.

East Fridmundarvatn is located 435 m above sea level with a surface area of 2.36 km². It is a shallow lake with a maximum depth of 1.15 m and an average depth of 0.8 m. Two small springs empty into the southern end and a small brook drains from the northern end to Lake Gilsvatn. The bottom of the lake is soft mud, mostly covered with Myriophyllum sp. and the bluegreen algea Nostoc sp. The annual primary production has been estimated to be in the range of 200-400 g C/m²/yr.

The fish population consists predominantly of Arctic char, a few brown trout and sticklebacks.

The lake was lightly fished until 1975, but since then it has been fished intensively in order to improve the size and quality of the fish. Prior to 1975 the annual catch was about 2000 fish. The following years the catches was as follows:

<table>
<thead>
<tr>
<th>Year</th>
<th>Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1976</td>
<td>10000</td>
</tr>
<tr>
<td>1977</td>
<td>14300</td>
</tr>
<tr>
<td>1978</td>
<td>7300</td>
</tr>
<tr>
<td>1979</td>
<td>1400</td>
</tr>
</tbody>
</table>

The average annual harvest in the years 1975-79 was 7.5 kg/ha/year with a maximum of 15 kg/ha/year in 1977. Both gill nets of various mesh sizes, and traps were used to catch the fish.

The size composition of the stock has changed in these years. In 1975 the 28 cm length class (200 g) dominated the catch, and there were fish up to 40 cm, some of them cannibals (Fig. 1).

In 1978, 31 cm (270 g) fish were most common, but the maximum size was down to 36 cm, and the relative number of 20-25 cm fish was increasing. Test fishing in 1980 (450 fish) showed that the population had changed drastically in length/frequency composition (Fig. 1). Now 18 cm fish were dominating and the maximum size was down to 36 cm.
The net result of increased fishing pressure in the years 1975-79 is that the population has increased in number and decreased in mean size. This is an opposite result of what was expected when the experiment was started. The present explanation is that by removing predators (cannibals) and grown up fish, thus reducing mortality and increasing space for the youngs, the recruitment will increase. The recruitment (in numbers) must have been greater than the removal of old fish.
Fig. 1 Length distribution of char from E-Frimfundarvatn 1975-80. Dominating length class each year used as unity (100%). 1975 and 1980 samples were caught with gill net series (19.5-45 mm) 1976-78 samples were caught with trap nets (20 mm mesh) and beach seine (20 mm mesh).
THE CHARS OF NORTHERN FINLAND

Eero Niemela

The char is nowadays limited to the southeastern, eastern and the most northern corners of Finland (Seppovaara 1969). The species has disappeared from many lakes in the central part of the country because of lake and river regulations for hydroelectric purposes, acidification, severe fishing pressure and introductions of whitefish. Even today stocking of fish as a management procedure is a common practice, like in e.g. Lake Inarinjärvi - Finland’s largest lake containing char. This lake (120 m.a.s.l.) is regulated for the benefit of the Soviet Union, the eastern neighbour. The amplitude is 2.7 m and the total area approx. 1 000 km². Whitefish, lake trout, char and brown trout are stocked in the lake annually. Two types of char are differentiated by local anglers:

1) Harmaaraauto, isonierä (typical of Inarinjärvi) = great char: grey, short and broad, normal weight from 300-600 g, but specimens up to 8 kg have been caught. Minimum weight at spawning approx. 500 g.

2) Paltasarauto = small char: weight 250-300 g, sometimes up to 700 g. Occurs e.g. in Lake Kilpisjärvi and many more lakes in the north.

The distribution of the salmonid fishes in Lake Inarinjärvi as evidenced in the catch statistics are thus:

<table>
<thead>
<tr>
<th>Fish Type</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>whitefish</td>
<td>63 %</td>
<td>60 %</td>
</tr>
<tr>
<td>&quot;great char&quot;</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>&quot;small char&quot;</td>
<td></td>
<td>0.7</td>
</tr>
<tr>
<td>lake trout</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>brown trout</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>landlocked salmon</td>
<td>0.3</td>
<td>0.6</td>
</tr>
</tbody>
</table>
The char occurs in another 30-odd lakes in the Utsjoki district and also in many brooks and small rivers. As stated earlier many of the original char lakes have been destroyed by whitefish introductions. Lake Luomusjärvi, 475 hectares and 324 m.a.s.l., has a mixed fish fauna of whitefish, char, brown trout and burbot. The fishery statistics of the lake shows a typical trend of a predominantly char/whitefish lake with char dominating the winter catches and whitefish the summer catches:

<table>
<thead>
<tr>
<th></th>
<th>summer</th>
<th>winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Luomusjärvi (1979)</td>
<td>1700 kg</td>
<td>100 kg</td>
</tr>
<tr>
<td>whitefish</td>
<td>860 kg</td>
<td>140 kg</td>
</tr>
</tbody>
</table>

This is mainly caused by the different methods used in the two seasons, sportfishing with jiggers dominating in the winter and netting in the summer season. This is, however, not a rational way of harvesting the lake, because the nets catch the whitefish too early and too coarsemeshed nets are further used thus being unable to catch the smallsized char. This situation is a common feature of the Nordic countries. Finally, some data can be given concerning an experiment with homing in char. The experiment was performed in Lake Kevojärvi. In a small river (River Rässijoki) 58 char were caught by electro-chocking, tagged with Carlin tags and transported downstream to Lake Kevojärvi. The average length was 40.7 cm. Twelve specimens were later recaptured in their native stream.

REFERENCES

Seppovaara, Ossi 1969. Char (Salvelinus alpinus L.) and its fishing industrial importance in Finland. Suomen Kalatalous 37: 75 p. (In Finnish with Swedish and English summaries and legends.)
THE POPULATION GENETICS OF ARCTIC CHAR: A STATE OF THE ART

Lennart Nyman

Studies on local populations of morphologically almost indistinguishable species of fish pose well nigh insurmountable problems to the fisheries biologist. When meristic and morphological data fail and tagging returns are few and give little information on the distribution of populations all kinds of data must be scrutinised for clues pertaining to the specific level of taxonomic organization which we term a local population. This problem is particularly relevant within the Arctic char complex and other sibling species groups of salmonids, like e.g. the whitefishes, smelts and ciscoes of previously glaciated regions of the northern hemisphere. Traditional methods are inadequate to delimit populations within such groups and the obvious alternative should be the use of biological tags particularly in form of population specific gene frequencies as indicated by protein electrophoresis.

Extensive studies have been performed on fish populations by employing protein markers, and screening of numerous polymorphic loci have usually yielded heaps of gene frequency data which have been taken to represent population characteristics. However, such studies, no matter how technically elegant they may seem, often fail to realize that our lack of knowledge as to the function of the gene products we visualize also hampers our possibilities to translate the results properly. Some of the limitations of electrophoretic techniques and meristic data have a common denominator, viz. the problem of giving proper "weight" to a character as a taxonomic clue. It must be pointed out that the seemingly self-evident conclusion that the number of pyloric caeca, the mean number of vertebrate or the number of gill rakers are not necessarily correlated with population status, but merely represent anything from climatic conditions, subspecies rank or even morphological sibling species. All of these criteria, however, reflect variation which may or may not have a genetic basis. The same is true of many polymorphic gene loci. Some polymorphisms show extremely limited variations in allelic frequencies within a species, whereas others may yield
highly significant differences between numerous neighbouring local populations. Furthermore, since some polymorphisms may be of little consequence as determinators of viability or else be more or less selectively neutral whereas others are strongly connected to the function of the individual or the population they can not be treated in the same manner. Lack of breeding data, technical imperfections of electrophoretic techniques and lack of supplementary ecological criteria are other severe complications. Generalizations about average "heterozygosity" as a means to assess amount of inbreeding and thus fitness are also dubious in some cases - like in the char group.

Our present knowledge is based on one well studied polymorphism and three more, which have shown the basic criterion of Castle-Hardy-Weinberg equilibrium, and sixty-odd more loci lacking both intraspecific and intrageneric variation in the Arctic chars. Based on these criteria alone one could seemingly safely assume that the Arctic char complex consisted of a number of extremely similar populations, almost similar to the degree of inbreeding depression. From the functional plasticity of the chars we know that this can not be true, and needless to say, we need supplementary data to achieve a more complete understanding of how the chars have diverged genetically and ecologically.

This is the reason why a large number of more or less independent characters are used to describe discrete populations or sympatric sibling species of char. The "basic" esterase polymorphism, which is inherited in a codominant Mendelian way, differs in frequency range in the three species so far discovered in Scandinavia, but introgression, fixation of the commonest allele and overlapping ranges preclude classification not only of individual fish but sometimes even of population samples. However, inclusion of meristic and ecological data, such as size/age relationship, time at spawning, parasite infestation, food preference as examined by stomach analyses, snout length in relation to eye diameter, colouration etc. considerably increase the magnitude of successful classification - as shown by e.g. some of the papers in this volume. These criteria and their relevance speak for themselves, what need be pointed out once
more perhaps is the thorough knowledge we now have of the esterase polymorphism. Careful breeding experiments showed the simple codominant manner in which it is inherited. The polymorphism was not correlated with either sex, size, age or disease. It was furthermore found that in one of the species there was a correlation between latitude or rather temperature (climate) and the frequency of the two alternative alleles, which was explained by different temperature optima expressed as peak enzyme reaction rates. Thus the frequency of the most anodal allele (often termed "F" - for fast) decreases in populations in colder environments in what is usually called the "normal char". There are also indications that similar physiological differences occur between the probably homologous allelic pairs in the so called "F-char" even though the total genome in this species creates another genetic environment as evidenced by considerably higher F frequencies in higher latitudes. The third species, the "S-char", is not known from enough localities to allow for speculations as to possible clinal distributions of the alternative alleles.

Transplantation experiments, where fish of known extraction have been released in formerly fishless lakes and then followed for several generations have further substantiated the hypothesis of geographical and temporal stability of the taxon-specific allele frequency ranges. This information now helps us to record the pace and mode of introgression that may take place in sympatric char combinations and also record migrations of char and the success of colonization.

In summary, the three species of char so far detected are best separated on the species and population levels by a combination of genetic, meristic and ecological parameters.
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