NORDIC JOURNAL *of* FRESHWATER RESEARCH

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NORDIC JOURNAL*of* FRESHWATER RESEARCH

Aims and Scope

Nordic Journal of Freshwater Research is a modern version of the Report of the Institute of Freshwater Research, DROTTNINGHOLM. The journal is concerned with all aspects of freshwater research in the northern hemisphere including anadromous and catadromous species. Specific topics covered in the journal include: ecology, ethology, evoulution, genetics, limnology, physiology and systematics. The main emphasis of the journal lies both in descriptive and experimental works as well as theoretical models within the field of ecology. Descriptive and monitoring studies will be acceptable if they demonstrate biological principles. Papers describing new techniques, methods and apparatus will also be considered.

The journal welcomes full papers, short communications, and will publish review articles upon invitation.

All papers will be subject to peer review and they will be dealt with as speedily as is compatible with a high standard of presentation.

Papers will be published in the English language. The journal accepts papers for publication on the basis of merit. While authors will be asked to assume costs of publication at the lowest rate possible (at present SEK 250 per page), lack of funds for page charges will not prevent an author from having a paper published.

The journal will be issued annually.

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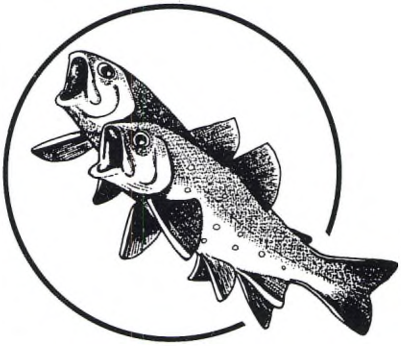

Proceedings of the

Third International Charr Symposium

June 13-18 1994, Trondheim, Norway

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Preface

At the International Symposium on Charrs and Masu Salmon, in Sapporo, Japan 1988, it was proposed that a third symposium on charr biology should be held in Scandinavia. The meeting in Japan was successfull and well attended, as was the first charr symposium in Winnipeg, Canada in 1981. With the continued effort in *Salvelinus* research around the world, the audience in Sapporo felt the need for a subsequent symposium in a few years′ time. After some time and discussions, Norway took the challenge and started the planning of the Third International Charr Symposium, to be convened in Trondheim in June 1994. The host institutions were the Norwegian College of Fishery Science, University of Tromsø; the Norwegian Directorate of Nature Management (DN); and the Norwegian Institute of Nature Research (NINA). The aim of the symposium was to provide a forum for the interchange of ideas and recent developments in charr (*Salvelinus* spp.) biology. Contributions on brown trout (*Salmo trutta*) were also invited as long as they were related to charr biology.

The opening session of the symposium took place on 13 June. Welcome addresses were given by Director Peter Johan Schei of DN and Director Karl Baadsvik of NINA. Both emphasized the importance of charr biology in nature management and research. Schei viewed charr in relation to biodiversity issues whereas Baadsvik focused on developments in Norwegian Arctic charr science. Lionel Johnson, Canada, had been invited to give the key-note lecture, which was given directly after the opening addresses and marked the start of the symposium. His contribution is printed as the first paper in the proceedings.

The symposium had 101 participants from 10 countries (Austria, Canada, France, Iceland, Japan, Norway, Russia, Sweden, UK and USA). A participant list with addresses appears at the end of the proceedings.

The oral presentations were organized in the following consecutive sessions: **Genetics** (Chair: James D. Reist, Canada), **Life History** (Chair: Hiroya Kawanabe, Japan), **Ecological Interactions** (Chair: Tor G. Heggberget, Norway), **Management** (Chair: Odd Terje Sandlund, Norway), **Speciation** (Chair: Johan Hammar, Sweden), **Parasitology** (Chair: Per-Arne Amundsen, Norway), **Aquaculture** (Chair: Alexander Chernitsky, Russia) and **Conservation and Management** (Chair: Geoffrey Power, Canada). Every session started with a lecture by an invited speaker. The invited papers are printed at the beginning of the proceedings, in the order of the sessions as listed above. All sessions were well attended and 37 presentations were given. A poster session was held on the afternoon of 13 June and 24 posters were on display until the last day of the symposium. All oral and poster contributions appear in the Book of abstracts which was distributed to the participants.

By invitation, John E. Thorpe, UK, summed up his impressions from the symposium at the closing session on 18 June. His contribution is printed as the last paper of the proceedings. The closing session ended with a general discussion.

Manuscripts from both oral and poster presentations were invited for publication in the proceedings. All submitted manuscripts were reviewed, and 42 papers were accepted for publication.

At the symposium banquet, the insignia for outstanding research on *Salvelinus* were awarded to two distinguished scientists, Dr Lionel Johnson, Canada, and Professor Ksenia A. Savvaitova, Russia.

A mid-symposium excursion to Selbusjøen was arranged by NINA. Arnfinn Langeland gave a lecture on the ecology of the lake with emphasis on charr/*Mysis* interactions, and Hans Mack Berger presented an exhibition of live fish and *Mysis* on the beach.

A post-symposium excursion and workshop was arranged by the Norwegian College of Fishery Science to northern Norway directly after the symposium. Emphasis was placed on demonstrating the charr part of the Norwegian sea ranching programme and discussing problems connected to sea ranching with charr. Sessions were first held at the Møkkeland water course, Harstad, where Martin-A. Svenning, Helge Eriksen and colleagues were responsible for the programme; and then at the Aquaculture Research Station, Kårvika, Tromsø, where Malcolm Jobling and colleagues hosted the session. The last two sessions were held on board the coastal steamer M/S *Richard With* from Tromsø to Øksfjord and at Talvik Research Station, Alta, where Bengt Finstad and Tor G. Heggberget from NINA were hosts.

The logo of the symposium, showing two spawning Arctic charr, was drawn by Johan Hammar, Sweden.

Målfrid Bølestrand Kristiansen, Jorun Vikan Larsen, Laila Saksgård and Brit Veie Rosvoll were in charge of the registration and other secretariat functions before and during the symposium. Their efforts were large, effective, kind and necessary.

Tor F. Næsje had the responsibility to give assistance during all oral and poster presentations.

Malcolm Elliott, UK, volunteered to serve on the editorial committee. His extensive experience as a science editor was a great help in producing the proceedings. He also corrected the English of many manuscripts. Monica Bergman at the Institute of Freshwater Research, Drottningholm, did a very professional job as the assistant editor for this volume of the Nordic Journal of Freshwater Research.

The symposium received financial support from the Norwegian Directorate of Nature Management, the Norwegian Institute of Nature Research, the Norwegian Research Council, the University of Tromsø and the Norwegian College of Fishery Science. The Norwegian Sea Ranching Programme PUSH supported the post-symposium workshop. The Nordic Publication Board for Natural Sciences supported the publication of the proceeedings.

We feel that the Third International Charr Symposium was a successful meeting. On behalf of the organizing committee and the host institutions, we want to express our gratitude to everyone, mentioned and unmentioned, who took part in the organizing and the running of the symposium and the excursions, to the invited speakers for their important contributions, to all participants for coming to Norway, and to the institutions that gave financial support.

We hope that the present volume provides interesting reading, and already look forward to the next international charr symposium.

Tromsø and Trondheim, August 1995

Anders Klemetsen and *Bror Jonsson*

Convenors

CONTENTS

Keynote lecture

Invited papers

Full papers

Closing lecture

Nordic J. Freshw. Res. (1995) 71: 9-22

Systems for Survival: of Ecology, Morals and Arctic Charr (*Salvelinus alpinus*)

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Abstract

Undisturbed Arctic charr populations in autonomous lakes in northern Canada, provide a reference system delineating the structures and behaviour contingent on stability and survival. Examination of the roots of moral behaviour by Jacobs (1992) reveals interesting correspondences with the basic biological dynamic. The origin and survival of organisms, it is hypothesized, is the result of interaction between two countervailing physical principles, one is the *Principle of Least Action* (the dissipation of energy as rapidly as possible), fundamental to modern physics, the other is a *Principle of Most Action* (energy capture and its retention for as long as possible). This principle is most readily apparent in biology. *Action* governs the overall process of energy transfer; its dimensions are energy *times* time. Application of these principles to living, interacting organisms results in a hierarchical structure. Asymmetric interaction between levels accelerates energy transfer (decreased *action);* but within hierarchical levels symmetric interaction is necessary for survival (increased *action*). A further prerequisite of survival is the dominance of the *Most Action* principle over 'successional' or 'ecological' time; conversely, over 'evolutionary' time *Least Action* predominates.

Keywords: Arctic charr, action principles, balance-of-nature, symmetry, asymmetry, survival, stability, ecosystem dynamics, ethics.

Introduction

Honourable Chairman, Members of the Symposium Committee, Fellow Fanatics, Scholars and Friends:

It is a great honour to be asked to deliver the keynote address on this most auspicious occasion. We have assembled today in this ancient and magnificent city of Trondheim from all circumpolar lands, as well as from those countries in more southerly latitudes blest with Arctic charr populations, to discuss and honour one of the world's great species. Not only is this an important scientific meeting, it fulfils also the ideals of nineteenth century scientists who believed that through science we can reach mutual understanding between nations, for it has frequently been observed by participants at Charr gatherings that they far exceed most scientific meetings in their warmth and friendliness. Therefore we are here not only to learn more of this wonderful species, to discuss new scientific findings and new ideas, but also to seek new friends and to strengthen old bonds. I have no doubt that this will be the warmest and friendliest meeting yet, brought together as we are by the common goal of understanding the universe of charr.

But in the great outside, the world we know is changing fast: on all sides ecological disasters are actually occurring or in the making as we continue to run up ever greater fiscal, social and environmental deficits. Only if we understand the living world and eliminate our ecological ignorance and gross arrogance, shall we be able to counter these forces of outrageous fortune. As you will recall, after all the miseries of the world had escaped from Pandora's box, the only one that could not get out before the lid was closed was Hope. But Hope is not enough if we are to survive the ecological miseries we have released. and for which we alone are responsible. As biologists, we cannot be mere voyeurs, intruding into the lives of other organisms for our personal gratification: we must recognize that we are simply another organism, albeit a complex and interesting one, governed by biological reality. In addition, as the dominant species in so many ecosystems, we are charged with the cardinal responsibility for order and good government within the universal Laws of Nature. Therefore, we must try to elucidate and understand these Laws, drawing inspiration and verification from the species we study.

Having spent many years fascinated by northern ecosystems, and particularly the role of Arctic charr, perhaps I may be allowed a few thoughts on what I believe these relatively simple systems can tell us concerning the structure of the world's ecosystems in general and the part played by mankind in particular? These relatively simple, autonomous Arctic ecosystems may be regarded as pots of gold at one end of a spectrum of increasingly complex ecosystems, stretching from the poles to the tropics. This spectrum of systems enables us to extend our views beyond the Arctic and hopefully gain insight into the fundamental workings of the natural world. Initially, we must concern ourselves with generalities more than specifics, for, as always in biology, there are exceptions and complications as exemplified by the bacteria living deep in the anoxic mud of the ocean floor and the open systems of the ocean basins. Fortunately, many Arctic lakes have been exempt from significant disturbance permitting us to observe and dissect their essential dynamics.

Nevertheless, even within a relatively simple autonomous ecosystem, there are many variable factors, acting either simultaneously or intermittently, which obscure the precise trajectory of such a system through time. Despite these difficulties, I believe with the early Greeks "that a single order underlies the chaos of our perceptions; furthermore we are capable of comprehending that order" (Lederman 1993).

"Systems *for* Survival" is the title I have chosen for this address in the belief that our survival depends on decyphering the coded messages displayed by all ecosystems and their translation into a working philosophy. It is a title plagiarized from a recent book by Jane Jacobs, the eminent authority on the growth and function of the city, entitled "Systems *of* Survival: a Dialogue on the Moral Foundations of Commerce and Politics" (Jacobs 1992). This intriguing book explores social relationships and how we must conduct ourselves if we are to survive with our dignity intact. Interestingly, I believe that analysis of the social and ecological worlds yields a similar message. The introduction of a moral note thus confounds the notion that science is completely neutral on ethical questions and to mix science and ethics is extremely dangerous to the objective view. Notwithstanding, as biology is the 'subversive science', let us then live subversively.

Systems of Survival

Jane Jacobs divides human beings into two groups, a division that she believes has existed in all cultures since the dawn of civilization. Interaction between these two groups is the foundation of all civilized conduct. Beyond the universals, which apply to all people of goodwill, such as responsibility, cooperation, courage, moderation, mercy, common sense, foresight, judgement, competence, perseverence, faith, energy, patience, and wisdom, these two groups each live by what Jacobs terms distinct *moral syndromes,* one characteristic of the commercial community, the other characteristic of the *guardians* whose function is to control and regulate affairs. This dichotomy is clearly illustrated in our own particular field, where the commercial side is represented by the fisherman always trying to increase his catch and improve the efficiency of his gear, whilst the guardians are clearly the enforcement authority controlling and regulating catch for the good of all. Each of the two groups, according to Jacobs, has a different mind set determined by their different strategies for making a living. The *commercial syndrome* (Table 1) is characterized by, among other qualities, competitiveness, openness, inventiveness, industriousness, thrift and honesty. These qualities (although not invariably apparent) are essential for effective commercial activity upon which we all depend for our comfort and convenience. Guardians, on the other hand, are responsible for order, good government and the regulation of affairs; they shun trading, respect hierarchy, are loyal, decisive, fatalistic and exclusive, and they treasure honour.

The commercial group is concerned with new ways of doing things, accelerating the interchange of goods and promoting what we generally regard as *progress,* whereas guardians ensure continuity and stability. Scientists, and at first sight this may seem somewhat incongruous, are included in the commercial category; however, on closer examination it is evident that essential qualities for a scientist are those of competitiveness, openness, inventiveness and industriousness, and above all, honesty. The fabric of human society and civilization, Jacobs contends, is held together by the symbiotic application of these two syndromes; both are equally important and *each must be held in relative balance by the other*. Difficulties arise when a member of either group crosses the invisible dividing line and mixes the mind set of the other with her or his own: when, for example, the Fisheries Officer begins to trade in fish. Most important today, Jacobs believes, is it necessary for those in administrative positions to be able to appreciate the existence of both syndromes and, at the same time, clearly differentiate between them. Of course this division must not be applied too narrowly, for always there are changing circumstances, imposing a change of stance on the individual, as he or she moves from one role to another in our complex society. The essential feature is to recognize the mode in which one is currently operating and to abide by the relevant rules. How, you may well ask, can these two *moral syndromes* be, in any possible way, related to Arctic ecosystems?

Table 1. The Commercial Moral Syndrome and the Guardian Moral Syndrome (after Jacobs 1992).

The Commercial Moral Syndrome	*The Guardian Moral Syndrome*
Shun force	Shun trading
Come to voluntary agreements	Exert prowess
Be honest	Be obedient and disciplined
Compete	Adhere to tradition
Respect contracts	Respect hierarchy
Use initiative and enterprise	Be loyal
Be open to inventiveness	Take vengeance
Be efficient	Deceive for the sake of the task
Promote comfort and convenience	Make rich use of leisure
Dissent for the sake of the task	Be ostentatious
Invest for productive purposes	Dispense largesse
Be industrious	Be exclusive
Be thrifty	Show fortitude
Be optimistic	Be fatalistic
Collaborate easily with strangers and aliens	Treasure honour

Systems for Survival

In the first place, Arctic charr *(Salvelinus alpinus)* are perhaps the greatest survivors of all. Charr are not survivors in the same sense as the famous Coelacanth, *Latimeria,* sequestered in the languid waters of the Comores Islands, but a species that thrives in the extremely rigorous inland and coastal waters all around the periphery of the Arctic Mediterranean, where life is rugged and mean and every day a struggle against a lean and hungry environment. At the other extremity of its range, Arctic charr thrive in mountain lakes of southern Europe left behind by the retreating ice cap of the Pleistocene epoch, as well as in the British Isles, Central Siberia, Japan, and the more favoured states among the 'Lower Forty Nine' of the U.S.A.

In many lakes in Arctic Canada, lake-dwelling, or so-called 'land-locked' charr populations, frequently exist in relatively simple, self-contained ecosystems; in many of these lakes Arctic charr is the only fish species present. For 9 to 10 months each year the lakes are ice-covered, effectively isolating them from contact with the outside world. Additionally, such lakes are frequently found in drainage basins entirely free from human disturbance. From a research point of view, these lakes are an experimental ecologist's dream for they are, in effect, a fully equipped laboratory in which we can examine the behaviour of a single species free from competitors or predators in a relatively self-contained ecosystem. They are, in fact, the super-computers of the biological world.

The capacity of Arctic charr to live in rigorous northern conditions appears to be its lack of specialization, hence its suitability for studies of general significance. Populations of Arctic charr may be either anadromous, making an annual trip to the ocean for feeding, or entirely lake-dwelling; occasionally, such populations live sympatrically. Anadromous charr reach their greatest size and abundance between latitudes 65° N and 75° N, attaining in this region a mean length of about 700 mm and a mean weight of 3-5 kg. Having few predators in the adult stage, Arctic charr is always the dominant species in an ecosystem, occupying the terminal position in the food chain. In fresh waters they adapt to an extremely wide range of niches, adjusting their phenotype accordingly, and where conditions permit, they may even occupy two or more different niches in the same waters, each each having its own characteristic phenotype. The existence of two or more distinct populations living sympatrically has caused great discussion among evolutionists and zoogeographers, for this contravenes a basic tenet on which our generation was raised: "one species, one niche." This apparent conflict has given rise to the great "Charr Problem" about which so much has been written (Nordeng 1983, Hammar 1984, Klemetsen 1984, Nyman 1984). Whether resulting from a division of the habitat, or the multiple invasion of sibling species, as you may believe, the process appears to have reached its maximum in Thingvallavatn in Iceland where as many as four different *morphs* have been observed (Sandlund 1992).

Many Arctic charr populations live at the very edge of existence. They can withstand a lifetime of conditions in which temperatures seldom rise above a few degrees Celsius, and they are able to withstand up to 2 years fasting in this frigid environment. They consume the widest possible variety of food items, ranging from plankton and invertebrates, to small fish; but at best, the food supply is meagre and declines as latitude increases. When the hard times are over and conditions become favourable charr show a remarkable capacity for rapid recovery (Johnson 1980).

Physiologically, too, charr show great flexibility, accommodating each spring to salt water then returning to fresh water in the fall (anadromy), repeating this migration each year for many years, except in those years when they remain in fresh water to spawn. Of all anadromous salmonids, charr are the least specialized to marine life and, despite their cold environment, they are devoid of the blood-stream anti-freeze, characteristic of specialized Arctic marine species. Because of this lack of anti-freeze, it seems that charr are unable to overwinter in the Arctic

Ocean, where temperatures remain below zero for most of the time. Perhaps their most extreme specialization is their incredible olfactory capacity explored by Hans Nordeng (Nordeng 1983) and Hakon Olsén (Olsén 1985). Arctic charr, in fact, emerge as supreme generalists: perfect guests at life's koldtbord.

From the present perspective, the most important characteristic of the populations in these lakes is that they almost invariably exist in a relatively stable state as witnessed by their constant structural pattern (Johnson 1972, 1976, 1983, 1994a,b,c). In each case, the population was found to be either unimodal as in the charr population from Little Nauyuk, on the Kent Peninsula (68° N) (Fig. 1), or bimodal as in Lake "H" (80° 5′ N), at the head of Borup Fjord, in northern Ellesmere Island (Parker and Johnson 1991) (Fig. 2). Thus a population may have a minor mode composed of relatively small fish and a major mode of large, adult fish. Within each mode, the individuals, although very similar in size, exhibit considerable variation in age. In Little Nauyuk Lake ages ranged from 5 to 14 years within the modal length class of 200-249 mm.

This stable structure is not a property confined to Arctic charr, but a general property observed in all northern freshwater fish stocks. It is perhaps best illustrated by the long data series (1971-85) from Baptiste Lake (Fig. 3), 50 km north of Yellowknife in the Canadian Northwest Teritories, an otherwise undisturbed lake, 365 ha in area in the northern boreal forest (Healey 1975, Johnson and Gyselman unpubl.). Although these data were gathered from lake whitefish *(Coregonus clupeaformis)*, identical structure is shown by all dominant Arctic fish stocks.

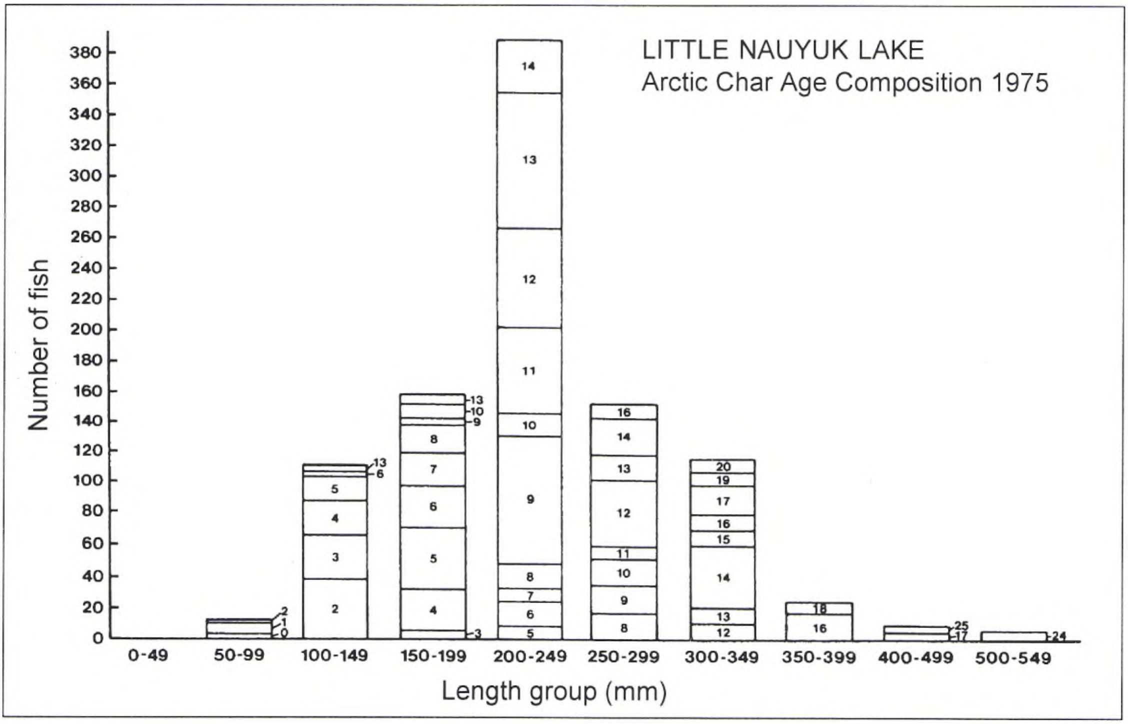

Fig. 1. Arctic charr *(Salvelinus alpinus)* from Little Nauyuk Lake (68° N) on the Kent Peninsula, N.W.T. Fish lengths are tightly clustered around the modal value (225 mm), but ages range from 5 to 14 years.

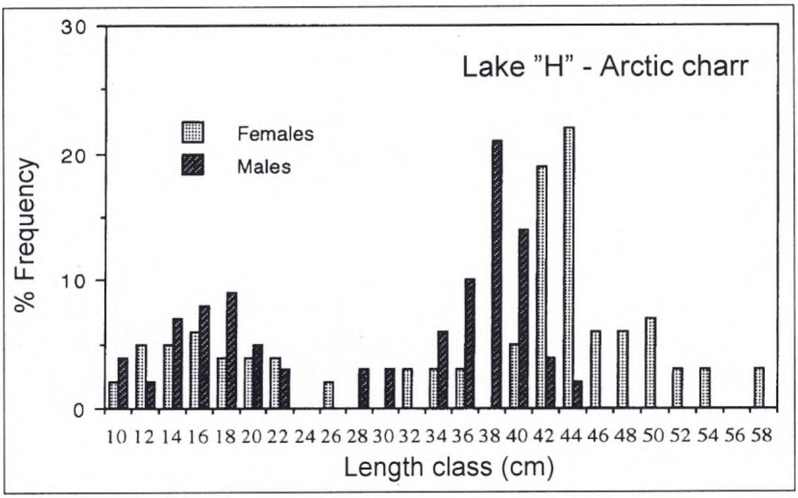

Fig. 2. Arctic charr *(Salvelinus alpinus)* in Lake "H" (82° N) Borup Fjord, Elllesmere Island, N.W.T. Showing two charr populations living in the same lake. These populations start breeding at different sizes and occupy different habitats. (Data from Parker and Johnson 1991).

Arctic ecosystem structure

Arctic lakes have a relatively linear food-chain, in which Arctic charr, whitefish or lake trout, occupies the terminal and dominant position. The dominant population is made up of large, mature, relatively uniformly sized fish of variable age, forming a stable *establishment,* constant in mean size and abundance (Johnson 1976, 1983, 1994a,b,c). This establishment, regulating its own abundance, imposes a *top-down* stability on the rest of the system (Northcote 1988). Year-to-year variability in the environmental regime is absorbed by the population, which thus becomes an expression of the environmental variables integrated over the recent history of the population, within the more constant parameters of lake morphometry and water quality.

When displaced from the steady state by intensive fishing and then allowed to recover, the fish population of an Arctic lake returns in a well-damped manner to its original configuration. This was shown by work on Keyhole Lake and (Hunter 1970, Johnson 1983, Vanriel and Johnson 1995) and Little Nauyuk Lake (Johnson 1994a).

In these isolated lakes a steady state has evidently been reached, comparable with the *climax* of vegetation theorists, but without the semantic clutter surrounding the term as used in plant ecology. Their capacity to maintain a particular configuration, and, following massive disturbance, to return to it without significant oscillation, is clear evidence of an effective internal damping mechanism (Johnson 1983). In that growth in fishes is generally considered to be indeterminate, the wide variation in age of fish of modal length implies internal regulation of growth and abundance (Johnson 1994a).

Thus, an isolated Arctic lake closely reflects the view of Forbes (1887) (one of the fathers of limnology), as expressed in his paper "The Lake as a Microcosm":

> ". . . . It forms a little world within itself—a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp."

In terms of the physicist such a system approaches a *closed* condition; that is a system which functions within boundaries such as prevent the exchange of materials with the external world, but permit the exchange of energy and entropy.

The high degree of stability, attained by fish populations within the relatively impermeable lake boundaries, supports the view of Sir Arthur Tansley, dean of British plant ecologists, that

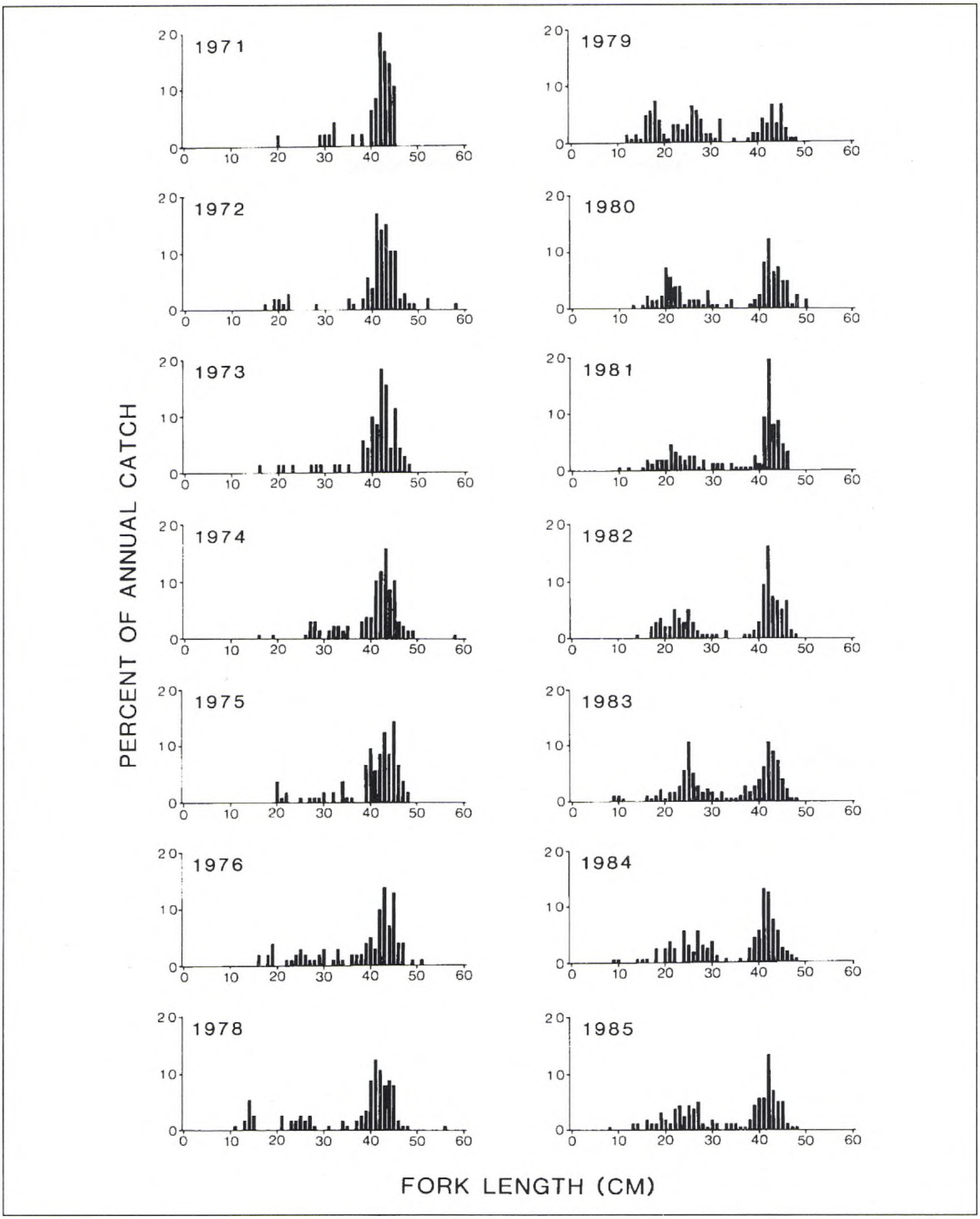

Fig. 3. Lake whitefish *(Coregonus clupeaformis)* from Baptiste Lake, 50 km north of Yewllowknife, N.W.T., showing inherent stability of the population between 1971 and 1985. Apart from annual sampling, the lake remained undisturbed over the period of observation. (From Healey 1975, and Johnson and Gyselman unpublished data on file at the Freshwater Institute, Dept. of Fisheries and Oceans, Winnipeg).

there is a "universal tendency to the evolution of dynamic equilibria" (Tansley 1935), but,

> ". . . The more relatively separate and autonomous the system, the more highly integrated it is, and the greater the stability of its dynamic equilibrium. . . . The "climax" [or stable state] represents the highest stage of integration and the nearest approach to perfect dynamic equilibrium that can be attained in a system developed under given conditions and with the available components."

Such stability evidently results from the balance of processes operating within the lake boundaries and is achieved through the agency of interacting forces creating a damping mechanism.

However, the view of a lake as a microcosm, has been largely discarded by modern limnologists because it has been clearly shown that lakes reflect disturbances and changes within their drainages. As disturbance within lake basins is almost universal today, limnological change can be understood only in terms of disturbance in the surrounding lands. Fortunately, this is not significant in the Arctic lakes under consideration, for they have low rates water exchange, and their basins are sparsely vegetated. Prior to investigation they had remained completely undisturbed since their formation some 8000 years ago.

The Balance of Nature

The existence of a climax, or dynamic equilibrium, as attained in a small Arctic lake, makes it necessary to revisit what is perhaps the oldest and most intriguing concept in biology: the Balance of Nature. The roots of this concept go back to the dawn of history, being first discussed by Herodotus in the 5th Century B.C. (Egerton 1973), although the first person to actually use the term *balance* in this connection was William Derham (1714). In his book *Physico-Theology* he states:

> "The Balance of the Animal world is, throughout all Ages, kept even, and by a curious Harmony and just Proportion between increase of all Animals and the length of their Lives, the world is through all Ages, well, but not over stored."

Soon afterwards, Linnaeus (1749) produced the first sketch of the science of ecology in his book *Oeconomia Naturae.* According to Egerton (1973):

> "Linnaeus used his economy-of-nature concept as an organizing principle to unify an important, but previously amorphous part of natural history. In so doing, he was also attempting to transform an important background concept into the central theory of a new science. Both his concept and his new science deserve close attention (p. 335) . ."

Unfortunately, as Egerton continues (1973 p. 343):

> "There was no science built, as Linnaeus would have had it, around the balance-of-nature concept."

Stability in the ecological sense has become a rather confused concept with many different connotations (Johnson 1994a); in fact Charles Elton (1930 p.17), the father of animal ecology, states categorically that there is no such thing as the balance of nature. In the final analysis there is, of course, no absolute stability, for without a degree of instability there would be no evolution. In an effort to clarify the situation Pimm (1991) lists three different usages of the term *stable* in addition to the mathematical definition, indicating, respectively: resilience, persistence and resistance, each with its own special definition. Mathematically, a system is stable if, and only if, the variables all return to an equilibrium position following displacement. Also implied in the definition is that a system is a bounded entity. This must be the starting theorem for any discussion of stability.

Ecological stability thus demands the existence of boundaries and constant environmental conditions, as exemplified in a small autonomous Arctic lake. Such a lake forms a reference system against which other systems may be compared (Vanriel and Johnson 1995). Manifestly, these circumstances occur only rarely in the real world and do not persist indefinitely.

In relatively *open* ecosystems, with fluctuating physical and biological environments, many of the same species may be present over the years, with individual abundances fluctuating in a seemingly chaotic manner in response to local energy gradients. However, if fluctuations are not to be self-augmenting and eventually lethal, a damping mechanism, operating at an underlying level, must exist. Open ecosystems, therefore, may be viewed as constantly trying to stabilize within the immediate environmental complex, but before stability can be achieved conditions change once more. Nevertheless, all systems are ultimately, closed by the boundaries of the biosphere. These global boundaries will be most effective during periods free from disturbance, when the biosphere is "full"; over evolutionary time, long periods of equilibrium existed, infrequently punctuated with periods of rapid change (Eldredge and Gould 1972). In the wake of disturbance reducing population abundances and eliminating local boundaries, the biosphere boundaries will be less effective and probably will have little impact at the local level until the system returns to equilibrium.

The important question is: What is the nature of the damping mechanism? To be effective such a mechanism must induce stability over a wide range of conditions; therefore it must result from a general system property and cannot be tied to a particular species or species complex. Only thus will an ecosystem be able to track environmental change, and only then provided the interval between significiant changes is sufficient to allow an appropriate response to develope.

Action Principles

The salient features of a stable Arctic lake charr population that require explanantion are: 1) high biomass of the dominant species despite very low primary productivity, 2) great mean age, 3) uniformity in length despite great variation in age, 4) regulation of recruitment to balance death rate, and 5) the functioning of the population as a coherent unit in the face of disturbance. Although first recognized in Arctic lakes these characteristics are found world-wide in autonomous ecosystems (Johnson 1985, 1994*a, b*)

These properties of an ecosystem may be accounted for by the application of *Action Principles. The Principle of Least Action* is perhaps *the* most fundamental principle of dynamical physics, for it governs the overall transfer of energy within physical systems both at the macro- and micro-level. The term *Action* in physics has little correspondence with its common usage: it is defined as the *product of energy and time* and is expressed in *Joule-seconds* in the International System of units (SI). The universal *Principle of Least Action* implies that the trajectory of a system can be described as that path for which the action, integrated over the period of observation, has the least value (Feynman 1963, Watson 1986). This implies that energy is dissipated from a system as rapidly as the internal constraints allow.

This being the case, acquisition and accumulation of energy in the biomass, and its retention over time, directly contravenes the *Principle of Least Action.* Therefore, it is necessary to postulate a contrary and over-riding principle: a *Principle of Most Action,* that stipulates that the *action* (energy x time) in any species population, tends to increase to the maximum permitted by the prevailing physiological and environmental constraints. This is the precise inverse of the *Principle of Least Action.* In all living creatures *most action* is manifest in the acquisition of energy and its condensation, concentration and conservation. As the *Principle of Least Action* is universal in its application, an ecosystem results from the interaction of these two countervailing principles. Thus, for an ecosys-

SUCCESSION

(A trend to Most Action dominates system behaviour)

Most Action <——————

——————> **Least Action**

Leads to:	
Energy concentration	Rapid energy dissipation
Long turnover time	Rapid turnover
Imposition of time-delay	Acceleration of energy flow
Species elimination	High diversity

culminates in the:

CLIMAX

(trends to Most Action and Least Action reach equality)

Most Action <———— = ————> **Least Action**

(hierarchy formation and stability)

Fig. 4 Interaction of Action Principles expressing "a universal tendency to the evolution of dynamic equilibria." Equilibrium is reached at the climax.

tem to survive, the *Principle of Most Action* must dominate system behaviour until equality is reached at the climax. This, in Tansley's words, is the " . . . universal tendency to the evolution of dynamic equilibria" (Fig. 4). Over the long-term, the position of this dynamic equilibrium may change as species composition alters, and species adjust to environmental change or adapt more closely to their environment.

The Ecosystem Hierarchy

Each species population within an ecosystem tends to conserve energy, but the combined effect of the rest of the system on that species is to reduce its action (i.e. energy x time), through grazing, predation, etc. Thus the maximum expression of the trend to most action is evident in the terminal or dominant species, which may be defined as that species which is largely free from grazers and predators.

The effect of the *Principle of Most Action* is directly observable in trends to increased size, increased abundance and increased life-span, both over successional and evolutionary time scales; but the countervailing *Principle of Least Action*, tending to accelerate energy transfer, cannot be observed in this way for it operates, like gravity, in a latent manner. Its effects can only be deduced from the system's dynamics. During succession, the two principles interact, but the *Principle of Most Action* dominates system behaviour until a stable state is reached at the climax as the two opposing forces approach equality.

If a chaotic state is to be avoided the various populations in an ecosystem must assume a hierarchical arrangement in which energy becomes more and more concentrated at each ascending level in the hierarchy. Only in this way can energy transfer be regulated, stability attained and the *Principle of Least Action* overcome at the system level. Thus, at each link in the food chain, energy concentration increases in *time and space,* as individual size and age increase, but, as Peter Vanriel and I showed at Keyhole Lake, not only do size and age reflect the increase in *action,* there is also an increase in the energy *concentration* of the tissues themselves (Vanriel and Johnson 1995) (Fig. 5). Energy, in effect, is captured by organisms having a relatively high energy concentration in time and space, from organisms having a relatively low energy concentration (Fig. 6). This is precisely the opposite process that would be expected in classical physics.

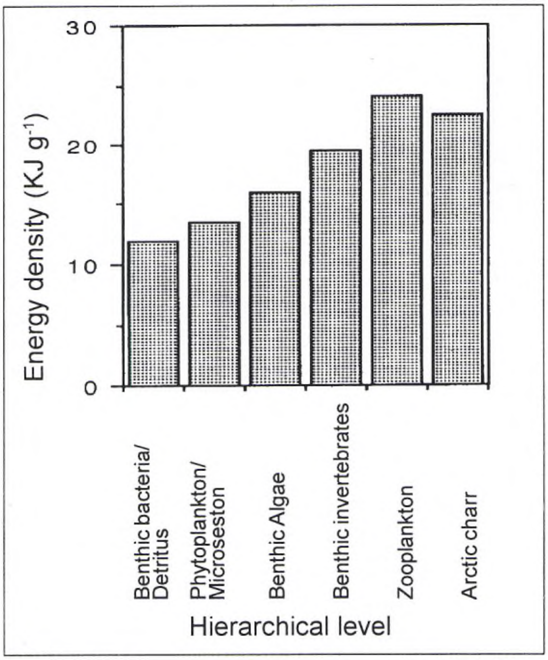

Fig. 5. Energy density (KJ·g^{-1}) of the various trophic levels in Keyhole Lake, Victoria Island, N.W.T. Zooplankton was shown to play only a very small part in the trophic heirarchy in which Arctic charr assumes the role of terminal predator. The plankton appears to form a virtually separate sub-system (from Vanriel 1989).

An ecosystem thus functions as a *homeorhetic* system[1], in which energy fluctuations are damped and *flows* equilibrated; this stands in contrast to a *homeostatic system* which maintains a specific state (e.g. the pH of the blood). Thus ecosystems move towards a balance of energy inflow and outflow, which, provided that inflow initially exceed or equal outflow, allows a stable state to be attained over a wide range of species and environments.

Stability is thus determined by universal thermodynamic considerations, not by a particular species or set of species; in this process lies the evident flexibility in systems allowing change and adaptation.

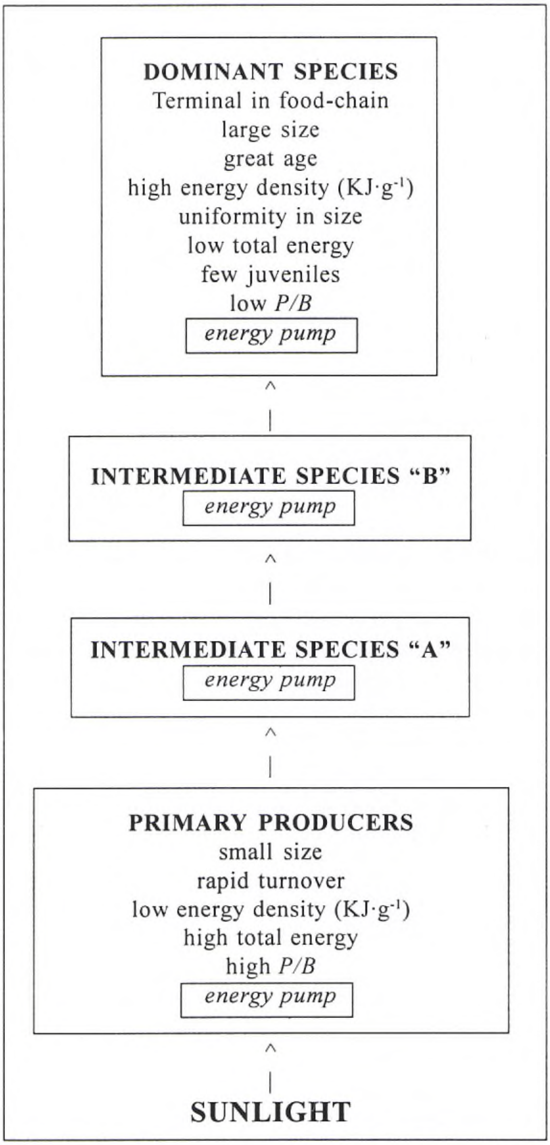

Fig. 6. Dynamics of a hierarchically structured aquatic ecosystem. Energy is "captured" by organisms having a relatively higher capacity to acquire, conserve, and concentrate energy from organisms with a relatively lower capacity.

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[1] A simple homeorhetic system is a water tank with an open drain, into which water initially flows faster than it is discharged. As the pressure at the outflow increases, discharge increases automatically, and the system attains equilibrium when inflow and outflow are equal. This is an extremely flexible system capable of reaching equilibrium over a wide range of inflow rates.

Energy is transferred 'up' the ecosystem hierarchy, or food chain, through the capture of energy in organisms at a lower hiererchical level by organisms at a higher level. This implies *asymmetric* interaction between individuals at different hierarchical levels. On the other hand, within levels (as demonstrated by Arctic charr), energy is conserved and uniformly distributed by *symmetric* interaction between individuals. In its most basic formulation asymmetric interaction stimulates energy flow: symmetric interaction imposes a time-delay on energy flow and permits energy accumulation.

However this is never a perfect state. In a symmetrically interacting population, individuals may fall into local asymmetry, as man may fall into sin, by exploiting opportunities of the moment. This must be limited, otherwise the population will fall into disarray and may be eliminated. When limited, slight asymmetry allows the formation of local hierarchies (as found in wolf packs) which may, through increased complexity, improve the effectiveness of energy capture. Thus hierarchies may develop within hierarchies.

Within a particular set of boundary conditions, ecosystem structure is maintained by a delicate balance between symmetric and asymmetric interaction. Although the trend to *Most Action* dominates system behaviour over the course of succession, over the long period of 'evolutionary' time, change allows the *Principle of Least Action* to dominate, that is, there is gradual "slippage" over the course of evolution leading to faster energy flow and greater complexity. It is the interaction between these two principles, dominating system behaviour in different time frames, that results in what we recognize as evolution. This, I believe, as Linnaeus advocated, is the *Economy-of-Nature Principle* on which the science of ecology should be established.

Integration

Life may thus be regarded as a striving to attain symmetry in an inherently asymmetric system. These opposing principles result in a hierarchical structure which attains stability and order within the prevailing boundary constraints. These are the "measures and institutions which impart to competition the framework, rules and machinery of impartial supervision which a competitive system needs as much as any game or match if it is not to degenerate into a vulgar brawl" (Ropke 1994, commenting on economic development).

Let us now return to Jane Jacobs' thesis. It should be apparent that her two *moral syndromes* reflect the two *Action Principles* as they operate within a human community. Understanding and combining them is therefore likely to provide both ecologically and ethically sound guiding principles for survival. The Guardian Syndrome represents the tendency to adhere to tradition, to be obedient and disciplined, to shun trading, and to respect hierarchy (hierarchies within hierarchies). Such activities impose resistance to change (inertia) on an inherently changing world. This is equivalent to the energy conserving and concentrating *Principle of Most Action.* In the human world, symmetry of interaction in social intercourse, codified and supported by a vast amount of civil and criminal law, allows the development of communities. Conversely, the Commercial Syndrome, stimulates increasing energy flow through competition, initiative and enterprise. Commerce is essentially a boundary breaking activity, opening up a system to external influences. To maintain stability and the capacity to adjust to change, demands that these two syndromes be held in balance.

As soon as humans appeared on the biological scene we began to change the primitive state, accelerating energy flow through most components of the system except ourselves by the use of tools, weapons, domesticated animals, agriculture and commerce, slowly at first, then greatly expedited by scientific discovery and technology. This is evidently a natural consequence of the *Most Action Principle*, rather than some defect in man's genetic make-up. Elimination of the local boundaries which formerly imposed constraints and limited fluctuation, now permits fluctuation on a global scale. In the process many ecosystems have been reduced to a state which can only be described as a "vulgar brawl."

In effect, we have largely decoupled the two moral syndromes as representing the countervailing biological drives of energy conservation and energy transfer, thereby allowing each principle to proceed toward the limit without adequate checks and balances. We have now reached a state that is essentially out of control and unsustainable as we head toward the ultimate boundaries (Meadows et al. 1992).

The biology of the planet has been "globalized" by the elimination of local boundaries and time delays. Similarly, the financial and industrial world has been globalized to stimulate commerce and currency trading, for it is only out of stability breaking and acceleration of energy transfer that 'profit' emerges, whether in the commercial or biological field.

Unfortunately, accommodation to accelerating flow rates and greater complexity appears to be largely irreversible except by system failure; as the Russian proverb indicates, "it is relatively easy to turn a fish into a fish stew, but no one really knows how to reverse the process" (Kennedy 1993). When something goes wrong with a complex ecosystem its only possible response is to drop back to a simpler state where the necessary 'impartial supervision' can once again be imposed and homeorhesis re-established. From this new position ecological processes can again flourish, but with a new set of components.

As Hope alone is not sufficient to alter our predicament, let Arctic charr provide a final word on how we might attain a balanced ecosystem, for charr, of necessity, live subject to the 'measures and institutions' imposed by thermodynamic and physical constraints. A stable dominant population must regulate its own abundance through coherence and the capacity to remain coherent under stress. Coherence is attained through mutuality (symmetric interaction) resulting in the equitable distribution of the available resources. By stabilizing its own population a damping moment is imposed on fluctuation at lower hierarchical levels. In turn, maintenance of the hierarchic structure necessitates a limit on the degree of asymmetry imposed by one level on another.

Thus I conclude, morals originate in the perception, through the haze of near-chaotic human activity, that certain principles governing our survival do exist. Perhaps in societies simpler than our own, the relationship between cause and effect was more readily apparent, for we appear to have largely discarded many of the former tenets of continued existence. The Golden Rule is simply a restatement of the need for symmetric interaction and this precept is replicated in most great religions. Only by near-symmetric behaviour can a population maintain itself in a healthy cohesive state within its boundaries. However, to push those boundaries to the natural limits ensures, as we see in charr, existence at a subsistence level. To live comfortably within the natural limits, we must establish our own boundaries and maintain them through self-restraint.

Thus, despite much that has been said to the contrary, morals have a physical/biological basis and are therefore intimately bound up with our survival. As both Plato and Aristotle agreed, although largely repudiated in modern scientific circles, nature exhibits reason, purpose, and design, inseparable from the foundations of human ethics (Provine 1982).

I would like to take this opportunity to thank most sincerely the Symposium Organizers for their magnificent efforts and to wish all participants a great scientific, social and moral experience over the coming two weeks.

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Molecular Approaches to the Study of Genetic Variation in Salmonid Fishes

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Abstract

The development of biochemical and molecular techniques over the past 40 years has enabled a direct appraisal of genetic variability within and among populations. The advantages and disadvantages of allozyme, mitochondrial DNA (mtDNA), and minisatellite DNA markers are discussed in relation to such studies. While these are illustrated by reference mainly to brown trout examples, similar applications are possible for Arctic char and other salmonids. MtDNA is particularly suitable for studies of population differentiation and postglacial colonisation. Highly variable minisatellite DNA can be applied to population studies where low levels of allozyme or mtDNA prevent the use of these marker systems. Many salmonids show intraspecific variation in their life history and behavioural traits. Both evolutionary studies and practical management activities require information on the relative Darwinian fitness of these alternative strategies. One of the major uses of the highly polymorphic minisatellite DNA loci is in the identification of parentage, thus enabling a direct estimation of fitness in natural and experimental populations.

Keywords: Allozyme, Arctic char, brown trout, fitness estimation, minisatellite DNA, mitochondrial DNA.

Introduction

A correct interpretation of the ecology, physiology, behaviour and systematics of salmonids requires an understanding of the genetic basis, evolutionary origins, and adaptive significance of the phenotypic variability which is typical of the group. Studies of polymorphic proteins have indicated that salmonid species are divided into a large number of more or less reproductively isolated genetically distinct populations among which genetic differentiation generally increases with increasing geographical distance. Such markers do not prove that the genetic differences observed among populations are of adaptive significance. However, there is increasing evidence from studies of morphological, behavioural, life history, and, to a limited extent, physiological traits that adaptively important genetic variation occurs among and within populations (Riddell et al. 1981, Taylor 1991, Gharrett and Smoker 1993). However, most of the evidence for local adaptation is purely circumstantial and fitness differences among phenotypic variants have been adequately demonstrated in only a few cases (e.g., Jonsson and Hindar 1982). As genetic variability is rapidly being eroded in most species through the reduction and extinction of natural populations, and the deliberate and inadvertent mixing with cultured stocks, it is important from a management standpoint, as well as for fundamental evolutionary studies, to understand the significance of this variability.

In this paper we give a somewhat simplified overview of the main molecular approaches which can be used for studies on salmonid populations. Fuller details of these methods are to be found elsewhere (e.g. Wright 1993, Park and Moran 1994). The development of biochemical and molecular techniques over the past 40 years has enabled a direct appraisal of genetic variability within and among populations. These studies use variants in protein or DNA sequences as "flags" or markers to provide information about the population or other unit being studied, and in most cases there is no direct interest in the polymorphism as such. Early studies involved starch gel electrophoresis of proteins such as haemoglobin and transferrin but attention quickly turned to enzymatic proteins (allozyme variation). Although a considerable number of polymorphic proteins have been detected in most populations of salmonid species such as brown trout, *Salmo trutta*, (Ferguson 1989), other species such as Arctic char, *Salvelinus alpinus*, have shown low levels of variability (Anderson et al. 1983). In this latter species, lack of suitable protein markers has severely limited population studies. However, even in brown trout, one of the most polymorphic of all fish species (Ferguson 1989), usually only two or three alleles segregate at a protein-coding locus in a particular population and heterozygosity levels are generally less than 10%.

In the past decade attention has turned to DNA studies, first to mitochondrial DNA (mtDNA) and then, as molecular techniques developed, nuclear DNA. Although more costly and technically demanding, DNA studies offer a number of practical advantages over protein studies. Since we are not dealing with expressed genes, a single tissue is sufficient for analysis, whereas, to obtain sufficient polymorphic protein loci, several tissues are generally required. Protein studies also require the use of fresh or frozen tissue while DNA techniques can use alcohol preserved or, in some cases, dried tissue. The requirement for only a limited amount of a single tissue means that biopsy sampling can be undertaken, or, for example, embryos from "eyed eggs" can be used. Also adipose fin biopsy samples can be routinely used for salmonid studies. The development in recent years of DNA amplification using the Polymerase Chain Reaction technique (PCR) has meant that, for some approaches, even smaller amounts of tissue are sufficient. In PCR, two short synthetic DNA sequences are used as primers and the section of DNA between them is enzymatically copied thousands of times. This makes it possible, for those approaches which are PCR based, to potentially use, for example, a single fish scale or degraded DNA from museum specimens. The ability to use archive material has opened up the possibility of examining genetic changes in salmonid populations over the past 100 years or so and gives a new lease of life to the many scale collections in fisheries laboratories throughout the world and also to museum specimens. PCR amplification can also allow specific gene regions to be isolated more easily than by cloning in micro-organisms. These amplified regions can then be examined directly by restriction enzyme analysis or sequencing.

MtDNA, by virtue of its higher mutation rate as compared with single copy nuclear DNA, plus its maternal mode of inheritance and lack of recombination, offers several advantages for population studies. Its one quarter effective population size, relative to nuclear DNA, results in greater genetic differentiation due to genetic drift and thus it is more likely to provide population specific markers. From a phylogenetic point of view, the lack of recombination means that mtDNA markers can be used to organise individuals into matriarchal lineages even after interbreeding, and thus nuclear introgression, has taken place. The first techniques used to examine mtDNA variation generally required the isolation of mtDNA in the purified form. This is a slow procedure and consequently in many early studies too few individuals were examined for valid conclusions to be drawn. The use of mtDNA probes, and more recently PCR amplification of specific mtDNA regions (e.g. Cronin et al. 1993), has considerably speeded up the analysis to the extent where mtDNA analysis is now approaching allozyme studies in terms of speed of screening, although not cost.

Protein or mtDNA markers are based on changes in DNA sequence generally as a result of point mutations involving base substitutions.

Recently attention has turned to another type of variation, that of differences in the number of repeated copies of a segment of DNA. This variation is a result of internal genomic mechanisms such as unequal crossover and slippage. Sequences that display a variable number of tandem repeats are classified on the basis of decreasing size into satellites, minisatellites and microsatellites (Tautz 1993). Except for the alpha satellite DNA that organises the centromere, none of these repetitive DNAs has a clearly defined function. Satellites consist of units of up to several thousand base pairs repeated thousands or millions of times. Minisatellites consist of DNA sequences of some nine to 100 base pairs in length which are repeated from two to several hundred times at a locus. Microsatellites have a unit length of one to six base pairs repeated up to about 100 times at each locus. The alternative name VNTR (Variable Number Tandem Repeats) is also used for both minisatellites and microsatellites although Tautz (1993) uses this term as a synonym for minisatellites only. Individual alleles at a locus differ in the number of times the sequence is repeated in tandem. Since many different alleles are possible and mutation rates are often high, these hypervariable regions potentially overcome the problems of low number of alleles and slow rate of evolution which limits allozyme and other protein studies. Some minisatellites, in humans at least, show the greatest known variability for DNA sequences with very high mutation rates (0.05 per gamete) and consequently high numbers of alleles and heterozygosity. We will restrict our consideration to minisatellites although it should be noted that many similar applications are possible with microsatellites, one of the advantages of the latter being that their smaller size makes them amenable to PCR amplification (Wright and Bentzen 1994). Satellite DNA may also be a useful source of genetic markers (Wright 1993).

Detection of minisatellites is carried out using a complementary DNA fragment as a probe to highlight the sequence(s) of interest following electrophoretic separation of restricted genomic DNA. Both isotopic (P_{32}) and non-isotopic (colourimetric, chemiluminescent) methods for probe labelling can be used. There are two distinct types of repeat DNA screening. The first involves generalised probes (e.g. Jeffreys 33.6 and 33.15; bacteriophage M13 DNA) which give a multi-banded pattern as a result of the simultaneous detection of multiple chromosomally dispersed loci. Since most of the detected loci have a large number of alleles, no two individuals are likely to have the same combination of alleles at all loci. Thus the pattern of DNA fragments produced is individual specific and is referred to as a DNA fingerprint. The same probes can be used on a wide range of organisms, from plants to humans. DNA fingerprinting is of limited value in population studies since neither the number of loci nor the locus affiliation of alleles can be inferred directly.

The alternative and more valuable approach is to dissect the mutilocus pattern into its individual loci. This can be done by using specific locus probes (SLPs) which detect only a single locus. In this case individual patterns are either single-banded homozygotes or double-banded heterozygotes. Because of their higher sequence specificity such probes need to be isolated from the species under study, or at least from a closely related one. It has been claimed that one advantage of minisatellites (and microsatellites) is that, since they are non-coding, they are selectively neutral. However, an association has been found between the risk of cancer and rare alleles at a human minisatellite locus (Krontiris et al. 1993) and there is current evidence to suggest that microsatellite "allele" size may affect gene regulation (Epplen et al. 1993). So, as with other types of genetic markers, VNTR selective neutrality should not be invariably assumed (Ferguson 1994).

While many SLPs have been isolated for humans, the specialised nature of the cloning procedures required has so far limited application of this technique to fish studies (Prodöhl et al. 1994b, Wright 1993). To date our laboratory has isolated six SLPs from a brown trout genomic library (Prodöhl et al. 1994a, 1994b) and six SLPs from an Atlantic salmon (*Salmo salar*) library (Taggart and Ferguson 1990, Taggart et al. 1995). With the exception of one probe derived from Atlantic salmon, all probes cross hybridise with the other species to reveal a single locus. Some of these probes can also be used to detect single locus minisatellite polymorphisms in other salmonid species, including Arctic char (Prodöhl et al. 1995, S. E. Hartley pers. comm.). An essential prerequisite for the application of these markers to population or family studies is the verification of inheritance and germline stability of each locus, and also that linkage relationships be identified. This is of particular importance in the salmonids where aberrant segregation at protein coding loci has been recorded for many species, this being thought to reflect residual tetrasomy within the tetraploid salmonid genome (Wright et al. 1983). Analyses of family sets showed Mendelian segregation for all loci in both brown trout and Atlantic salmon. Linkage of one locus with the sex determining region was found in brown trout. Mutation rates were estimated to be less than 10^{-3} per allele per locus per generation. The loci detected by the SLPs show from one to over 20 alleles in brown trout and Atlantic salmon, with considerable variability occurring among loci in respect of the number of allelės. The relative advantages and disadvantages of allozyme, mtDNA and minisatellite DNA markers will be assessed by reference to selected studies mainly undertaken in the authors' laboratory.

Population structure studies

Sympatric populations

Morphogically distinct and ecologically specialised sympatric forms have been described for many salmonid species including Arctic char (Hindar et al. 1986, Skúlason et al. 1989, Hartley et al. 1992) and brown trout (Ryman et al. 1979, Ferguson and Mason, 1981). In some cases these reflect phenotypic variation of a single population while in other cases they represent genetically distinct and reproductively isolated populations. For example, Lough Melvin, a lake of some 21 km^2 situated in NW Ireland, supports three types of brown trout, known locally as gillaroo, sonaghen and ferox. They are distinct morphologically (Cawdery and Ferguson 1988) and have different feeding preferences (Ferguson 1986). Do these three types represent ecotypic variation or do they form separate populations? Allozyme studies (Ferguson and Mason 1981) have indicated that the three types are reproductively isolated (Table 1). Thus, only gillaroo possess the *LDH-1*QO* allele, while ferox show a high frequency (0.65) of the *LDH-5*100* allele which does not exceed a frequency of 0.02 in the other two types. Sonaghen are characterised by relatively high frequencies of the *CK-2*115* and *GPI-2*135* alleles. This reproductive integrity is maintained by geographical separation of the spawning sites (Ferguson and Taggart 1991). The gillaroo spawn in the only outflowing river of the lake, whereas sonaghen spawn in the inflowing rivers. The ferox spawn in the lower deeper section of one of the inflowing rivers, which is also used further upstream by sonaghen. While the allozyme evidence for the reproductive isolation of the three types is convincing, it is of interest to examine what mtDNA and VNTR markers can tell us about this situation.

Table 1. Frequencies of variant alleles at enzyme-coding loci showing statistically significant heterogeneity among Melvin trout types. (Based on Taggart and Ferguson 1991.)

Locus	Allele	Gillaroo (*N*=202)	Ferox (*N*=37)	Sonaghen (*N*=341)
*AAT-1,2**	*140*	0.27	0.60	0.41
*AAT-1,2**	*45*	0.21	0.00	0.15
*AAT-4**	*74*	0.11	0.00	0.05
*CK-2**	*115*	0.06	0.00	0.31
*GPI-2**	*135*	0.07	0.00	0.37
*GPI-3**	*110*	0.06	0.00	0.03
*G3PDH-2**	*50*	0.08	0.12	0.17
*IDHP-1**	*160*	0.11	0.00	0.09
*IDHP-1**	*10*	0.02	0.00	0.10
*LDH-1**	*QO*	0.17	0.00	0.00
*LDH-5**	*90*	0.99	0.35	0.98
*MDH-2**	*152*	0.49	0.23	0.45

Examination of mtDNA variation in 139 Melvin trout with six enzymes (*Ava* II, *Eco*R V, *Hae* III, *Hinf* I, *Mbo* I and *Xba* I) resulted in the detection of ten mtDNA haplotypes (Hynes et al. 1995). The frequencies of these haplotypes are given in Table 2. All ferox surveyed were monomorphic at all restriction sites examined (haplotype I). The occurrence of four unique mtDNA haplotypes in gillaroo and three in sonaghen, coupled with the significant frequency differences among all types adds further convincing evidence that the three types are genetically distinct populations. This extensive variation found in the mtDNA of the Melvin trout samples contrasts with the sequencing study of Bernatchez et al. (1992), involving 640 bp of the mitochondrial control region (D-loop), where no variation was found in samples from various parts of the Atlantic basin. Similarly no sequence variation was found in this region in representative samples of the Melvin haplotypes (L. Bernatchez pers. comm.).

A multi-locus DNA fingerprint analysis of ferox, sonaghen and gillaroo populations using the 33.6 human minisatellite probe provided further evidence of the reproductive isolation of the three types (Prodöhl et al. 1992). Although no unambiguous diagnostic fragments were observed for any of the types, lower band sharing coefficients were found in inter-type comparisons as compared with the relevant intra-type comparisons. In addition, ferox showed a significantly higher level of band sharing among its individuals in agreement with its lower level of allozyme and mtDNA gene diversity.

Table 2. Frequencies of mitochondrial DNA haplotypes in Melvin trout populations. Haplotypes comprise *Xba* I, *Ava* II, *Hinf* I, *Hae* III, *Mbo* I, and *Eco* RV morphs respectively. (Based on Hynes et al. 1995.)

Haplotype	Composite genotype	Gillaroo (*N*=47)	Sonaghen (*N*=55)	Ferox (*N*=37)
I	BAAAAA	0.13	0.25	1.00
II	ABAAAA	0.04	0.29	0.00
III	BADAAA	0.00	0.22	0.00
IV	BADAAB	0.00	0.04	0.00
V	ACEAAA	0.00	0.16	0.00
VI	ACAAAA	0.23	0.04	0.00
VII	ABAABA	0.46	0.00	0.00
VIII	ABAACA	0.06	0.00	0.00
IX	ACCBAB	0.06	0.00	0.00
X	ACCBAA	0.02	0.00	0.00

Table 3. Frequencies of alleles at the minisatellite *Ssa-A45/1* locus in the Melvin trout types. (Based on Prodöhl 1993.)

Allele	Gillaroo (*N*=114)	Ferox (*N*=56)	Sonaghen (*N*=152)
A	0.11	0.18	0.30
B	0.09	0.00	0.00
C	0.17	0.49	0.63
D	0.44	0.00	0.01
E	0.13	0.33	0.03
F	0.06	0.00	0.02
G	0.00	0.00	0.01

Screening with five single locus minisatellite DNA probes showed from three to eight alleles at each locus in the three types. Significant differences were found at all loci in the frequencies of these alleles (Table 3) but no unique alleles were found in any of the three types with the exception of rare alleles (frequency ≤0.09) (Prodöhl 1993). Given the large number of alleles at each locus and sample sizes of 50 to 150 these low frequency private alleles may represent sampling artefacts. Although minisatellite analysis did not identify any unique alleles capable of distinguishing the three types, there were however substantial frequency differences. For example, gillaroo and sonaghen exhibited frequencies of the "D" allele at the *Ssa-A45/1* locus of 0.44 and 0.01 respectively and this allele was absent in ferox.

Overall mtDNA, with the combined frequency of the unique haplotypes being 0.60 in gillaroo and 0.42 in sonaghen, provides the most discriminating marker system for these two types. As indicated earlier, this is to be expected from the one quarter effective population size of the mtDNA genome. If a low level of gene flow exists then common genes in one type are likely to be introduced into the gene pool of another type. However, such introduced genes are more likely to be lost by drift in the case of mtDNA. It could also be that males are more likely to stray and interbreed with another type than females. Since the θ value (Weir 1990; equivalent to Wright's F_{st}) of 0.33 based on mtDNA is almost exactly twice that of the allozyme (0.17) and single locus minisatellite (0.15) θ values, as expected from the haploid nature of this genome, this is clearly not the case. While mtDNA is obviously a valuable marker for population genetic studies, the greater susceptibility to genetic drift of this genome can also lead to spurious conclusions. Thus, random lineage sorting in small subsets of a panmictic population can result in apparent population structuring. It is therefore important in studies of mtDNA in small populations to demonstrate that the pattern of differentiation is temporally stable. In the case of the Melvin trout populations, comparison with an earlier sample (McVeigh et al. 1995) showed consistency of population specific haplotypes.

MtDNA is of no value in the identification of ferox as it only possess a single shared haplotype. *LDH-5** provides the highest level of discrimination of ferox from the other two types. It suffers, however, from the drawback that, being expressed in eye tissue, it cannot be non-destructively sampled. While the minisatellite DNA loci contribute little further information on the population genetics of the Melvin populations, the fact that these data are in accord with other studies provides an important validation of the approach in an already well characterised situation. These minisatellite markers can then be applied, with confidence, to situations where other markers are not available or appropriate. Examples of two such situations are now considered.

Icelandic brown trout populations

Past studies have revealed that Icelandic brown trout populations exhibit reduced levels of protein polymorphism as compared with those examined from Britain and Ireland (Hamilton et al. 1989). Our analysis of Icelandic trout populations from north, south, east and west coast drainages for mtDNA variation showed a common single mtDNA haplotype. Thus the mtDNA marker is uninformative for genetic studies of these populations. In contrast a more recent examination of nine minisatellite DNA loci in three Icelandic populations has detected an appreciable level of genetic variation albeit at a lower level than in the Melvin brown trout populations. Two of the loci examined were found to be monomorphic while at other loci a maximum of six alleles was observed. On average, three alleles per locus were found in the Icelandic samples compared with seven in the Melvin trout. The mean heterozygosity of the Icelandic samples was 0.32 compared with an equivalent value for the Melvin populations of 0.59. Private alleles were also present at higher frequencies compared with the Irish populations (Table 4) (Prodöhl 1993), as expected from the greater genetic drift which has clearly operated in these populations. In spite of this there is sufficient variability at the minisatellite loci for these to be used as markers for population genetic studies in this situation of reduced allozyme and zero mtDNA polymorphism.

Isolated Scottish populations

In brown trout samples which were examined from two small isolated lakes in northern Scotland, no variation in allozymes or mitochondrial

Table 4. Frequencies of alleles at the minisatellite *Ssa-A45/1* locus in Icelandic trout populations. (Based on Prodöhl 1993).

Allele	Sandsá (*N*=46)	Litlisjór (*N*=45)	Stora Fossvatn (*N*=43)
A	0.33	0.00	0.00
B	0.03	0.01	0.00
C	0.26	0.04	0.00
D	0.25	0.81	0.84
E	0.09	0.14	0.15
F	0.04	0.00	0.00
G	0.00	0.00	0.01

DNA was found (Hynes et al. 1995). Indeed these are the only brown trout populations, from the many examined throughout western Europe, which do not show any evidence of allozyme variation (Ferguson 1989). Application of both multi-locus and nine single locus minisatellite DNA probes also showed a complete lack of variation (Prodöhl 1993). Not only is the complete monomorphism surprising in this otherwise highly polymorphic species, but also the fact that fixation is for the same alleles in the two populations. Although they are only a few kilometres apart there is no connection between them and indeed one of the lakes has no inlet or outlet streams. Presumably transfer of fish has taken place at some time, possibly even to both lakes from an unknown source. This lack of variation could only come about from extreme and repeated bottlenecks. It also brings into question the importance of genetic variability in natural populations.

Postglacial colonisation of brown trout

A basic question concerning the genetic diversity that we see today among brown trout, Arctic char and other salmonid populations in formerly glaciated areas is how much of this has arisen postglacially from a common ancestor and how much is the result of independent colonisation of already differentiated forms which diverged from each other during or prior to the last glaciation. Considerable debate has taken place as to the number of Arctic char colonisations (Behnke 1989). Based on the differential occurrence of the two alleles at *LDH-5** it has been proposed that there were two postglacial colonisations of brown trout in NW Europe (Ferguson and Fleming 1983, Hamilton et al. 1989). Thus the *LDH-5*100* allele, since it is present in at least 12 salmonid species, is the ancestral one and its carriers are referred to as the "ancestral" race. The unique brown trout *LDH-5*90* allele seems to have arisen in NW Europe during or after the last glaciation, possibly in the Baltic Sea, with allelic substitution taking place under the action of natural selection (Henry and Ferguson 1985). The *LDH-5*90* allele can thus be used as a phylogeographic marker to trace the post-glacial spread of what has been denoted as the "modern" race which colonised NW Europe at a later time than the "ancestral" race.

In an attempt to provide further resolution of brown trout postglacial colonisation, analysis of mtDNA variation was undertaken (Hynes et al. 1995). Overall 18 mtDNA haplotypes (I-XVIII) were found in NW Europe with two further haplotypes (XVIII and XIX) being found in a small outgroup sample from Mediterranean France. Three haplotypes (I, VI, and XII) were common and widespread in populations fixed for both **100* and **90* alleles and seem likely to be sympleisiomorphic, i.e., they were present in the ancestor of the "ancestral" and "modern" race. Each of the supposed "ancestral" (high **100* frequency) populations appears to have become fixed by random lineage sorting for one of these lineages. The low mitochondrial diversity of the presumed "ancestral" populations is in keeping with their lower allozyme diversity and with postulated colonisation bottlenecks (Hamilton et al. 1989). The isolation of "ancestral" populations from present day migratory trout has prevented the acquisition of further mtDNA haplotypes by gene flow. The elapsed post-glacial period is too short for new mutants to be present in frequencies detectable with the sample sizes used in the study. The low **100* frequency ("modern" race) populations have a much greater mtDNA diversity in keeping with larger population sizes and opportunities for spread of haplotypes by interpopulation migration. Thus while the mtDNA data are compatible with the dual post-glacial hypothesis, at the present level of resolution, they provide no further insight.

It has been previously suggested (Cawdery and Ferguson 1988, Ferguson and Taggart 1991), on the basis of morphological and allozyme data, that the Melvin ferox with its high *LDH-5*100* frequency represents the "ancestral" race. Furthermore, it was argued that gillaroo and sonaghen are descendants of the "modern" race that diverged sympatrically. However, the extent of mitochondrial DNA divergence between these two forms is not consistent with a post-glacial splitting but rather suggests a separation of about 80,000 years, perhaps brought about by the onset of the last glaciation which occurred about this time (Hynes et al. 1995). Thus the mtDNA information in this case is in disagreement with allozyme data. Several authors (e.g. Hindar et al. 1986) have argued that the greater allozyme similarity of sympatric populations, compared with possibly homologous allopatric ones, indicates sympatric "speciation". However, a small amount of inter-breeding could produce nuclear gene, but not mtDNA, convergence.

The above examples demonstrate that allozyme, mitochondrial DNA and minisatellite DNA markers each have strengths and weaknesses in the examination of population structuring. It is important to assess the requirements in each particular study situation and choose the appropriate technique. The relative simplicity of the allozyme methodology and the existence of an extensive data base means that this approach will continue to be productive for the foreseeable future.

DNA profiling and fitness estimation

There is one area of study at least in which minisatellite (and microsatellite) markers have a unique application. Many salmonids show intraspecific variability in their life history and behavioural traits. Both evolutionary studies and practical management activities require information on the relative fitness of these alternative strategies, i.e. to what extent are these differences adaptive? For example, Northcote (1992) pointed out the need to test the relative fitness of resident and migratory forms of stream salmonids. Fitness is the contribution to the next and succeeding generations and estimation of it requires identification of the offspring produced by specific parents. One of the major uses of the highly polymorphic minisatellite DNA loci is in the identification of parentage, allowing direct estimation of fitness in natural populations. The ability to identify parentage and to directly assess the contribution of two parents, not just to the first generation, but to succeeding generations, opens up many possibilities for studies on natural and experimental populations of all organisms (Burke, 1994). Examples of possible studies which could be undertaken on salmonid fishes are shown in Table 5. Parentage identification is also allowing field scale studies of the fitness implication of the escape of farmed Atlantic salmon into natural populations. A similar approach can be used in breeding studies by allowing multiple families to be maintained in the same tank thus avoiding the confounding effects of different environmental conditions which occur when fish are maintained separately.

Multi-locus DNA fingerprints, based on universal DNA probes such as those produced by Jeffreys and colleagues (Jeffreys et al. 1985), can be used for parentage identification only in situations of discrimination between a small number of potential parents and offspring. Such identifications can be considerably extended by making use of single locus minisatellite DNA probes, a procedure known as DNA profiling. DNA pro-

Table 5. Examples of life history characteristics which could be examined in natural salmonid populations using DNA profiling to identify parents and offspring in F_1 and later generations.

- Identification of redds for each adult - number, position - relate to adult parameters.
- Contribution of mature parr in each redd - relate to adult parameters.
- Migratory behaviour of juveniles - relate to adult parameters.
- Survival and behaviour of juveniles in relation to sex.
- Survival of offspring relative to:
    - Mature parr vs. adult fathers;
    - Migratory vs. non-migratory parents;
    - Parental age;
    - Time of river entry;
    - Spawning time;
    - Original age of smolt migration;
    - Spawned in home vs. foreign river.
- Do migratory individuals derive from non-migratory parents and vice versa?

filing is based on the determination of genotypes at specific loci and an individual's profile is its composite genotype at all loci examined. For example, a five locus genotype profile would be given as - AB BG CD EH CC - where A, B, C etc. denote the alleles segregating at each locus. If we have five loci each with five alleles, there are 15 possible genotypes at each locus and 759375 potential composite genotypes. Extending this to ten alleles, at each of five loci, gives over 500 million composite genotypes. The exponential increase in the number of composite genotypes with the increasing number of alleles illustrates why the hypervariable minisatellite DNA loci are particularly applicable for parentage identification. Populations do not possess each of the alleles at equal frequencies, however, and the likelihood that any two individuals will show the same genotype will not be the same for all genotypes but will depend on the relative frequencies of the alleles at each locus in the population under investigation. This means that in practice the number of loci required for parentage identification needs to be assessed for each individual situation. Identification is carried out by matching the composite genotype of an unknown offspring to the potential composite genotypes present in a particular family. An alternative, but less powerful, approach is to match alleles rather than genotypes, using the fact that, barring mutation, an individual's alleles must be present in its parents.

Current genetic markers provide the opportunity for studies from the individual to the species level. While significant advances have been made over the past 25 years on the population structure of salmonids, our knowledge of the adaptive significance of variability within and among populations is still very limited. In this respect, as well as studies of relative fitness of life history traits in natural populations, it is in the expanding area of developmental and regulatory genetics that exciting future discoveries are likely to be forthcoming. Such studies are potentially capable of defining the genetic triggers which control the stages of the life cycle and "choose" alternative pathways. This will require a more detailed knowledge of the structure of the salmonid genome. The high heterozygosity of minisatellites and microsatellites provide markers by which such mapping can be undertaken. However, as with the human genome project, this will require collaborative efforts by many groups of workers. But on which species should the work be undertaken. Is it to be brown trout, Atlantic salmon or Arctic charr, or one of the north American salmonids?

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The Ecology of Arctic Charr, *Salvelinus alpinus*, and Brown Trout, *Salmo trutta*, in Windermere (northwest England)

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Abstract

The two resident salmonid species in Windermere, the largest natural lake in England, are Arctic charr and brown trout, but migratory brown trout (= sea-trout) and Atlantic salmon (*Salmo salar*) move through the lake to and from their spawning streams. All English populations of Arctic charr are found in the Lake District (northwest England). Windermere has the largest population with at least four races; the north and south basins of the lake each containing two races that spawn in spring and autumn respectively. Three methods provided comparable estimates of fluctuations in the charr stocks: gill-netting in November at a spawning site in the north basin (1939-present), anglers' catches from both basins (1966-present), echo-surveys at least monthly in both basins (July 1989-present). Two major changes have occurred in recent years: a decrease in numbers and catches of charr in the south basin compared with the north basin; an increase in brown trout caught by charr anglers fishing the pelagic zone in the south, but not the north, basin of the lake. These changes are associated with eutrophication, especially in the south basin. It is not known why brown trout have moved into the pelagic zone but some possible reasons are proposed. As both charr and brown trout now occur in the pelagic zone, it is important to compare their ecology and examine the possibility of competition between them. A summary is therefore provided for the most important ecological similarities and differences of these two species in Windermere.

Keywords: population dynamics, lake fisheries, catch statistics, eutrophication, echo sounding.

Introduction

This contribution commences with a brief description of Windermere and recent changes in its trophic status, then describes fluctuations in the numbers and catches of Arctic charr (*Salvelinus alpinus* (L.)) and pelagic brown trout (*Salmo trutta* L.) in the lake, and finally summarises the most important ecological similarities and differences of these two species in Windermere.

Windermere is the largest natural lake in England and is situated in a National Park (English Lake District). The lake provides part of the water supply to North West England and is a focus for tourism and recreation. The main fish association in the lake consists of resident Arctic charr, brown trout, perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.) and catadromous European eel (*Anguilla anguilla* (L.)). Anadromous brown trout (= sea-trout) and Atlantic salmon (*Salmo salar* L.) also pass through the lake as smolts and adults returning to spawn in streams flowing into the lake (Fig. 1). Several species of smaller fish are found in the littoral; namely stickleback (*Gasterosteus aculeatus* L.), bullhead (*Cottus gobio* L.), stoneloach (*Noemacheilus barbatulus* (L.)) and minnow (*Phoxinus phoxinus* (L.)). Two species of lamprey have been recorded but are not abundant (*Lampetra planeri*

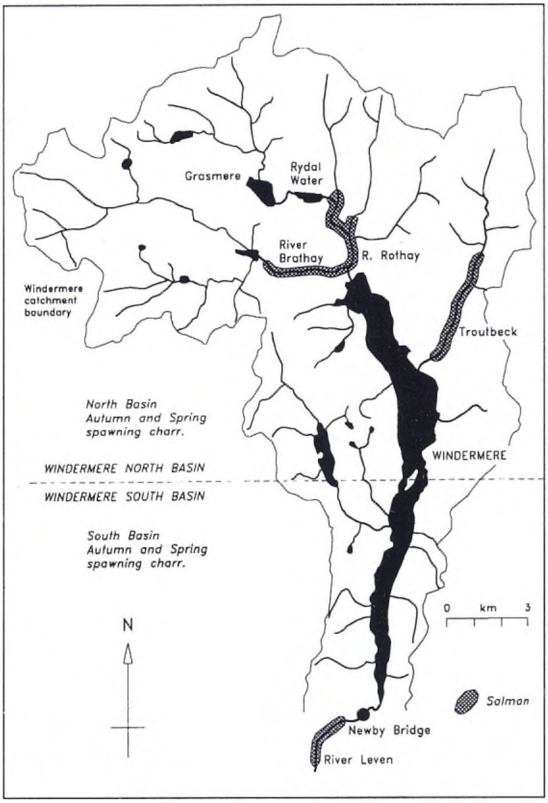

Fig. 1. Windermere and its catchment: Atlantic salmon spawn in the larger Rivers Brathay, Rothay and Troutbeck, as well as the lake outflow, the River Leven (marked areas on map); brown trout spawn in virtually every stream from large to small; and Arctic charr spawn in the lake, apart from one small group spawning just upstream from the mouth of the Brathay. Note that the north and south basins of the lake each have autumn and spring spawning charr, i.e. at least four races of charr occur in the lake.

(Bloch) and *L. fluviatilus* (L.)). The rudd (*Scardinius erythrophthalmus* (L.)), roach (*Rutilus rutilus* (L.)) and tench (*Tinca tinca* (L.)) are generally rare but locally frequent in the lake; these three species were probably introduced as a result of anglers disposing of their live bait.

General accounts of the research on the fish populations are provided by Bagenal (1970), Macan (1970) and Le Cren et al. (1972). The early work on Windermere charr was summarized by Mills (1989), apart from a paper on their food by Frost (1977). All the English populations of Arctic charr occur in eight lakes in the Lake District of Northwest England, but there are over 45 populations in Ireland, over 175 in Scotland and five in Wales (Maitland and Lyle 1991). The only other member of the genus *Salvelinus* in the British Isles is the introduced American brook charr, *Salvelinus fontinalis* (Mitchill), that is very local and rare (Maitland and Campbell 1992). There are at least four races of Arctic charr in Windermere with the north and south basins of the lake each containing two distinct races that spawn in spring and autumn respectively (Fig. 1). The term 'race' is used here to mean an interbreeding group of individuals, all of whom are genetically distinct from other such groups of the same species. The four races in Windermere appear to be reproductively isolated and therefore there are barriers to gene flow. Alternative terms, used by some authors, are 'subspecies' or 'deme' (strictly 'gamodeme') for such local interbreeding groups of individuals. Most of the Windermere charr are autumn spawners with spring spawners representing less than 4-6% of the adult population (Mills 1989, Mills and Hurley 1990, Elliott and Baroudy 1992). Recent work on charr from Windermere has examined their oxygen tolerance, their critical thermal limits, racial differences in their eggs and juveniles, and some of the problems in estimating their numbers by hydroacoustic methods (Baroudy and Elliott 1993, 1994a,b,c).

Compared with charr, relatively little is known about the brown trout in Windermere. Allen (1938) sampled trout by using a seine net along the littoral of the north basin and provided the first account of their biology. All the trout spawn in the numerous streams flowing into the lake (Fig. 1), and the lake population may well be limited by the space available in the streams for rearing the fry. Their growth rate in the lake is high and trout of up to 5 kg wet weight have been caught in the lake. Swift (1961) studied the seasonal growth of trout released into a netted-off portion of the lake. More recently, Craig (1982) sampled trout in six afferent streams of

Windermere. He found that the age of entry into the lake was variable in the young trout; the majority (70%) entered the lake in the third year (age 2+ years) of their life cycle, with 16% in their second year (1+) and 14% in their fourth year (3+). Although there is relatively little information on the ecology of brown trout actually in the lake, there are detailed studies on trout populations in streams within the Windermere catchment, one on juvenile sea-trout having continued for over 25 years (references in Elliott 1989, 1993, 1994). There is also a large amount of experimental work on the ecological requirements and growth of brown trout obtained locally (reviewed by Elliott 1994). All the sea-trout and Atlantic salmon have to enter and leave the lake via the River Leven which flows for 3 km before entering the sea. The sea-trout often spawn in small tributaries but salmon spawning is restricted to the larger Rivers Brathay, Rothay and Troutbeck, as well as the Leven (Fig. 1). Adults of both sea-trout and salmon are occasionally caught in the lake by anglers, but the chief fishery is in the River Leven.

Against this broader background, the present account is restricted to the two resident salmonid species in Windermere. It also places most emphasis on the Arctic charr because they are the subject of this Symposium.

Windermere and its trophic status

The lake originated about 12,000 years ago and occupies a glacially excavated valley rock basin. It is divided by an area of shallow water and islands (Fig. 1) into a north basin (area 8.1 km^2, volume 201.8 • 10^6 m^3, mean depth 25.1 m, maximum depth 64 m) and a south basin (area 6.7 km^2, volume 112.7 • 10^6 m^3, mean depth 16.8 m, maximum depth 42 m). Shallow littoral areas are more frequent in the south basin. The two basins differ in their inflow-outflow characteristics but water retention time of the lake as a whole is approximately 9 months (Sutcliffe and Carrick 1983). Due to its smaller volume and additional input of some streams, the south basin has a nominal retention time of around 3.3 months. At an altitude of only 39.3 m, Windermere is one of the few lowland lakes with a substantial population of Arctic charr.

Since 1945, regular measurements from both basins have shown that the lake has become nutrient enriched (Lund 1972, Sutcliffe et al. 1982, Heaney et al. 1988, Talling and Heaney 1988). The increasing concentrations of NO_3-N may be due to a large increase in the use of nitrogenous fertilizers with subsequent winter fluctuations conditioned by climatic factors, including temperature. Large increases in winter concentrations of soluble reactive phosphorus, especially in the south basin, are probably due to increases in sewage-borne phosphorus discharged to the lake (see also Mills et al. 1990). Associated with this increasing enrichment, there has been an increase in hypolimnetic deoxygenation during summer and autumn in the south basin, first recorded during 1981. This deoxygenation was particularly severe during 1988. In the south basin, anoxia occurred for a prolonged period between the end of September and mid-November, and extended upwards to a depth of about 25 m. Complete anoxia does not occur in the north basin, but oxygen concentration fell to less than 20% saturation below 30 m depth during the first half of November 1988, this being the most severe on record.

Although nutrient enrichment is not directly harmful to charr or trout, the associated anoxia will restrict the water volume available to the fish and this will be reduced further in hot summers when surface temperatures may be higher than the preferred values for the fish, especially the charr (Baroudy and Elliott 1994b). It is also possible that summer water temperatures will increase as a result of climate change. Evidence from other European lakes indicates that increasing enrichment can lead to a reduction and eventual extinction of charr populations (Mills et al. 1990). New sewage treatment plants should markedly reduce the quantity of phosphates entering both basins of Windermere, but recovery may be slow because the lake sediments accumulate phosphorus which may be released back into the water column over many years. It is therefore important to continue the monitoring programme on the fish populations of Windermere.

Long-term and short-term fluctuations in the numbers and catches of charr and pelagic trout in Windermere

Three methods have been used in Windermere to obtain relative estimates of the levels of charr stocks; namely gill-netting each November (1939-93) for autumn spawners in the north basin, anglers' catches from both basins (1966-93) and echo-survey data from both basins (July 1989-December 1993). The two latter methods also provide information on pelagic trout. All three methods are described in detail by Elliott and Baroudy (1992) who also document changes up to the end of 1991. The following account adds two years (1992, 1993) to the data set, this being especially important for the relatively shorter records from the echo surveys. Some of the problems in obtaining estimates of fish abundance with the echo-sounder are discussed in Baroudy and Elliott (1993).

Gill-netting of autumn and spring spawning charr has confirmed that both races are present in both basins. There is no evidence to suggest that age structure and the mean age of the spawning male and female charr has changed significantly since the earlier surveys in 1986, 1987, 1988 (Mills 1989). Gill-net catches of autumn spawning charr in the north basin showed a general upward trend from 1945 to about 1965 (Fig. 2a). This increase was associated with a cull of larger pike, the pike biomass being reduced by about 65%, and this removal of a major predator could be responsible for the increase in charr numbers (Kipling 1984). Since 1965, gill-net catches of charr have fluctuated considerably

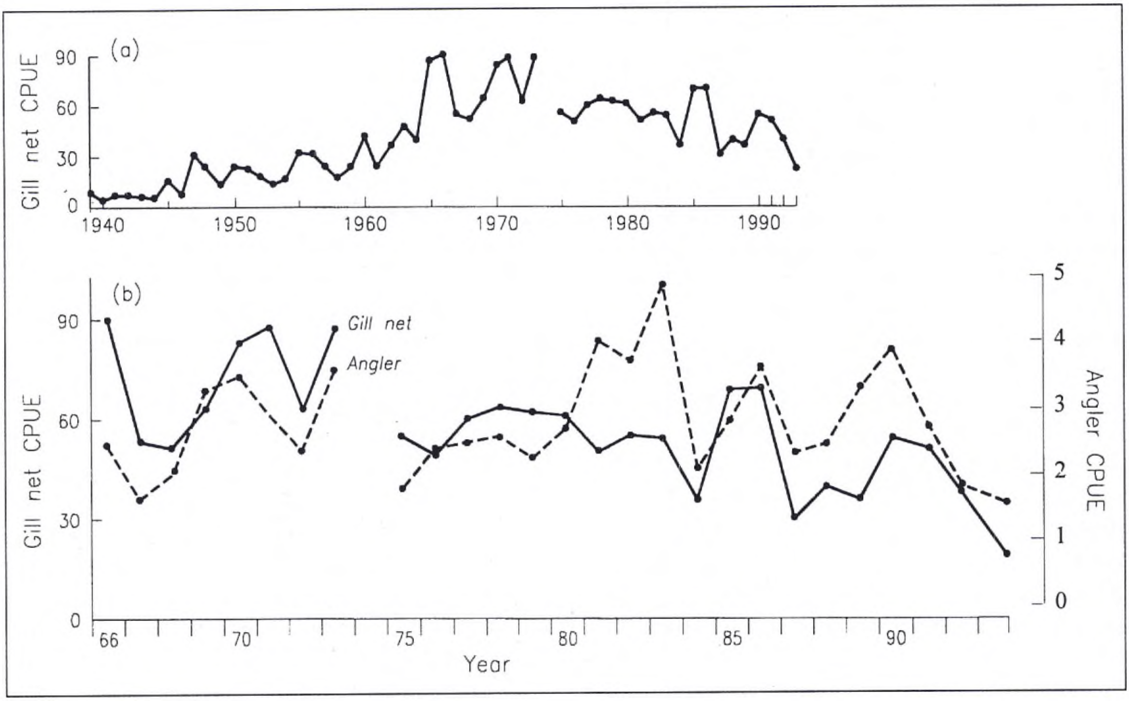

Fig. 2. (a) Gill-net catch-per-unit-effort (CPUE) for charr at Windermere north basin spawning sites from 1939-93. CPUE is the mean catch per gill-net day in November near Low Wray Bay (1939-73) and North Thompson Holme (1975-93) spawning sites.

(b) Gill-net CPUE (solid line) and angler CPUE (broken line) from 1966 to 1993. Angler CPUE is the mean catch per boat per hour. The scales for gill-net and angler CPUE have been arranged so that the overall means for each coincide.

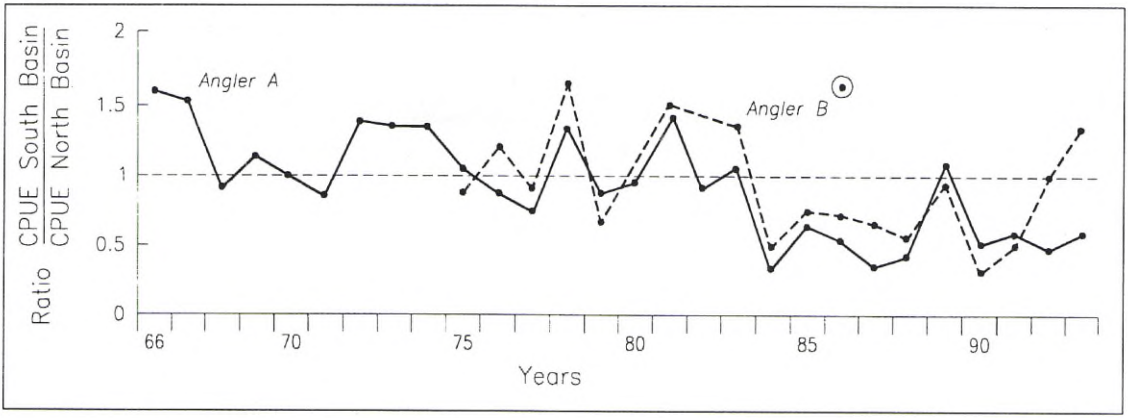

Fig. 3. Ratio of angler CPUE for south basin to north basin for angler A (solid line) from 1966 to 1993 and angler B (broken line) from 1975 to 1993. (Note: the high encircled value for angler B in 1986 was due to the inclusion of one exceptionally high catch in the south basin; when this was excluded from the analysis, the estimated ratio was very similar to adjacent values).

with no obvious discrepancy caused by a change of site from 1973 to 1975 (break in series in Fig. 2a). Gill-net and anglers' catches generally followed a similar pattern (Fig. 2b), but there was a marked discrepancy about 1980 when the relative catches crossed (note that both sets of catches were scaled so that their overall means coincided in Fig. 2b). Both sets of catches have shown a marked decline in recent years.

As the anglers' catches generally reflected changes in charr abundance (Elliott and Baroudy 1992), they were used to compare population changes in the two basins of the lake. A simple, but useful, index of these changes was provided by the ratio of mean catch in the south basin to mean catch in the north basin. Values of one angler's catches from 1966 to the present showed that, prior to 1983, catches were similar in both basins or were higher in the south basin (angler A in Fig. 3). The marked decrease in the ratio for the next five years indicated the relative decline in south basin catches from 1984 to 1988. The ratio of catches for a second angler over a shorter period (1975 to 1988) followed a similar pattern (angler B in Fig. 3). There was a clear improvement in 1989 with similar catches in both basins (ratio c.1) for both anglers. A decline in 1990 and 1991 for both anglers, and in 1992 and 1993 for angler A, to earlier values indicated that the 1989 improvement was temporary, not permanent. The increase in the ratio in 1992, and especially 1993, for angler B compared to angler A was chiefly due to the lower catches by angler B in the north basin compared with previous years rather than increased catches in the south basin.

Charr fishermen on Windermere have expressed the general, but subjective, view that more brown trout have been taken on charr tackle in recent years. Records obtained from the two anglers confirmed an increase in the percentage of pelagic trout taken in the catches, especially in the south basin (Fig. 4). It is notable that the latter increase commenced in 1984, the same year which marked the onset of changes in the ratio of catches in the north and south basins (cf. Fig. 3). The change in the latter ratio could have been due to the increased proportion of trout in the catches, but a comparison of the ratio for total catches (charr + trout) in both basins revealed little change in the temporal pattern from that obtained for charr alone (Elliott and Baroudy 1992). Increases in the catches of trout in the south basin were not therefore responsible for the lower catches of charr relative to those of the north basin.

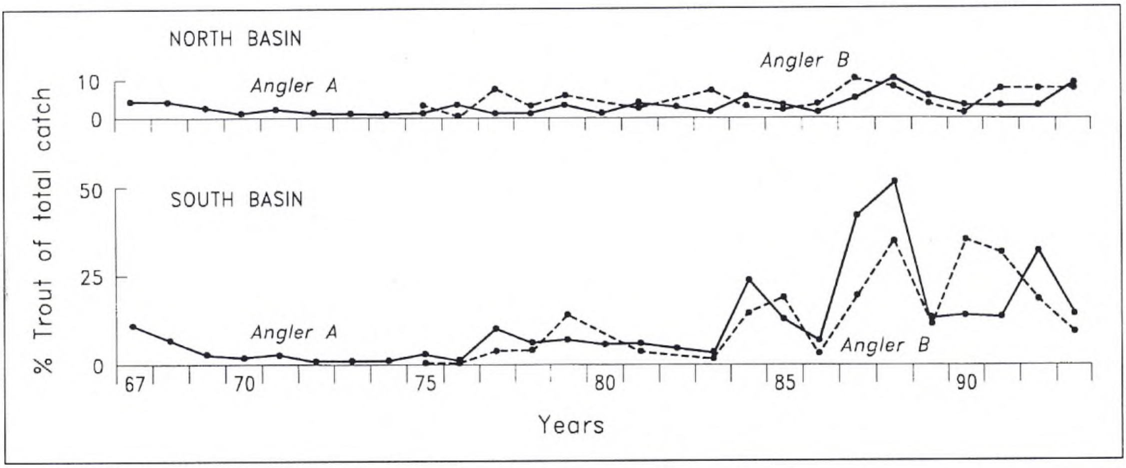

Fig. 4. Percentage of brown trout taken in the north and south basins in annual catches by anglers A and B.

Monthly catches were compared for both anglers in the fishing season (March/April to September) from 1989 to 1993. These years were chosen for more detailed examination because the anglers' catches could also be compared with fish density estimated by the echo sounder (Fig. 5). Apart from one large catch by angler B in April 1991, brown trout were rarely taken by both anglers in the north basin. They were, however, frequently taken in the catches in the south basin, especially in spring and early summer. These comparisons also show that in most months, catches were lower in the south basin than in the north basin. As it was impossible to separate charr from pelagic brown trout in records from the echo sounder, the latter therefore provided estimates of the total number of pelagic salmonids (charr + trout) in the north and south basins (Elliott and Baroudy 1992, Baroudy and Elliott 1993). The methods used by charr anglers take fish at water depths from about 1 m to no more than 20 m, and charr taken from the lake must have a fork length greater than about 20 cm. The results from the echo sounder were therefore filtered to leave those from water depths down to 20 m and fish longer than 20 cm, i.e. those fish that should, in theory, be available to the angler (Fig. 5).

The results confirmed the earlier conclusion from the anglers' catches that fish density was consistently higher in the north basin. There was also a similar pattern in the fluctuations in fish density and anglers' catches in the north basin, e.g. a late summer peak (August), especially in 1989, 1990. Similarities were less evident for the lower numbers in the south basin, but more fish were usually available in months in which anglers fished. Estimates of fish density at night were usually higher than the corresponding estimates during the day but there were exceptions in which the reverse was true. These were predominantly in autumn (October 1990, September, October 1991 for both basins; September, October 1992 for north basin; August, October 1993 for south basin).

These comparisons are generally encouraging because they show that the results obtained with the echo sounder are generally comparable to anglers' catches. The echo-sounder data not only confirmed the higher numbers in the north basin but also demonstrated lower numbers of pelagic fish in winter in both basins, and the decline in numbers of larger fish (Fig. 5). Both gill-net and anglers' catches continue to decline, and an increase in the ratio of south basin anglers' catches to north basin catches was due to a decline in catch in the north basin rather than an increase in catch in the south basin. The echo-sounder data confirm these conclusions. Pelagic trout taken by charr anglers continue to be mark-

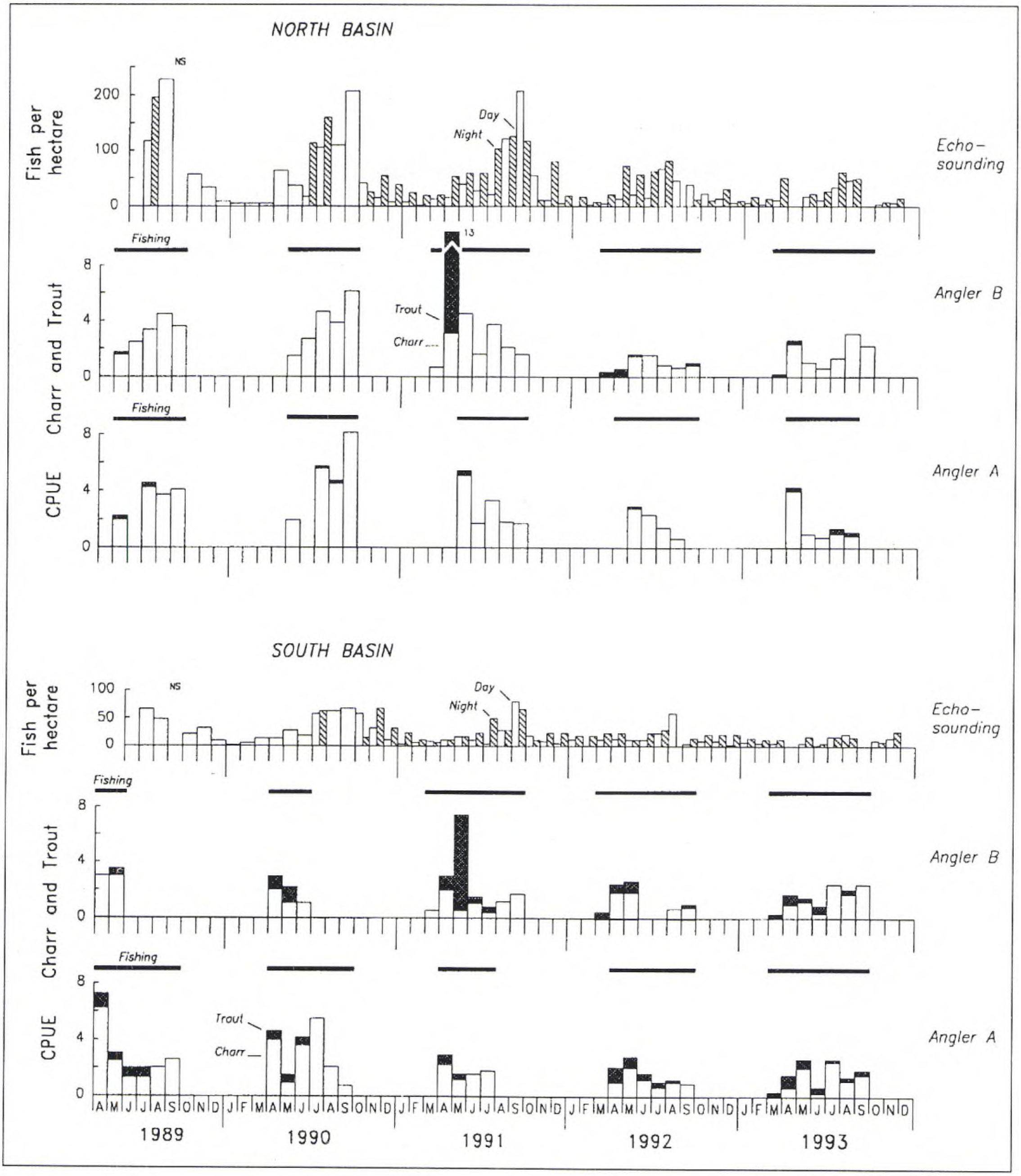

Fig. 5. Comparisons of monthly CPUE for charr (open columns) and trout (black portion of columns) taken in north and south basins by anglers A and B; estimates of fish density from echo-sounding are also provided.

edly higher in catches from the south basin compared with the north basin, but were lower in the south basin than in previous years. It is not known if this decline will continue.

Comparative ecology of charr and trout in Windermere

As both charr and brown trout now occur in the pelagic zone of the lake, it is important to compare their ecology and examine the possibility of competition between them. The following aspects are considered to be important and will therefore be examined for different stages in the life cycle: oxygen tolerance and critical thermal limits; growth and feeding; movements and survival, especially during the early critical period of the life cycle. Information is available on the following life-stages for some, but not all, of these comparisons: eggs, alevins (newly hatched fish with yolk sacs), fry (fish with little yolk and starting to feed exogenously), parr in their first (0+), second (1+) or third (2+) year (immature fish feeding independently) and adults (mature fish about to spawn or having spawned already). Salmon may also be mentioned briefly because, as stated earlier, they pass through the lake whilst moving to and from their spawning streams (Fig. 1).

Very little information was available on the oxygen requirements of Arctic charr until some recent experiments were performed to determine the lower limits of tolerance to reduced oxygen concentrations for Windermere parr kept at acclimation temperatures of 5, 10, 15, 20°C (Baroudy and Elliott 1994a). No significant differences could be found between races. The parr tolerated lower oxygen levels (1.8-2.0 mg l^{-1} = 15-17% saturation) at lower (5, 10°C) than at higher (15, 20°C) acclimation temperatures (2.2-2.4 mg l^{-1} = 22-25% saturation). Windermere charr alevins were less tolerant of low oxygen levels than parr; alevins required at least 9 mg l^{-1} (= 70% saturation) for maximum survival over 7 days or longer at 5°C, and all died at less than 30% saturation (Baroudy 1993). Parr of Arctic charr are therefore amongst the most tolerant of salmonid parr to low oxygen levels, but are only slightly more tolerant than parr of brown trout (see comparisons in Baroudy and Elliott 1994a). As mentioned earlier, marked decreases in oxygen concentration have occurred only at depths below 25-30 m in Windermere, and therefore there have been no major problems for the pelagic fish. However, if oxygen concentration decreased markedly in the pelagic zone, then parr of charr could probably cope better than those of trout. Incidentally, smolts of Atlantic salmon, that must pass through Windermere, are less tolerant with lower limits of 24-29% saturation at 13-15°C (Alabaster et al. 1979).

In contrast to the parr, the values for the charr alevins are high when compared with tolerance limits of 0.3 mg l^{-1} at 5°C for alevins of brown trout and Atlantic salmon (Bishai 1960). The charr alevin values are, however, similar to those recorded elsewhere for charr eggs (Gruber and Wieser 1983). Alevins and eggs of charr would therefore appear to be the most vulnerable life-stages. Fortunately, oxygen concentrations are high on the spawning grounds in Windermere during the appropriate season; autumn spawners spawn in shallow, well-oxygenated water in November and spring spawners in deeper, well-oxygenated water in May. The spawning grounds of the trout and salmon are, of course, in the well-oxygenated streams flowing into the lake.

A paucity of detailed studies on the critical thermal limits for charr was also the stimulus for an experimental study (Baroudy and Elliott 1994b). Comparisons between lethal temperatures for four acclimation values (5, 10, 15, 20°C) revealed negligible differences between races of Windermere charr and therefore the data were pooled to estimate the lethal values for survival over 7 days (incipient lethal temperature) and over only 10 min (ultimate lethal temperature) for three life-stages (alevins, fry, parr). Upper lethal values increased with acclimation temperatures for alevins but this effect was negligible for fry and parr. Alevins were generally less tolerant than fry and parr at lower, but not higher, acclimation temperatures; e.g. after acclimation at 5°C, mean upper ultimate values were 23.3, 25.1, 25.7°C and mean upper incipient values were 18.7, 21.5, 21.5°C for alevins, fry and parr respectively; after acclimation at 20°C, mean upper ultimate and incipient values were 26.2, 26.1, 26.6°C and 20.8, 20.8, 21.6°C for alevins, fry and parr respectively. The lower temperature limits were close to 0°C for all three life-stages.

A comparison with other salmonid species showed that parr of Arctic charr are the least tolerant to high temperatures but the most resistant to low temperatures (Baroudy and Elliott 1994b). One advantage of the comparisons between charr, brown trout and Atlantic salmon is that the parr of the two latter species were obtained from the Windermere catchment for use in the experiments (Elliott 1981, 1991). These differences are summarised in Fig. 6 that also compares the temperature requirements for egg hatching, feeding and growth, using values from the literature (references in legend to Fig. 6). In all these comparisons, the lowest values are for charr and the highest are for salmon, with trout in between. Although the optimum temperature range for growth is similar in charr and trout, the lower limit for growth is about 4°C in trout but close to 0°C in charr. Charr therefore continue to grow, albeit slowly, at low winter temperatures when trout growth has ceased. The chief food organisms of Windermere charr are planktonic Crustacea, especially Cladocera, but larval and pupal chironomids are sometimes abundant in the diet, and charr eggs are taken during both spawning seasons (Frost 1977, Mills 1989). Studies on the diet of brown trout in Windermere indicate the chief food organisms to be benthic macroinvertebrates, with the larger trout also feeding on fish (Allen 1938, Frost 1977). However, small samples of trout taken recently in gill nets set in open water indicate that the diet of these pelagic trout is closer to that of charr.

The most obvious difference in the life cycle is that the charr spend their entire life in the lake, apart from one small group that spawn in the River Brathay instead of the lake. Trout and salmon spawn in the streams; all juveniles remain there for at least one year and most do not leave their natal stream until they are at least two-years old (age 2+ years). The life-stages of charr and trout that occur together in the lake are therefore the parr that are at least one-year old and the adults. Juvenile trout have already been through the first critical period of their life cycle before they enter the lake. This critical period occurs when the fry leave their gravel nest and start to feed on small invertebrates in the stream. Mortality is high during this period and is often density-dependent (see reviews by Elliott 1989, 1994). It has been found for trout in the Windermere catchment that the size of newly emerged fry is related directly to egg weight, the latter is related positively to female size, and therefore larger females produce larger eggs that hatch to larger fry. These larger fry survive longer without food than smaller fry and therefore have a longer time in which to learn to feed (Elliott 1984, 1989). One consequence of these relationships is that the fry of the larger sea-trout have a survival advantage over those of the smaller resident trout (for further discussion, see Elliott 1994).

Although the relationship between egg size, fry size and ultimate survival is unknown for charr in Windermere, some recent experimental work strongly suggests that there may be similarities with trout (Baroudy and Elliott 1994c). There were no major differences between races for egg incubation times and the percentage of eggs hatching successfully, the latter being high (mean values 76-96%) with a negligible proportion of abnormal alevins (<0.8%). Although there were no significant differences in the lengths of female parents, both eggs and alevins were significantly larger for the autumn spawners than the spring spawners. Size differences in alevins, especially live weight, were positively related to egg size but not female parent size. Mean percentage survival for juveniles attaining the independent feeding stage was higher for the larger progeny of autumn spawners (32%) than the smaller progeny of spring spawners (3%). Racial differences in the egg and alevin stages therefore appear to have a significant effect on subsequent survival in the laboratory, and could be ultimately responsible for the relatively small proportion of spring spawners (only 4-6%) in the Windermere population of charr. It is dif-

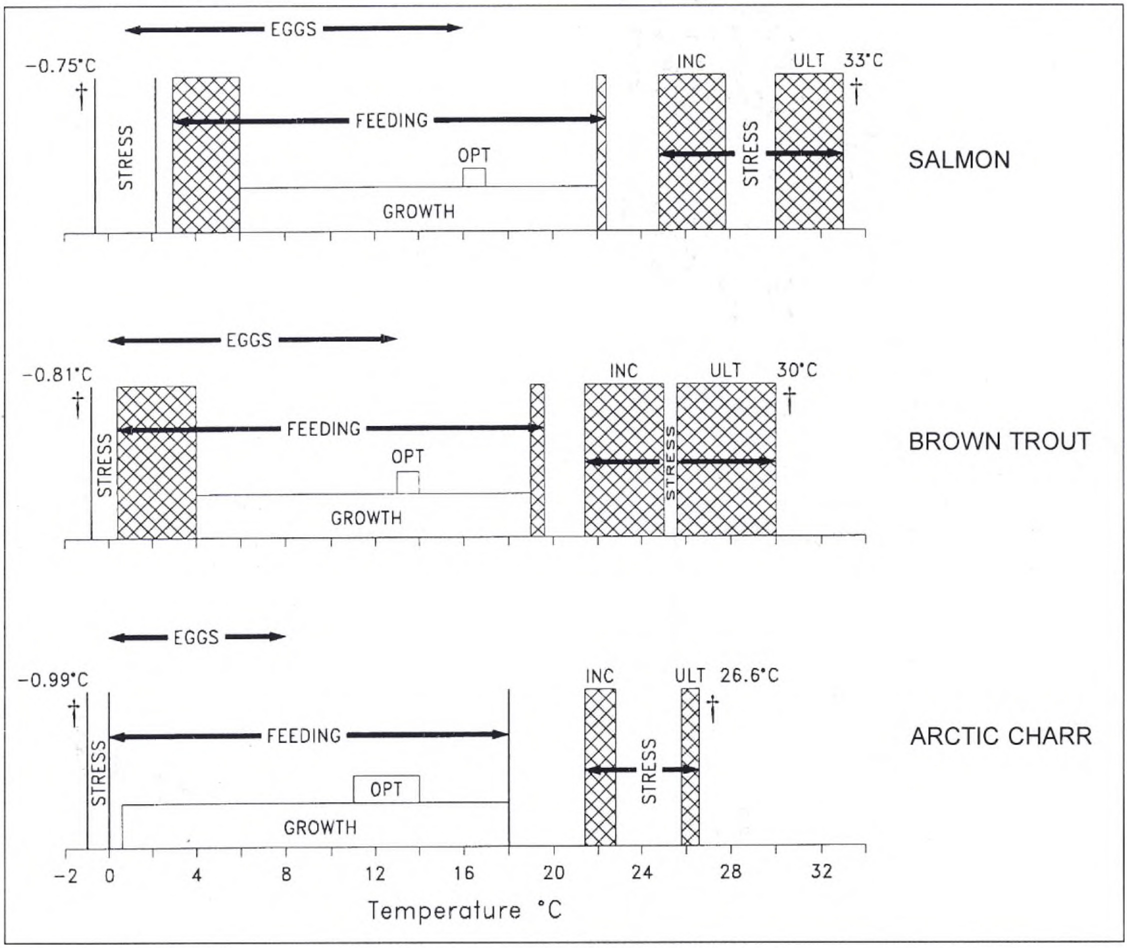

Fig. 6. Comparison of the temperature requirements for Arctic charr, brown trout and Atlantic salmon: critical thermal limits for parr (Inc = incipient lethal temperature, Ult = ultimate lethal temperature, hatched areas indicate the range over which both change with acclimation temperature); extreme lower and upper lethal limits are given as actual temperatures for each species; range for successful egg development; ranges for feeding and growth with optimum range for maximum growth (hatched areas indicate the range over which values change with acclimation temperature). Values collated from: Swift (1964,1965), Siginevich (1967), Elliott (1975a,b,1981,1991), Gunnes (1979), Crisp (1981,1988), Wandsvik and Jobling (1982), Jobling (1983), Steiner (1984), Jungwirth and Winkler (1984), Wallace and Aasjord (1984), Humpesch (1985), Jensen (1985), Jensen and Johnsen (1986), Brännäs (1987), Dwyer and Piper (1987), Elliott et al. (1987), Wallace and Heggberget (1988), Jensen et al. (1989), Jobling et al. (1993).

ficult to draw a firm conclusion because the progeny of the spring spawners attain the independent feeding stage at a slightly later time (May, June) than those of the autumn spawners (March, April), and this could affect their subsequent survival.

Although these summaries have shown that there is some information on the comparative ecology of charr and trout in Windermere, there are still many unanswered questions. A large amount of quantitative information now exists on the ecology of brown trout in their stream habitat (see review by Elliott 1994), but there is relatively little information on their ecology in the lake before they return to spawn in their natal stream. Most of the returning females are three-years old whilst most returning males are two- or three-years old. Their size indicates rapid growth in the lake. Nothing is known about their movements in the lake. From anglers' catches, it was assumed that they occurred chiefly in the littoral but, as shown earlier, they now occur in the pelagic zone, especially in the south basin of the lake.

Little is known about the growth and movement of the charr in the lake. Mark-recapture studies have shown that adults return each year to the same spawning site (Frost 1963, Le Cren and Kipling 1963), and differences in allele frequencies at esterase and malate dehydrogenase loci have been found between fish spawning at similar times but on different sites (Partington and Mills 1988). The charr mature at a much older age than the trout and their growth rate is much slower. The mean age of spawning female charr (c. 8 years for autumn spawners, c. 9 years for spring spawners) is slightly higher than that of spawning males (6-7 years for autumn spawners, 7-8 years for spring spawners). Most male charr mature at an age of 5 years whereas females mature at 6 years or older and live longer than males. About 80% of charr between 9 and 14 years old are female. There are no obvious differences in age structure between basins, and male and female charr grow at similar rates. As there is a high proportion of old charr in both basins, mortality through angling cannot be high or few fish would survive to reach such ages. These conclusions are based on recent information, and comparisons with earlier data are difficult because the previous use of scales for ageing led to marked under-ageing of older fish when compared with the use of otoliths for ageing in recent years (Mills 1989, Mills and Hurley 1990, recent unpublished data). These conclusions are also based on data obtained from mature fish caught in gill-nets. Virtually nothing is known about the growth and movements of the immature charr in Windermere.

Discussion

The Arctic charr and brown trout of Windermere have now been studied scientifically for over 50 years and observations on their natural history extend over a much longer period. For example, it has been known for over 300 years that there are autumn and spring spawning charr (Fleming 1671, see also Frost 1955). Worthington (1950) implied that there had been a change in the eighteenth and nineteenth centuries from a lake dominated by trout and charr to one dominated by perch and pike as a result of eutrophication. Although there is no doubt that Windermere has become more eutrophic, there is plenty of historical evidence that all four species have coexisted for at least 200 years, and certainly long before the onset of eutrophication (Le Cren et al. 1972). The historical records also show that a successful net fishery for the four species was in operation for several centuries until overfishing for charr and an increased interest in sport fishing for salmon and trout brought it to an end in 1921 (Le Cren et al. 1972). Old records of charr catches show the classic signs of overfishing such as reduced fish size and increased effort with smaller-mesh nets yielding lower catches. Cessation of the net fishery and later annual culls of large pike were probable responsible for the increase in the charr population from 1945 to about 1965, as shown by the gill-net catches (Fig. 2a).

In recent years, there has been a marked increase in quantitative information, especially for the charr. It is now known that there are at least four, genetically distinct, races of charr in the lake. Although there are slight morphological and major meristic differences between these races (Partington and Mills 1988), no differences could be found in their tolerance to low oxygen concentrations, their critical thermal limits for survival, their egg incubation times and hatching success (Baroudy and Elliott 1994a,b,c). This lack of differences is perhaps not surprising if, as seems likely, the different races share the same feeding habitats. Both eggs and alevins were, however, significantly larger for the autumn spawners than the spring spawners, even though the female parents were of similar size (Baroudy and Elliott 1994c). As mentioned earlier, survival in the laboratory was much higher for the progeny of autumn spawners than those of spring spawners, possibly because of their larger size, and this could be ultimately responsible for the small proportion of spring spawners in the Windermere population (4-6%). It has already been noted, however, that the later emergence of the fry of the spring spawners could also be a contributory factor. The newly emerged, smaller fry of the spring spawners would be not only more vulnerable to predation, but also inferior to the larger, and already established, fry of autumn spawners in any competition for food. There do not appear to be any major differences between races in either their morphology or feeding preferences, as seen in other charr lakes with dwarf and normal charr (see references in Hindar and Jonsson 1982, Hindar et al. 1986, Jonsson et al. 1988, Svedäng 1990, Hartley et al. 1992). Recent experimental work indicates that this ecological polymorphism in a Norwegian population is largely environmentally, rather than genetically, determined (Hindar and Jonsson 1993).

There was general agreement between the three methods (gill-netting, anglers' catches, echo-surveys) used to estimate fluctuations in the charr stocks of Windermere. Two major changes have occurred in recent years. First, there has been a decrease in numbers and catches of charr in the south basin compared with the north basin (Figs 2, 3). Second, there has been an increase in the number of pelagic brown trout caught by charr anglers in the south basin but not the north basin (Figs 4,5). Both changes are associated with increasing enrichment of the lake, especially in the south basin. It is not known why the trout have moved into the pelagic zone of the south basin. One possible explanation could be the marked increase in plant growth, especially blanket weed (*Cladophora),* in the littoral, once again associated with increasing eutrophication in the south basin. The plants provide excellent shelter for invertebrate animals and thereby reduce their availability as food for the trout. A general increase in trout abundance, especially in the littoral, could also be responsible for increased numbers of pelagic trout, but it is difficult to see why this would occur in the south, but not the north, basin of the lake. This hypothesis is also unlikely because anglers report that catches of trout from the littoral are still good in the north basin but have decreased markedly to negligible numbers in the south basin.

It is not known if the pelagic trout and charr compete for food because there have been no detailed comparative studies of the diets of the two species or of different life-stages of charr, as available for other lakes (e.g. Langeland et al. 1991, Klemetsen et al. 1992, L'Abée-Lund et al. 1993). Detailed studies in Norwegian lakes have shown that the food-overlap index is typically lower than 70% for sympatric trout and charr; the pelagic trout usually feed in the upper 1-5 m chiefly on surface insects and zooplankton, whilst charr feed over a greater range of depths and chiefly on zooplankton with zoobenthos being important at certain times of the year (Hindar and Jonsson 1982, Jonsson and Gravem 1985, Langeland et al. 1991).

The comparisons between Windermere charr and trout have shown that the eggs and alevins of the charr require higher oxygen concentrations than those of trout, but that charr parr can tolerate lower oxygen levels than trout parr. In terms of temperature tolerance, charr are less resistant than trout to higher values but more resistant to lower values, and grow slowly at low temperatures (0-4°C) when trout growth has ceased (Fig. 6). Although there is little detailed quantitative information on the life cycles of the two species in the lake, some major differences have been identified and these are summarized in Fig. 7. Differences between the autumn and spring spawning charr are almost as great as those between trout and charr. The major difference between the two species is the very slow growth of the charr compared with the trout, and the much older age for the spawning charr. Although the mean age of spawning charr is slightly lower for autumn spawners than for spring spawners, the latter grow slightly faster (cf. ages and lengths in Fig. 7). This suggests

Trout	**Charr (autumn spawners)**	**Charr (spring spawners)**
	c. 94-96% of spawning population.	c. 4-6% of spawning population.
Spawn November, December in streams, eggs hatch February. Critical period (high mortality) in April, May when fry disperse. Most parr (70%) migrate into lake at 2+ years.	Spawn November, December in shallow water in lake(one small group spawn in R. Brathay). Critical period probably when fry disperse in March, April.	Spawn February, March in deep water of lake. Critical period probably when fry disperse in May, June.
	Larger eggs, alevins and fry: higher survival (32%) to independent fry stage.	Smaller eggs, alevins and fry: lower survival (3%) to independent fry stage.
Live chiefly in littoral in north basin and in pelagic zone in south basin of lake. Grow fast in lake, e.g. attain length of c. 340 mm at age of 4-5 years.	Live chiefly in pelagic zone. Growth slow, e.g. attain length of c. 340 mm at age of 9-11 years.	Live chiefly in pelagic zone. Growth slow, e.g. attain length of c. 340 mm at age of 8-10 years.
Most trout mature and return to spawn in streams at 2+ years (males) and 3+ years (females), then return to lake. Survivors repeat spawn at 4+ years, 5+ years etc.	Mature and spawn at much older age than trout; mean age of spawners is 6-7 years (males), 8 years (females).	Mature and spawn at much older age than trout; mean age of spawners is 7-8 years (males), 9 years (females).

Fig. 7. Major differences in the life cycles of brown trout and both autumn and spring charr in Windermere.

that once the progeny of spring spawners have overcome their problems of smaller size and later emergence compared with the progeny of autumn spawners, their subsequent growth is good. A detailed study of energetics in a Norwegian population of Arctic charr has shown that differences in growth in the early life stages (age 0+ years) influences the age for a niche shift from zooplankton to zoobenthos feeding and also the age at maturity (Forseth et al. 1994).

There is clearly a need for more information on charr and trout in Windermere. Virtually nothing is known about the food, growth and movements of the immature charr in the lake. There is no information on the food of the pelagic trout or to what extent they are competing for food with the charr. Although there is some information about the temperature requirements of the two species, little is known about the growth and energetics of Windermere charr so that comparisons can be made with the extensive data already available for the trout. Such a comparison may help to explain the slower growth of the charr and their higher age at maturity. Recent declines in the charr stocks, especially in the south basin, are a cause for concern and it is important to continue the monitoring programme to ensure that there is advance warning of any marked changes in population density. The present contribution has also shown that there are still many unanswered questions on the ecology of charr and trout in Windermere. There is therefore an urgent need for more research to ensure the successful conservation and management of these two species that provide naturally sustainable resources of economic importance.

Acknowledgments

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Confessions from a Four Decade Affair with Dolly Varden: a Synthesis and Critique of Experimental Tests for Interactive Segregation between Dolly Varden Char (*Salvelinus malma*) and Cutthroat Trout (*Oncorhynchus clarki*) in British Columbia

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Abstract

Validation of the competitive exclusion principle has been attempted over a forty year period for species pairs of British Columbia freshwater fishes, mainly Dolly Varden char and cutthroat trout, by field comparisons in sympatry and allopatry on their use of space and food resources, by laboratory study of their trophic and visual structures, by large-scale field manipulation experiments, and by controlled laboratory behavioural experiments. Although much information has been obtained on ecological interactions between the species pairs, little insight has been gained into the validity of the principle itself or the mechanisms which might support it. Probably this is a result of difficulties and lack of precision in concept definition as well as in design of appropriate experiments to test its assumptions. Precise definition of the principle may not be practical and it may be more useful to consider competitive exclusion between closely related species pairs as a quasi-permanent final state of genetically determined difference realized by a series of less fixed steps brought about by interactive segregation.

Keywords: competitive exclusion, interactive segregation, salmonids.

Introduction

Competition and interactive segregation between closely related species pairs has commanded the attention and study of biologists throughout the western world at least since the time of Charles Darwin. In essence the concept is that two species with similar resource demands cannot occupy for long the same ecological niche, or cogently stated by Hardin (1960) as the competitive exclusion principle, "complete competitors cannot coexist". One should eventually displace the other, if not physically then temporally, or by shifts in niche requirements. Though attacked by Cole (1960a,b), the "principle" continued to serve as a focus for ecological theory as well as for both field and laboratory experiments with various attempts at redefinition, the most common following that of Colinvaux (1973, 1986) as "stable populations of two or more species cannot continuously occupy the same niche". In a review which examined some 527 field experiments and some 215 species to evaluate evidence for interspecific competition, Connell (1983) concluded that it could be reasonably demonstrated for about two fifths of the experiments and for over half of the species, but that more studies were needed for freshwater ones.

The competitive exclusion principle and its offshoots have been thoroughly discussed by a long series of well known ecologists such as Hutchinson (1978), Brewer (1979, 1988), Krebs

(1985) and Ricklefs (1990) to name but a few. Some have pointed out problems and shortcomings of the principle. McNaughton and Wolf (1979) noted that it is probably a truism but that it can lead to very interesting work on how two coexisting species differ. Others have regarded it as a transient phenomenon (Connell 1980) with little critical evidence of how it comes about (Andrewartha and Birch 1984), and perhaps the best evidence of it having taken place being when the poorer competitor disappears (Ricklefs 1990). Much recent attention has been directed to a range of mechanisms which can permit competing species to coexist (Briggs 1993, McLaughlin and Roughgarden 1993). These include ones which increase resource number or supply, prevent one species always being a superior competitor, result in environmental variation in space (patchiness) or time (diel, seasonal or longer term change), or bring about ontogenetic (and often asymmetric) change in resource demands.

So it was into this morass of controversy that we launched our long-term study of competitive interaction between Dolly Varden char (*Salvelinus malma*) and cutthroat trout (*Oncorhynchus clarki*) in the 1960s, anointed with some of the background but blissfully unaware of much of the further conflict that would surround the subject.

First beginnings

In the summer of 1949 I was involved in a limnological survey of the Arrow lakes in south-central British Columbia. Part of our work included beach seining to collect representative samples of shoreline fishes and in these, two species of cottids, the prickly sculpin *Cottus asper* and the torrent sculpin *C. rhotheus*, were frequently captured together in the same haul. Having recently read the work of David Lack on cohabiting cormorants and other birds of prey (Lack 1945, 1946), I became interested in questions centering around how these two closely related species of fish could apparently occupy the same or at least very similar ecological niches. Attempts to resolve the questions formed the basis of my B.A. Honours thesis (Northcote 1950) and eventually my first publication in a refereed scientific journal (Northcote 1954). In

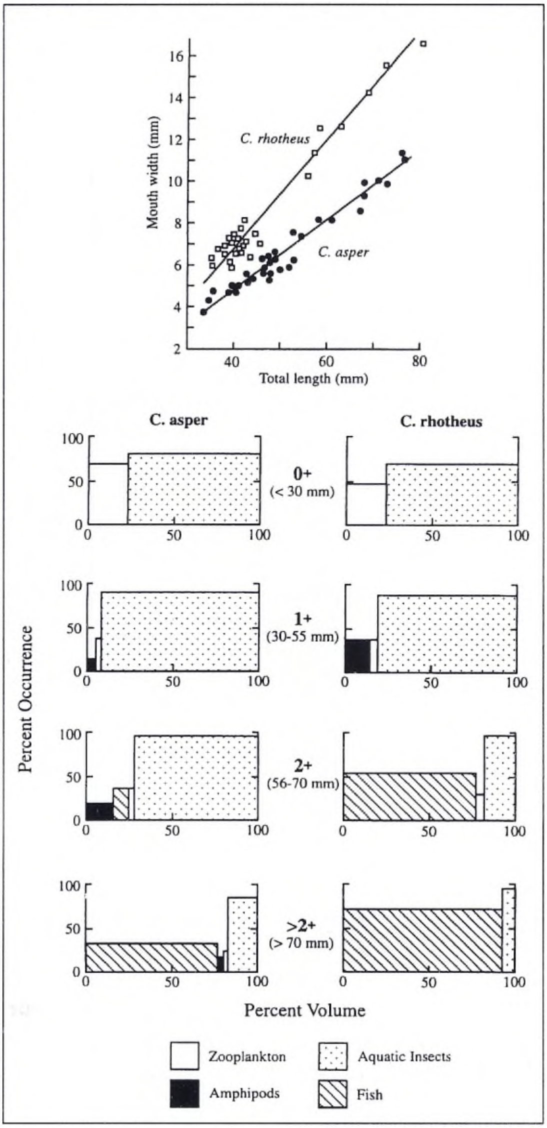


Fig. 1. **Upper**: changes in mouth size with body length in two cohabiting sculpins, Arrow lakes, British Columbia, 1949. (Adapted from Northcote 1954.) **Lower**: changes in prey taken with age (size; see above) in two cohabiting sculpins, Arrow lakes, British Columbia, 1949. Prey size increases from top to bottom in legend.

summary it turned out that these two species not only showed some differences in habitat preference (prickly sculpin being more associated with low current velocity, muddy shoreline and torrent sculpin with higher velocity, gravel shoreline) but also had differences in mouth gape which allowed the larger mouthed torrent sculpin to feed earlier on larger sized prey (Fig. 1). Thus this seemingly glaring exception to the competitive exclusion principle was nicely "explained", or so I thought then.

In 1951 I was on limnological survey of a series of lakes in the coastal region of the province and was struck with the sharp vertical differences in distribution shown by two salmonid species, Dolly Varden char and cutthroat trout - hereafter called char and trout respectively in this paper - which frequently cohabited in these lakes. The char were most commonly taken in nets set offshore in deeper waters (often below 10 m) whereas the trout were most abundant in shallow sections of onshore nets. Later observations on the same species pair in Queen Charlotte Islands streams showed that, though they often occurred together in the same reach, the char usually were under the cover of cutbank areas whereas the trout were most common in open off-edge waters.

By the early 1960s my first graduate student and I became interested in two cohabiting species of cyprinids, longnose dace (*Rhinichthys cataractae*) and leopard dace (*R. falcatus*) from the Fraser River of British Columbia. During the period of early summer freshet, marginal flooding, and abundant food supply, the two species live together along the river edge but even then show some differences in current preference. These become intensified especially in older fish during lower flow periods when food is less abundant. The habitat shift may result from ontogenetic changes in their buoyancy as expressed by swim bladder volume in relation to body weight (Fig. 2).

Thus by the early 1960s I had pondered problems of cohabitation in three different species pairs - sculpins, char/trout and dace. In each case, apparent solutions lay in subtle shifts in microhabitat use associated with differences in body structure for feeding or depth position, and in overlaps of resource requirements occurring mainly at times of abundant supply.

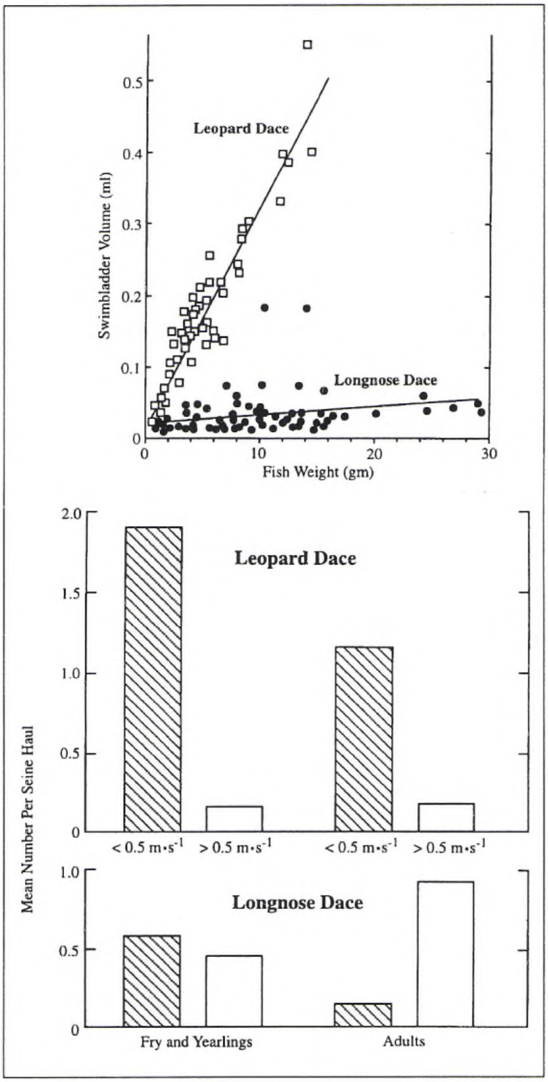


Fig. 2. **Upper**: changes in swimbladder volume with body weight in two cohabiting dace, Fraser River, British Columbia. (Adapted from Gee and Northcote 1963.) **Lower**: relative abundance of two cohabiting dace in slow and fast current, Fraser River, British Columbia. Based on 342 seine hauls in slow current (<0.5 m • s^{-1}) and 101 in fast current (>0.5 m • s^{-1}).

Insights from Nils-Arvid Nilsson

But our "explanations" to resolve apparent contradictions to the competitive exclusion principle were not entirely satisfactory, either to ourselves or to our critics! In the summer of 1962 I attended the 15th International Limnological Congress held in Madison, Wisconsin and there heard a presentation by Dr Nils-Arvid Nilsson on his research with Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) interaction in Swedish lakes and reservoirs. He made extensive comparisons between sympatric and allopatric populations of this species pair (see Nilsson 1967, 1978 for reviews), showing that in allopatry each species had a broad use of space and food resources whereas in sympatry these were greatly narrowed with each presumably focussing on its region of most effective specialization. The question then centred on whether or not these differences actually represented shifts brought about by direct interaction between the individuals involved (i.e. interactive segregation) or was the result of previously selected genetic differences between the species (i.e. selective segregation). For various good reasons Nilsson generally opted for the former explanation (see especially his 1967 review).

Comparisons of B.C. sympatric and allopatric populations

We followed Nilsson's lead, examining in an extensive field study (Andrusak and Northcote 1970, 1971) the differences evident in use of space and food resources by sympatric and allopatric populations of char and trout where

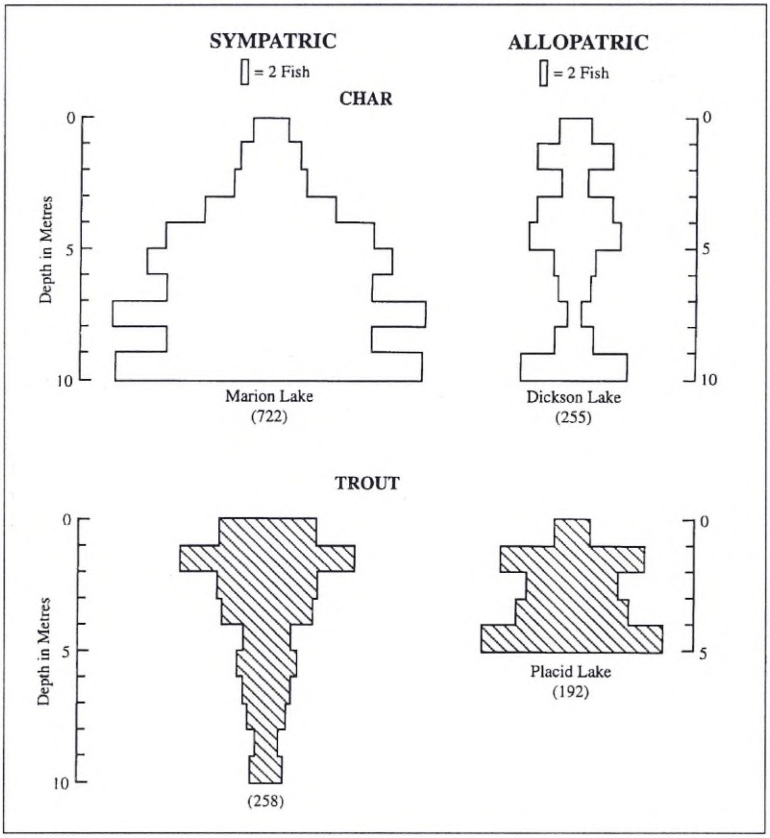


Fig. 3. Vertical distribution of sympatric and allopatric char and trout taken in gill nets from spring to autumn, 1967. Sample size in parentheses. Adapted from Andrusak and Northcote (1970, 1971).

neither was potentially confounded by interactions with other species of fish. As an allopatric population in Dickson Lake, char were widely distributed mainly within the upper 10 m with no marked concentration at any depths within that zone (Fig. 3). Echo sounder traces showed that some char were located at depths up to 25 m during the day (lake maximum depth 76 m) but were less deep in distribution at night. On the other hand in Marion Lake (maximum depth 12.1 m), sympatric char were concentrated at depths below 4 m (Fig. 3). Allopatric trout were abundant in shallow Placid Lake (maximum depth 6.7 m) at all depths except perhaps the uppermost metre (Fig. 3), but as a sympatric population in Marion Lake were clearly concentrated in the upper 4 m.

Allopatric char in Dickson Lake preyed heavily on all three major food categories with surface insects contributing well over 40% of their average food volume (Fig. 4), and bottom fauna about 20%. When sympatric with trout in Marion Lake, char reversed the relative contributions of the three major categories so that bottom fauna accounted for well over 60% of the volume and surface insects only about 6%. Allopatric trout in Placid Lake used all three major prey categories but when sympatric with char concentrated more on surface insects. Changes in diet for both species between allopatry and sympatry appeared to follow the shifts evident in their spatial distribution, the char being more bottom and deep water oriented and the trout more surface and littoral oriented.

Even though similar patterns in use of space and food resources by allopatric and sympatric char and trout were observed in several other coastal British Columbia lakes (Andrusak and Northcote 1970, 1971), it was difficult to demonstrate conclusively that the shifts were a result of interactive segregation rather than differences between lake conditions or other factors.

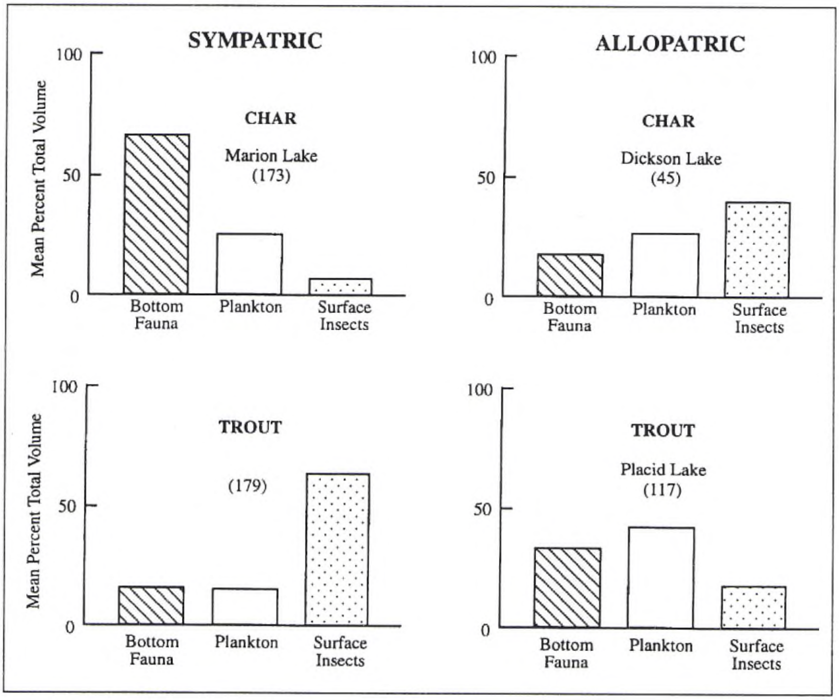


Fig. 4. Major categories of prey eaten by sympatric and allopatric char and trout from spring to autumn, 1967. Sample size in parentheses. Adapted from Andrusak and Northcote (1970, 1971).

Table 1. Behavioural differences between adult char and trout in the 0-4 m depth zone of Marion Lake in summer, 1968. Adapted from Schutz and Northcote (1972).

	Depth zone (m)			Group size			Feeding location		
	0-2	2-3	3-4	1	2-3	>3	Surface	Midwater	Bottom
Char	0	48	30	16	12	4	0	12	13
Trout	14	11	0	23	2	0	23	0	0

Early experimental approaches

Field observations in the shallow waters of Marion Lake (Table 1) indicated that char frequented the near-bottom waters, often in small groups, and commonly took prey close to or directly off the bottom by forays into the soft surficial sediments. Trout on the other hand were most frequently seen in the near-surface waters as solitary individuals and often took prey directly from the lake surface.

The field observations led to a series of laboratory experiments on the feeding behaviour of char and trout as solitary individuals and as interactive species pairs exposed to benthic and/ or surface invertebrate prey. Details are given in Schutz and Northcote (1972) but may be summarized as follows:

- solitary char have much a higher capture rate than solitary trout when feeding on benthic prey (Table 2);
- solitary char have much longer capture times than solitary trout when feeding on surface prey (Table 2);
- solitary char have much lower "surface grabs" than solitary trout when exposed to both benthic and surface prey (data not shown);
- solitary char are much more effective than trout in capturing benthic prey at low light intensity (10^{-1} to 10^{-3} lux), especially after a 40 min adaptation period at 10^{-3} lux (Fig. 5);
- char cohabiting with trout, when not subordinated, have moderate to high feeding success on benthic prey, and even when subordinated, have moderate to high benthic feeding success when benthic and surface prey are both available (Table 3).

Another series of field and laboratory experiments were run later with sympatric (Loon Lake) and allopatric (Dickson Lake) adult char using the same tanks, holding and feeding procedures as those of Schutz and Northcote (1972). Details are given in Armitage (1973) but two comparisons are of interest here. Allopatric char spent over half the time in the upper half of the test tanks whereas sympatric char were there for only about a third of the time and often rested on the bottom. The difference was significant

Table 2. Feeding success of solitary char and trout adults in laboratory tanks on different types of invertebrate prey. Adapted from Schutz and Northcote (1972).

	Benthic Mean captures per min searching		Surface[3] Mean capture time (s)
	Surficial[1]	Buried[2]	
Char	0.8-0.9	3.6-7.4	26-74
Trout	0-0.2	0.4	12-29

[1] Green *Psectrotanypus* larvae, [2] *Tubifex* oligochaetes, [3] Single *Drosophila* adults.

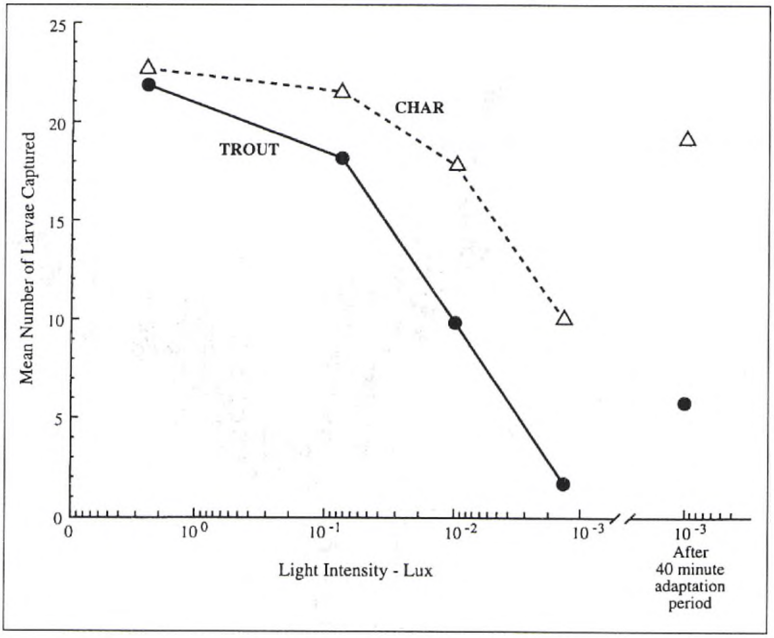


Fig. 5. Effect of light intensity after 10 min adaptation period on benthic prey capture rate in 10 min of red *Chironomus* larvae by solitary char and trout. Adapted from Schutz and Northcote (1972).

Table 3. Feeding success (% prey obtained) of adult char on benthic and surface prey when cohabiting with adult trout in laboratory tanks. Adapted from Schutz and Northcote (1972).

	Benthic prey alone	Surface prey alone	Benthic and surface prey together Benthic	 Surface
Char				
Subordinant	0-10	21-35	20-80	0-40
Not subordinant	42-85	52	-	-

($P<0.01$), using arcsin transformation. Feeding success on planktonic fourth instar *Chaoborus trivittatus* larvae was different between the two forms, with allopatric char showing higher mean capture efficiency (0.55 captures per attempt versus 0.37).

Whole lake experimental introductions

Our previous work on use of space and food resources of allopatric and sympatric populations was in part unsatisfactory because the study lakes were widely separated and in some cases had rather different limnological features. The Malcolm Knapp University of British Columbia Research Forest where Placid Lake was located also had several lakes with cohabiting char and trout as well as several other closely situated fishless lakes of similar size and other characteristics. Therefore in the late 1960s a "grand" experimental series of studies and introductions was conceived to exploit this unique opportunity in three phases:

1) a several year pre-introduction study of the zooplankton and zoobenthos communities in three nearby fishless lakes - Gwendoline, Eunice, and Katherine (Fig. 6);

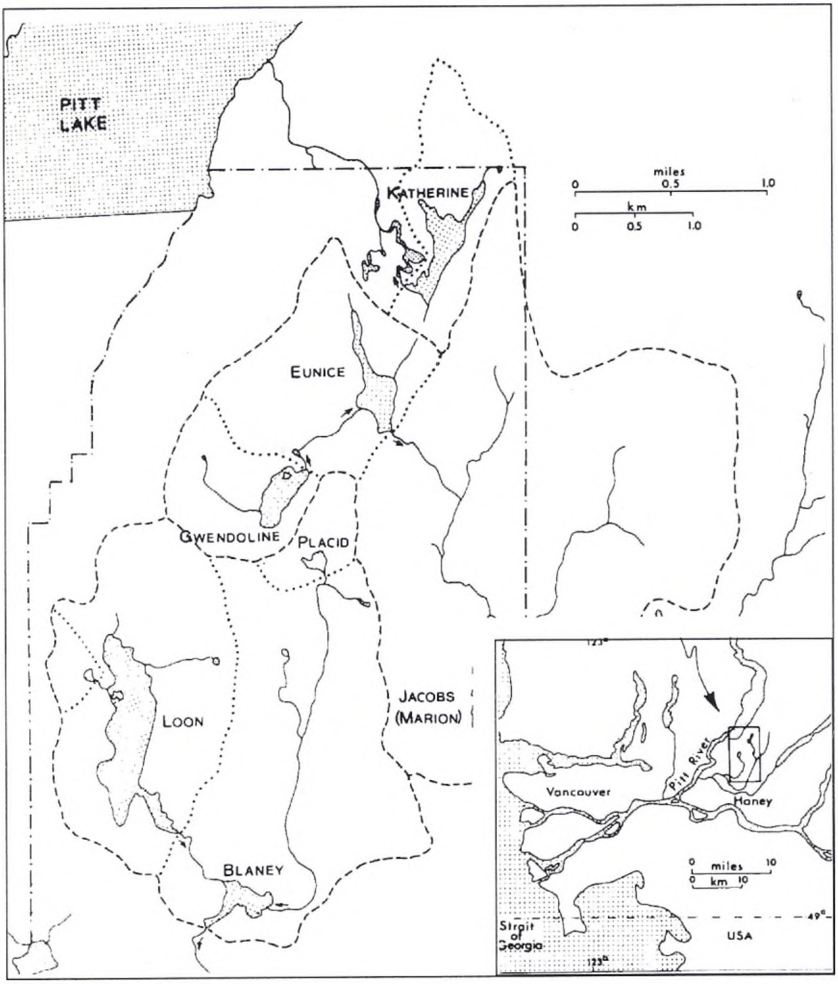


Fig. 6. Location of study lakes and their watersheds in the Malcolm Knapp University of British Columbia Research Forest. Inset shows general location in southwestern British Columbia.

2) introduction of Loon Lake sympatric char to form an experimental allopatric population in Katherine Lake, of Loon Lake sympatric trout to form an allopatric population in Eunice Lake, and maintenance of Gwendoline Lake as a fishless control, with a two decade study period to follow short and long-term changes in zooplankton communities as well as use of space and food by the experimental allopatric char and trout in their "new" lakes;
3) experimental introduction of Katherine Lake char into the allopatric Eunice Lake trout population, and vice versa, to establish experimental sympatric populations followed by a similar subsequent study period.

Pre and post introduction studies of zooplankton were completed (Fedorenko 1973, Fedorenko and Swift 1972, Northcote and Clarotto 1975, Northcote et al. 1978, Walters et al. 1987, 1990) and of zoobenthos (Northcote unpublished data, Hindar et al. 1988) as were the short and long-term effects of experimental segregation of formerly sympatric char and trout populations (Jonsson et al. 1984, Hume and Northcote 1985, Hindar et al. 1988, Rempel and Northcote 1989, Andrew et al. 1992). Only the latter studies will be reviewed briefly here.

A 3-4 m high waterfall on the stream connecting Gwendoline (the control lake) and Eunice proved to be unstable, giving away during a severe freshet and allowing upstream access of trout into Gwendoline Lake a few years after their introduction into Eunice Lake in 1974.

Spatial distribution changes

There were no statistically significant changes in vertical distribution of either allopatric char or trout during the first 18 months after the experimental transfers (pooled *G* tests, Table 2 in Hume and Northcote 1985) and the clear pattern for concentration of char in the near-bottom waters when sympatric with trout in Loon Lake remained following their experimental transfer to Katherine Lake (Fig. 7). Eight years after transfer to Katherine Lake, the char had broadened their vertical distribution to include the shallow littoral zone, were often seen to feed at the surface waters of the lake, but still were abundant in the deeper waters to 20 m (Fig. 8). The average vertical overlap in distributions between allopatric and sympatric lakes was less than 40%. Trout on the other hand had a much higher vertical overlap (>70%) between allopatric and sympatric lakes, apparently concentrating even more in near surface waters of

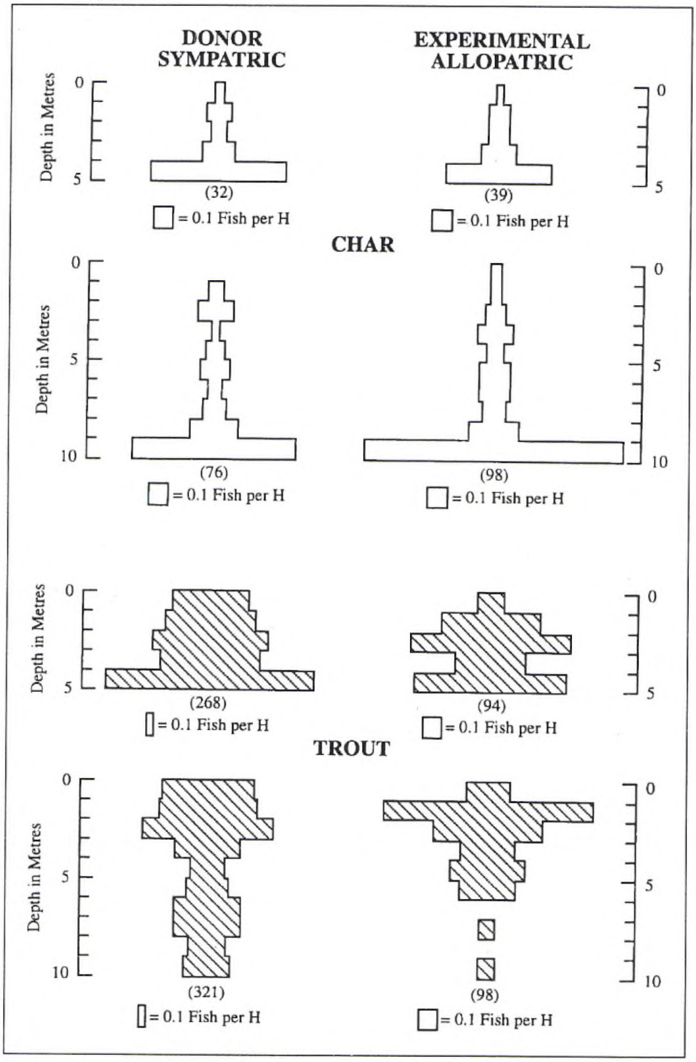


Fig. 7. Vertical distribution of sympatric char and trout (Loon Lake) and allopatric char (Katherine Lake) and trout (Eunice Lake) in surface to bottom gill net sets at 5 and 10 m contour stations from spring to autumn 1975 to 1976 (first 18 months after experimental introductions). Data from Hume and Northcote (1985).

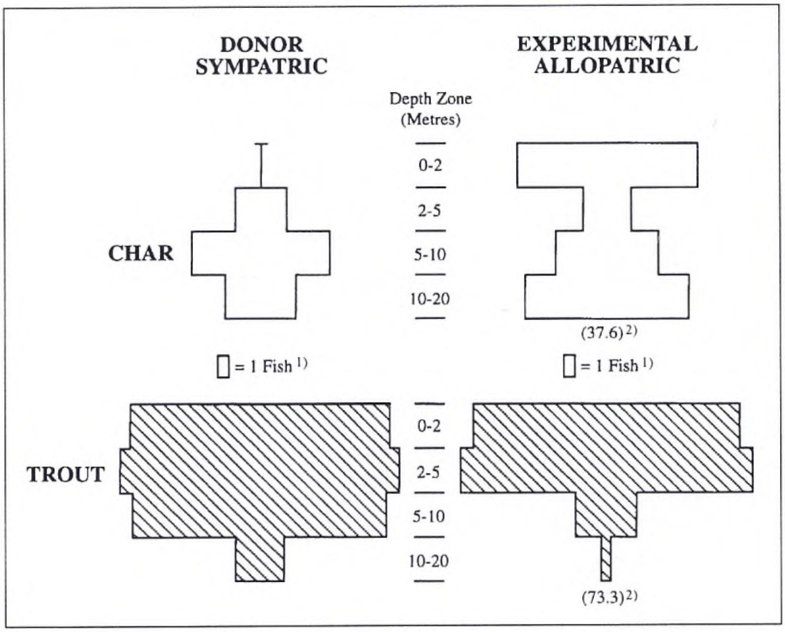


Fig. 8. Vertical distribution of sympatric char and trout (Loon Lake) and allopatric char (Katherine Lake) and trout (Eunice Lake) in surface to bottom gill net sets at 2, 5, 10 and 20 m contour stations from summer to autumn 1982 (eight years after experimental introductions). Data adapted from Hindar et al. (1988).

¹⁾ catch per net station per 48 h,

²⁾ average vertical overlap (percent similarity index) comparison with donor lake sympatric distribution.

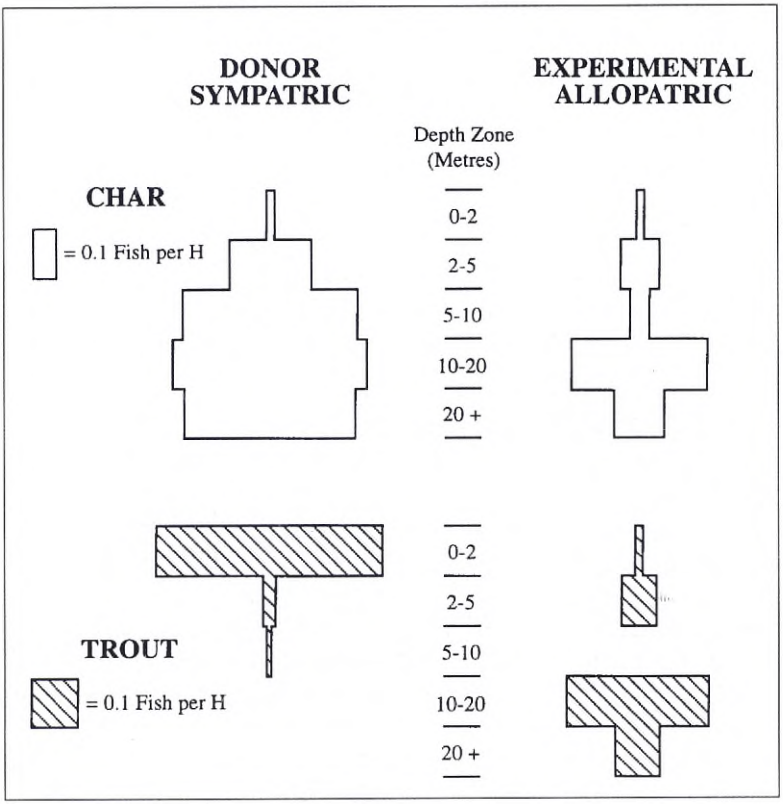


Fig. 9. Vertical distribution of sympatric char and trout (Loon Lake) and allopatric char (Katherine Lake) and trout (Eunice Lake) in bottom live traps during spring 1994 (20 years after experimental introductions).

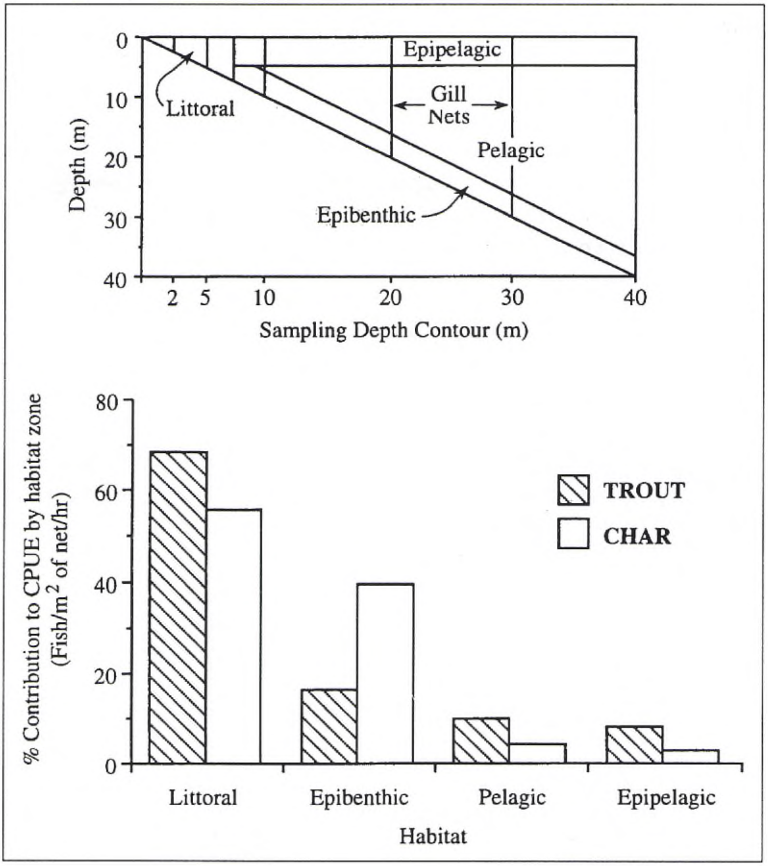


Fig. 10. **Upper**: schematic representation of the four habitat zones used in analysis of char and trout distribution. Adapted from Rempel and Northcote (1989). **Lower**: February 1988 percent contribution to catch per unit effort (CPUE) of char and trout in four habitat zones of Loon Lake.

their experimental allopatric lake (Fig. 8). These and other changes in use of lake habitat by experimentally segregated populations of char and trout have been documented in detail by Andrew et al. (1992).

Additional information on spring spatial distribution of char and trout in the study lakes was obtained recently in conjunction with their reciprocal transfer between Katherine and Eunice lakes to form sympatric populations there (Fig. 9). In the donor sympatric Loon Lake, char catch rates were very low in the littoral zone but high at depths of 10 to 20 m, whereas trout were mainly caught at depths less than 2 m and none was taken at 15 or 20 m. Allopatric char and trout were more broadly distributed vertically with highest catch rates at 15 m.

The high degree of spatial segregation evident between cohabiting char and trout (Figs. 3, 7, 8, 9) during spring to summer apparently breaks down during winter with char moving into the littoral zone where highest catches per unit effort were recorded for both species (Fig. 10). No significant differences were found between species in their distribution between four major types of habitat, nor in habitat and species interaction (Rempel and Northcote 1989).

Prey selection changes

Shortly after experimental transfer to their allopatric lakes both char and trout concentrated feeding on the larval midwater populations of *Chaoborus trivittatus* and *C. americanus*, virtually eliminating them within a year (Northcote et al. 1978). Then particularly char shifted to a much higher proportion of large benthic invertebrates (Fig. 11), mainly leeches, trichopterans and plecopterans. Eight years after experimental allopatry, plankton formed a very much less important prey item especially for char (Fig. 12), with non-chironomid zoobenthos dominating their summer diet (see Fig. 4 in Hindar et al. 1988).

Foraging experiments and visual prey detection

To investigate the extent to which prey detection by coexisting char and trout might be adapted to their patterns of spatial and prey segregation, we undertook a series of foraging experiments in relation to irradiance level and also examined the retinal structure of sympatric and allopatric populations (Henderson and Northcote 1985, 1988).

At a certain low irradiance level, the fish were incapable of detecting prey visually (designated the visual irradiance threshold - VIT), but that level for char, $7.0 \cdot 10^{14}$ photons • m^{-2} • s^{-1}, was about an order of magnitude lower than that for trout (Fig. 13). At irradiance levels above their VIT, reaction distance to both natural and artificial prey increased to a saturation irradiance threshold (SIT) above which no further increase occurred, that for char, $3.0 \cdot 10^{16}$ photons • m^{-2} • s^{-1}, being very much lower than that for trout at $6.6 \cdot 10^{18}$ photons • m^{-2} • s^{-1}. Furthermore the

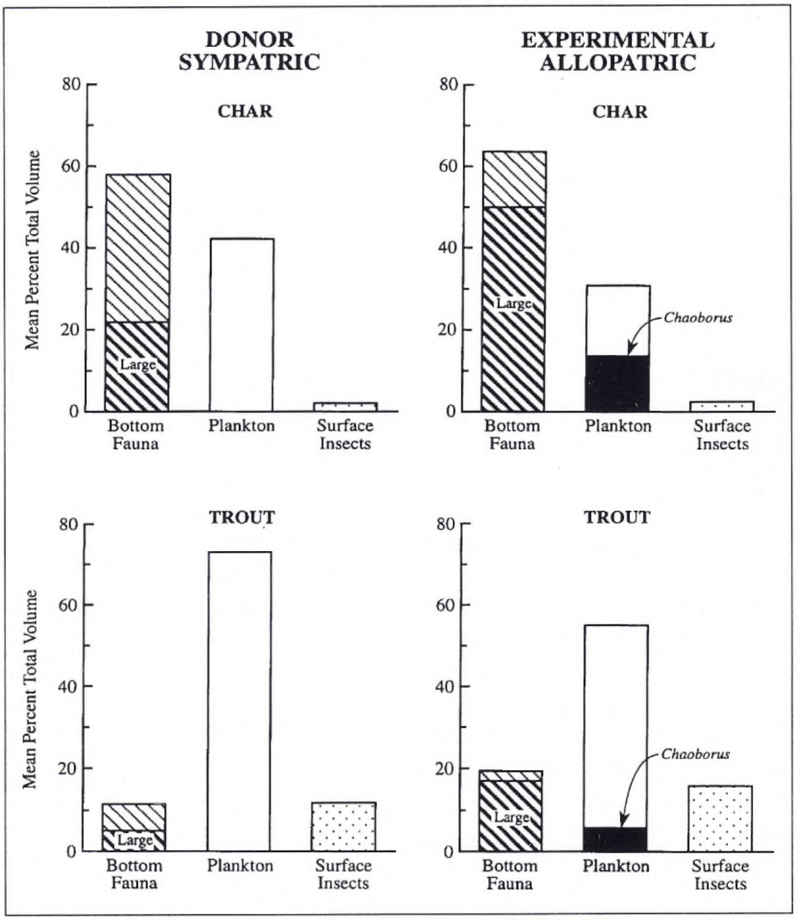
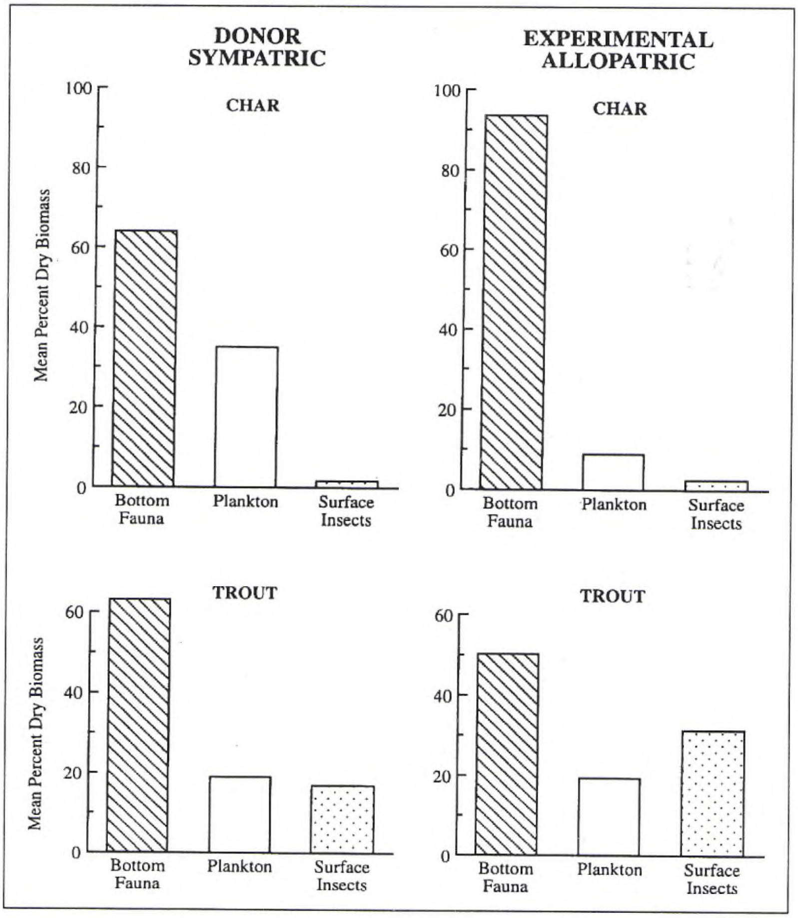


Fig. 11. Percent contribution of major prey types to diet of sympatric char and trout (Loon Lake donor stock) and allopatric char (Katherine Lake) and trout (Eunice Lake) taken in surface to bottom gill net sets from spring to autumn 1975 to 1976 (first 18 months after experimental introductions). Data from Hume and Northcote (1985).

Fig. 12. Percent contribution of major prey types to diet of sympatric char and trout (Loon Lake donor stock) and allopatric char (Katherine Lake) and trout (Eunice Lake) taken in surface to bottom gill net sets from summer to autumn 1982 (eight years after experimental introductions. Data adapted from Hindar et al. (1988); see for details.



reaction distance of trout exceeded that for char at all irradiance levels above about $4.2 \cdot 10^{17}$ photons $\cdot$ m^{-2} $\cdot$ s^{-1} and at their SIT was more than twice that for char (Fig. 13). By measuring diel changes in vertical irradiance in the waters of Loon Lake, we could estimate corresponding changes in the depth at which irradiance matched the VIT and SIT of both species (Fig. 14). Irradiance always exceeded the VIT for char in some part of the water column in midsummer (Table 4), but only above the uppermost 5 m between late evening and early morning, whereas even at the lake surface irradiance was less than the VIT for trout between late evening and early morning. Irradiance level was at the SIT for char over a longer period and extended to far greater depths than that for trout (Fig. 14, Table 4). Nevertheless because of the differential effect of irradiance level on mean foraging velocity of char and trout (that of the latter being higher than the former above about 10^{18} photons $\cdot$ m^{-2} $\cdot$ s^{-1}; see Fig. 6 in Henderson and Northcote 1985), we estimated that in July trout could *visually* search over 1000 m^3 of water for 1.5 mm *Diaptomus kenai,* whereas char could only cover about 150 m^3.

Our investigation of retinal structure in char and trout provided further insight into mechanisms supporting differences in their spatial distribution and foraging behaviour. Sympatric char have a much higher rod to cone ratio than do cohabiting trout (Table 5) and that for allopatric char is intermediate. Similarly the summation ratio of sympatric char is much greater than that

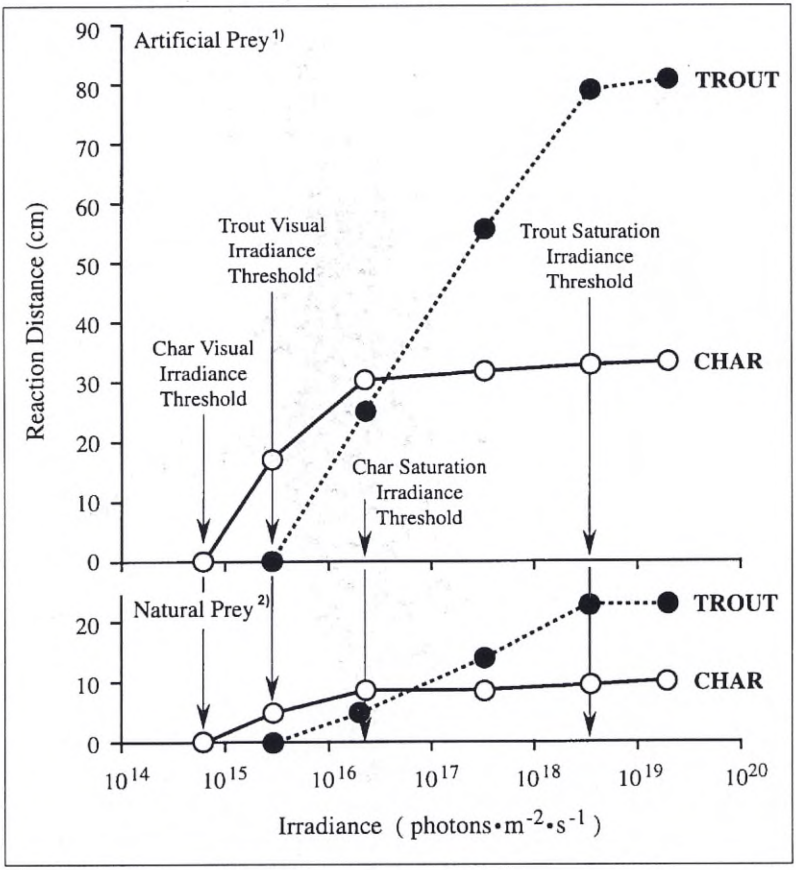


Fig. 13. Effects of irradiance on mean reaction distance of Loon Lake char and trout to prey. Adapted from Henderson and Northcote (1985); ±95% confidence limits lie within circle diameter of means.

1) 1 • 3 mm cylinders of chicken liver,

2) 1.5 mm *Diaptomus kenai.*

for cohabiting trout and intermediate for allopatric char (Table 5). These differences in retinal structure suggest that char could operate visually at lower irradiance levels than trout but that their visual acuity would be poorer, helping to explain differences in vertical distribution and foraging of the two species in sympatry. Furthermore the intermediate retinal features of allopatric char but not trout may correlate with behavioural differences between the allopatric forms, char but not trout having intermediate vertical distribution and food habits when in allopatry.

Table 4. Irradiance levels for visual prey detection by char and trout in Loon Lake, 8-9 July 1980. Data from Henderson and Northcote (1985). VIT=Visual irradiance threshold, SIT=Saturation irradiance threshold.

Species	Irradiance <VIT	Irradiance = SIT	
	Time period	Time period	Max. depth (m)
Char	Never	03:00-21:00	>40
Trout	21:30-02:45 (even at surface)	04:30-20:00	16.7

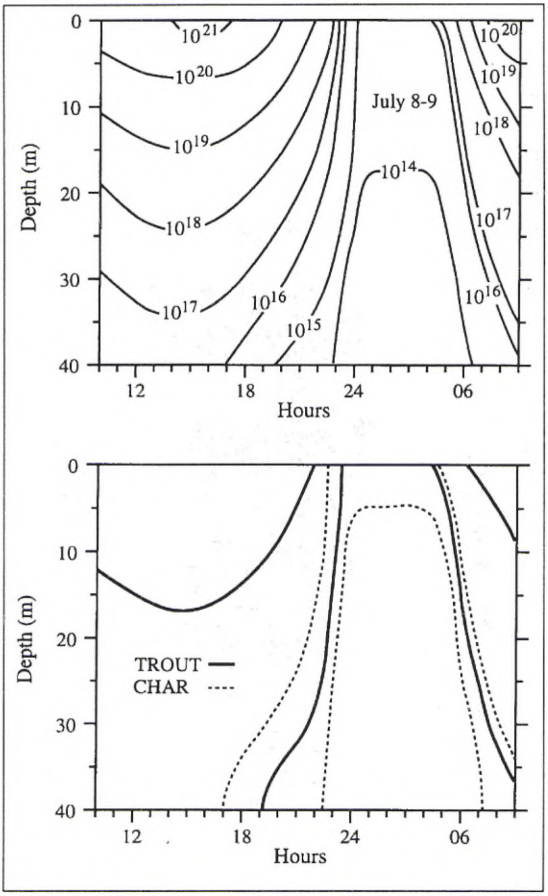


Fig. 14. **Upper**: depth-time isopleths of irradiance (photons • m^{-2} • s^{-1}) in Loon Lake on 8-9 July 1980. Adapted from Henderson and Northcote (1985). **Lower**: relationship between irradiance (photons • m^{-2} • s^{-1}) in Loon Lake on 8-9 July 1980 and visual sensitivity of char and trout. Upper line for each species gives depth where irradiance matches "saturation intensity threshold" (SIT); lower line gives depth where irradiance matches "visual intensity threshold" (VIT).

Synthesis and speculation

After more than four decades of work on interaction between closely related species pairs of freshwater fish, are we any closer to validation or vilification of the competitive exclusion principle? The uncharitable but probably realistic answer is no! But surely we now have greater understanding of the mechanisms involved in expression of resource use differences between cohabiting (sympatric) and isolated (allopatric) populations of the species pairs. These mechanisms may be based in structural differences between the species involved, as first suggested by such crude morphological measurements as mouth gape (Northcote 1954) or swimbladder volume (Gee and Northcote 1963) and most recently by more subtle histological differences in retinal cell structure and wiring (Henderson and Northcote 1988).

Unequivocal demonstration of interspecific competition's involvement in exclusion between species pairs often fails because of difficulties in determining not only the quantity of the specific resource being competed for, but more importantly its *availability* over a time span sufficient to bring about a shift in resource use. In temperate freshwater habitats subject to sharp seasonal change and with freshwater fish species whose resource demands undergo quick ontogenetic alteration, one often may be trying to prove the impossible! Hence the frequent frustrations and lack of relationships in field studies attempting to measure use of habitat space by gill net sets and seine hauls as well as prey availability by plankton nets and Ekman dredges.

One way out was to bring the problem into the laboratory where conditions could be more precisely controlled and replicated. And this we did, demonstrating differences in behaviour between char and trout when feeding on benthic and surface prey, in prey location at low irradiance levels, and in aggression and dominance relationships. These provided better understanding of interactions observed in the field but also seemed in part unsatisfactory because the scale had to be resolved in centimetres not metres. Spatial scale of experiments may not necessarily distort their numerical dynamics but other effects may occur (Gascon and Travis (1992). Surely the answer then was to effect whole lake experimental manipulations.

We were most fortunate in having a series of fishless lakes where experimental introductions could be made close to ones with natural

Table 5. Comparison of some structural features in retinas of sympatric and allopatric char and trout. Adapted from Henderson and Northcote (1988).

Species	Rod : Cone ratio	Summation ratio photoreceptor : bipolar : ganglion cells
Sympatric (Loon L.)		
Char	34.4 : 1	78.0 : 23.3 : 1
Trout	13.2 : 1	39.6 : 16.6 : 1
Allopatric		
Char (Dickson L.)	21.1 : 1	52.0 : 17.8 : 1
Trout (Placid L.)	14.1 : 1	36.5 : 15.3 : 1

sympatric and allopatric populations. Thus we were able to establish single fish species allopatric char and trout populations with similar genetic background from known donor populations and to follow their use of space and food resources over a twenty year span before creating sympatric populations in each by reciprocal introductions.

But separate lakes are never quite the same so we were bugged by the bogey of Hurlbert (1984) and by other differences making interpretation of natural experiments to test interspecific competition difficult (Begon et al. (1990). Though similar in many limnological variables, there were differences between the study lakes. These, discussed in detail by Hindar et al. (1988), are summarized in Table 6. The major morphological difference among lakes is the lower mean depth and greater area of shallow littoral zone in Katherine. Loon has the deeper late summer epilimnion depth and clearest water. All lakes have similar water chemistry with no serious oxygen depletion except occasionally below 40 m in Eunice. There are only minor differences in zooplankton species composition and no significant ones in abundance. Differences in zoobenthos density, size composition and vertical distribution do occur among lakes (see Hindar et al. for details) but these do not seem to explain the virtual absence of char in the shallow littoral of Loon Lake and their greater use of that zone when placed under allopatry in Katherine Lake. Also there probably are differences in intraspecific competition among the lakes (Table 6), but again these do not provide a convincing argument for the differences in resource use between Loon and Katherine lakes (Hindar et al. 1988).

Instead, the fact that experimentally allopatric char but not trout showed spatial and food shifts when placed in allopatry seems best explained by the view that interspecific competition is more severely expressed on char. Long-term (after 20 year) effects of experimental allopatry on their use of food resources must await analysis of the April/May 1994 samples. Nevertheless the niche shifts already observed and the suggestion of trout having greater impact on char than vice versa seem consistent with the field observations in other lakes (Andrusak and Northcote 1970, 1971) and laboratory behavioural findings of Andrew (1985) on these species, as well as those of Nilsson (1955, 1963) on Arctic char and brown trout. Reciprocal formation of sympatric char and trout populations in Katherine and Eunice lakes will provide further whole lake tests of competitive interaction, and one less dogged by the alternate lake difference hypothesis. These will require development of sizable flourishing populations from the founder ones recently introduced to the lakes.

But there will still be problems in interpretation of natural manipulative experiments as pointed out for work on percid species interaction many years ago by MacLean and Magnuson (1977) and more recently by Hanson and Leggett (1985). Furthermore our studies have dealt mainly with sub-adult to adult stages and much

Table 6. Review of major limnological and ecological characteristics in the three study lakes. (Northcote and Clarotto 1975, Hindar et al. 1988, and Northcote, unpubl. data.)

Characteristic	Study lakes		
	Loon sympatric	Katherine allopatric char	Eunice allopatric trout
Morphometry			
Area (ha)	48.6	20.7	18.2
Mean depth (m)	27.5	7.5	15.8
Shoreline development	2.2	1.9	1.5
Shallow littoral (0-2m, % total area)	7.1	24.5	10.4
Epilimnion depth (late summer, m)	5.5-8	2.5-6	2.5-6
Transparency (Secchi, m)	8-9	6.5-9	6-10
Irradiance extinction coefficient	1.1	1.4	1.7
Colour (Pt units)	5	10-15	15
pH	6.5	6.6	6.4
Total dissolved solids	32	15	16
Zooplankton composition, abundance	minor differences in composition but not in densities		
Zoobenthos composition, abundance	highest littoral density, profundal maximum at 40 m	higher proportion of large littoral zoobenthos	higher proportion of large deep zoobenthos (≥20 m)
Food resource availability	best in upper 2 m	best in upper 2 m	best in upper 2 m
Intraspecific competition	higher than Katherine L.	lower than Loon L.	higher than Loon L.
Vertebrate predation	occurs in all lakes from birds (loons, ospreys, mergansers) but impact or intensity not known (probably highest in Loon L.)		

needs to be done on juvenile stages as these may provide better understanding of asymmetries in interspecific interactions (Wissinger 1992). Size-scaling components have been regarded as "one of the most important attributes affecting mechanisms and expression of competition" (Werner 1994).

Also we may have relied too heavily on field observations and manipulations as well as laboratory studies in lake or lake-simulated environment. Even lake-dwelling (as adults) char and trout may spend up to a year or more in stream habitats. These we have not investigated although they clearly may be important (see reviews by Hearn 1987, Fausch 1988) and more recent studies by Dolloff and Reeves (1990), Glova et al. (1992), McIntosh et al. (1992), Nakano et al. (1992), Kessler and Thorp (1993).

As long-lived and stimulating as has been the competitive exclusion principle in ecology, its definition does not seem rigorous enough to subject to strong experimental test, certainly in the laboratory and probably also in the field. Many of the apparent "exclusions" that we observe in temperate natural populations of closely related species pairs may be the temporary (geological speaking) product of pioneer species invading habitats opening up after deglaciation and exploiting those habitats and conditions where previous selection provided them with long-term competitive advantages.

Acknowledgments

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Management of Charr Lakes

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Abstract

The population structure of Arctic charr (*Salvelinus alpinus*) may generally be characterized based on food and living habitats as having four individual forms: i) anadromous, ii) normal resident, iii) dwarf resident and iv) piscivorous. Throughout their life history, charr may shift from one form to another in association with changes in habitat use, food and growth. All of these forms can coexist in the same freshwater system or may be present in a lake as a single form. A mixture of different forms in the same lake has resulted in differing opinions about the importance of genetic versus environmental determination. Most studies, however, show that the forms within a lake are largely environmentally determined and belong to the same genetic pool. In this paper charr management is considered from an environmental and ecological point of view assuming that the charr within a lake belong to a common genetic pool. Examples are given to illustrate different populations. Annual yields and harvesting experiments of charr from different lakes are summarized. The possible effects of fishing on growth, mortality and maturation are discussed. Four scenarios of population structure are discussed. Based on present experience, two fishing stategies are recommended i) sustainable harvest by removal of both immature and mature fish with emphasis on the protection of large charr, and ii) sport fishery of predatory or cannibalistic fish.

Keywords: Charr, management, harvest.

Introduction

This species is commonly distributed in the northern hemisphere having both anadromous and landlocked forms. Arctic charr (*Salvelinus alpinus*) is typically a cold water species living in Arctic and temperate lakes with low productivity and few other fish competitors. The most commonly occurring fish competitors and predators are two other Salvelinus species lake trout (*S. namaycush*) and brook trout (*S. fontinalis)*, whitefish and cisco (*Coregonus* spp.*)*, brown trout (*Salmo trutta*), burbot (*Lota lota*), pike (*Esox lucius*), three-spined stickleback (*Gasterosteus aculeatus*) and nine-spined stickleback (*Pungitus pungitus*).

Since early historical times, the Arctic charr has been an important source of food for aboriginal people (LeDrew 1984, Kristofferson et al. 1984). Arctic charr, have in all likelihood, been exploited and utilized in northern Labrador since the arrival of the first Dorset Inuit, who occupied the region about 2,600 to 1,000 years ago (LeDrew 1984). In more recent times, the charr has become an important target for commercial and recreational fisheries. Thus, fishing has probably affected population structure in different ways. The introduction of monofilament nylon gillnets in the 1950's, coincided with a drastic change in population structure towards reduced fish size and high density (stunting) as observed in many Scandinavian Arctic charr lakes (Nyman 1984). To reveal the effects of fishing, it is necessary to look for unmanipulated stocks which still may be found in unpopulated northern areas and mountain lakes.

Here I will use the more general term form to describe charr occurring in different morphological types irrespective of whether the different forms are determined genetically or environmentally. All sympatric forms will be considered as belonging to the same gene pool. However, specific management may be implemented when a population is proven to be divided into different spawning populations separated by space and time. The genetic differences recorded between the dwarf and normal forms of Lake Sirdalsvatnet corresponded to differences in spawning time (Hindar et al. 1986). The coexistence of four morphs of Arctic charr in Lake Thingvallavatn, Iceland, was demonstrated by investigations of morphology, habitat use, diet, endoparasitic fauna, life history, time and place of spawning, early ontogeny and population genetics (Sandlund et al. 1992). Genetically, the morphs are very similar. The four morphs are conspecifics, although they may be reproductively segregated to some extent (Sandlund et al. 1992). In the following, Arctic charr is denoted as charr.

Why is it so difficult to manage charr lakes? Is it due to the charr's plasticity to inhabit lakes differing greatly in environmental conditions. We know that charr exhibit great variation in size and life history as a response to different lake charracteristics. Charr may spawn both in lakes and running waters, and it may utilize all habitats and most prey animals in lakes differ-

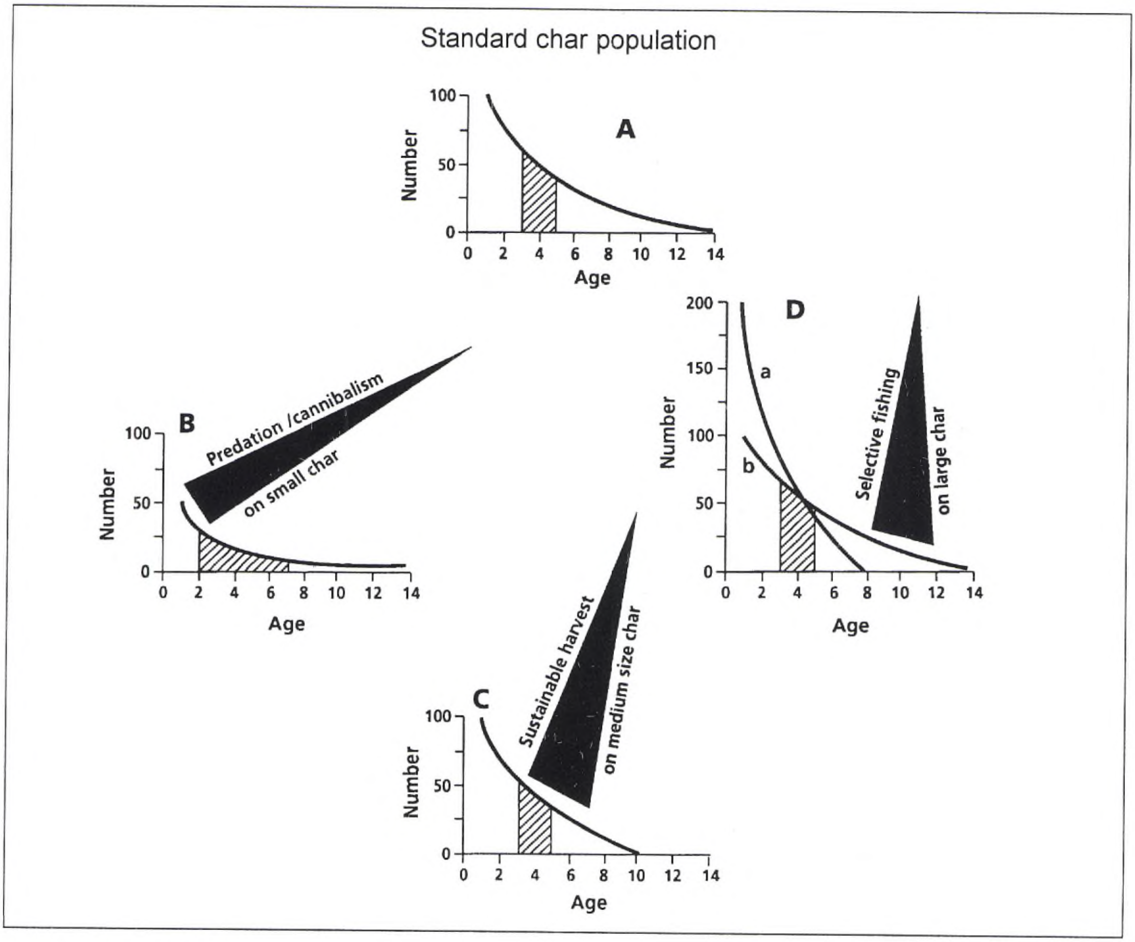

Fig. 1. Effects of different harvesting strategies on population age structures of Arctic charr (B-D) based on a basic age distribution (A). Hatched areas indicate age-at-first maturity.

ing in productivity potential. Charr are found in Arctic, alpine and temperate lakes. The anadromous charr may regularly migrate to feeding grounds in the sea during a few months in summer. Thus, preconditions are set for great variation in charr productivity and population structure (size and age). Perturbation by fishing may strongly affect population structure, which makes it difficult to predict the outcome of charr management. In this paper I review some yield and harvesting experiments and consider the most important interactions with other fish species. Finally, I discuss the management of charr based on four scenarios of population structure (Fig. 1). I conclude with two basically different strategies for managing charr lakes (sustainable harvest and sport fishery of predatory fish).

Forms of charr

There are four forms of Arctic charr, which are characterized by different sizes: dwarf of 10-100 g, normal charr of 100-500 g, sea or anadromous charr of 300-3,000 g, and large piscivorous charr of 500-3,000 g. In addition, forms may be characterized according to age at maturity, habitat and food (Johnson 1980). The sizes of the different forms overlap and are arbitrarily set for practical identification. One or several of these forms may be present in allopatry or sympatry in the same lake. Cannibalism in charr occurs throughout most northern regions as reported by Martin (1955), Nilsson (1955, 1965), Skreslet (1973a,b), Johnson (1980), Fraser and Power (1984), Sparholt (1985) and Riget et al. (1986). On the western side of the Atlantic, anadromous forms of charr are found as far south as Gander River in Newfoundland at latitude 49°N (Johnson 1980). In Norway, the anadromous form occurs on Spitsbergen and along the Norwegian coast south to 65°N (Jensen 1981). Therefore, one problem in management of charr stocks arises from the complexity and variation in size and morphology of the species.

Yield and harvesting experiments

Records of charr harvest in different lakes show that the harvest may vary greatly depending on lake size, lake productivity, fishing effort, competition with other fish species and predation (Table 1). Due to the short term records of fishing and restricted fishing intensity, no records of the maximum sustainable yield (MSY) exist.

Table 1. Harvest of Arctic charr in different lakes, change in surface is due to hydropower regulation.

Lake	Area (ha)	Change surface	Harvest kg/ha/yr	Yr	Reference
Tunhovdfjord	2,535	18.0 m	2.69	1961-80	Aass 1984
Pålsbufjord	1,950	24.5 m	1.83	1961-80	Aass 1984
Limingen	9,570	8.5 m	0.08		Aass 1984
Songsjøen	70	Natural	0.61	1968-84	Langeland & Jonsson 1990
Grønsjøen	163	Natural	2.75	1978-86	Kirkvoll 1987
Øvre Stavåtjønn	3	Natural	11.00	1979-84	Langeland 1986
Essand	2,730	6.6 m	0.7-1.7	1974-80	Jensen 1988
Nesjøen	3,870	23 m	4.7-9.8	1974-80	Jensen 1988
Takvatn	1,420	Natural	3.60	1984-88	Amundsen et al. 1993
Møkkelandsvatn	110	Natural	3.90	1990-93	Svenning pers.comm.
Foldvikvatn	100		3.00	1990-93	Svenning pers.comm.
Goulasjavri	240	20 m	3.00	1990-93	Svenning pers.comm.
Selbusjøen	5,788	6.3 m	1.70	1974	Langeland 1976
Keyhole	48	Natural	4.35	1962-66	Hunter 1970
Thingvallavatn	8,400	Natural	8.90		Kristjansson & Adalsteinsson 1984

In most recorded cases of harvest, the figures also include a reduction of biomass, which suggests that the sustainable harvest is lower than the amount of fish removed from the lake. Most of the lakes referred to are charr/trout lakes where both species compete for the same resources (Langeland et al. 1991). A general feature of harvest records is that sustainable harvest of charr in small oligotrophic lakes ranges between 2 and 3 kg ha^{-1}. In large, deep Arctic lakes the harvest is assumed to be lower or between 0.5 and 2 kg. The high yield of charr in Lake Nesjø and Icelandic lakes (see below) is outside this range. Yet, no studies have been performed to correlate yield of charr with environmental conditions, e.g. primary production. It seems justifiable to suggest that exceptionally high yields of charr are primarily caused by higher lake productivity.

Hunter (1970) estimated the standing stock of charr in Lake Keyhole in 1962 to be 43.5 kg ha^{-1}. During the years 1962 to 1966, 7,228 charr were removed from the lake. He belived that half of the stock could be removed once every 5 years, i.e. equivalent of 4.35 kg ha^{-1} (Table 1).

According to Kristjansson and Adalsteinsson (1984), the annual yield in Lake Tingvallavatn was 8.9 kg ha^{-1} (Table 1). On average, charr lakes in Iceland yield annually 10-15 kg, with better lakes yielding up to 45 kg ha^{-1} (Kristjansson and Adalsteinsson 1984).

The annual yield in large hydropower reservoirs varies greatly from 0.02 kg in Lake Limingen (Aass 1984) to 9.8 kg ha^{-1} in Lake Nesjøen (Jensen 1988). The differences between reservoirs were due to natural conditions, regulation height of the lake surface and management practice (Aass 1984). The Nesjø reservoir was made in 1970 impounding 3870 ha of new land which resulted in good conditions for fish productivity. Subsequently, high yields were recorded in this lake (Jensen 1988). Until 1976, the biomass of charr per net in Lake Nesjø was 4-6 times higher than normal in Norwegian lakes. Lake Selbusjøen is steep-sided and deep, with a maximum depth of 204 m and yields a low annual harvest of about 1.7 kg ha^{-1} (Langeland 1976).

Grønsjøen is a shallow lake with an area of 163 ha. The mean annual yield in the lake over a 9 year period was 2.75 kg (80%) charr and 0.66 kg (20%) brown trout, or a total of 3.4 kg ha^{-1} (Kirkvoll 1987). Lake Songsjøen with an area of 70 ha, has been harvested over a 17 year period yielding 2.3 kg (79%) of brown trout and 0.61 kg (21%) of charr, or a total of 2.9 kg ha^{-1} (Langeland and Jonsson 1990). The reason for the difference in dominance ratio between charr and brown trout seems to be caused by environmental conditions related to water quality, lake productivity and morphometry. The mountain Lake Grønsjøen is a clear water lake suitable for charr. The lower lying Lake Songsjøen is a brown water lake with low productivity. Both lakes offer good spawning areas for charr and trout. Although the fish yield is similar for both lakes, ca. 3 kg ha^{-1}, the population dominance of the species seems to depend on their ability to utilize different food resources. In a harvesting experiment lasting over 6 years in the small (4 ha) mountain lake Øvre Stavåtjønn, most of charr removal was due to biomass reduction (Langeland 1986). The mean yield for the last three years was 6.0 kg, or slightly less than the hypothesized estimate of annual surplus production of 7 kg ha^{-1} that could be harvested.

The larger Lake Takvatn, of 1,420 ha, was intensively fished using funnel traps (Amundsen et al. 1993). During the period 1984-89, a total of 666,000 charr were removed amounting to an annual mean of 3.6 kg ha^{-1} mainly due to a biomass reduction to less than 30% of the initial value. The effects of the fishing program were substantial and positive, with a shift in age structure towards younger fish and increased individual growth for charr older than 4 years. The experiment in Lake Takvatn showed that removal of substantial numbers of small charr in a large lake is feasible using funnel traps baited with fish roe or casein (Amundsen et al. 1993).

In the Lakes Møkkelandsvatn, Foldvikvatn and Goulasjavri, funnel traps were used to remove charr (Svenning pers. comm.). During the period 1990-93 annual removal of charr was estimated to be 3.9-3.0 kg ha^{-1}, mainly due to a biomass reduction (Table 1).

Commercial harvests of anadromous charr are well known from the Northwest Territories and Labrador, Canada (Kristoffersson et al. 1984, LeDrew 1984). In the 1980's, the commercial harvest of anadromous charr in Cambridge Bay was largest in the Northwest Territories, representing more than 50 tonnes annually (Kristoffersson et al. 1984). In comparison, the annual landings of charr in Labrador after 1977, exceeded 200 tonnes, accounting for more than 50% of the total commercial production of Canadian charr in 1980 (LeDrew 1984). It is difficult, however, to calculate anadromous harvests on a unit basis of lake surface area. This is because sea charr migrate to feeding grounds in coastal waters and remain 6-8 weeks during the summer before migrating back to the lake (Mathisen and Berg 1968). There are few records of anadromous harvests from Norwegian waters. In a mixed stock of charr, the genetic difference between resident and migratory individuals often appears to be small or non-existent (Jonsson and Jonsson 1993). According to these authors, preference towards migration to sea instead of stationary behaviour probably depends on individual growth rate, or a physiological process like metabolic rate which is correlated with growth rate. Little attention has been paid to studying the ratio between migrating and resident parts of sea migrating stocks. Studies from Lake Kobbvatnet, northern Norway, indicate that anadromous charr may decline simultaneously with a great reduction in individual weight and increased number of resident charr. In Lake Kobbvatnet, the population of charr consists of a small fraction of sea charr, a small fraction of normal charr and a very high portion of small dwarf charr (Jensen and Larsen 1985). According to Jensen and Larsen, the reason for the high density of slow-growing charr is reduced food availability and fishing, disallowing charr to reach a size suitable for smoltification and migration. They concluded that intensive fishing on resident charr may increase the fraction of anadromous charr. Decades ago the situation was opposite, with a large population of sea charr and a small fraction of resident charr (Berg 1964). Before the mechanisms determining the partial migration of anadromous charr and the interaction with resident charr are identified, it is difficult to develop harvesting strategies for mixed stocks. However, intensive fishing on the resident part of the population seems advisable to increase the migratory fraction.

High density of charr in lakes has led fishermen and scientists to believe that productivity and maximum sustaniable yield is very high. However, studies on turnover rate of accumulated charr biomass or ratio of productivity to biomass, give low values in nearly 3 years, with a P/B-ratio approximately of 1/3 (Langeland 1986). Through intensive fishing, the turnover time may be reduced to 15 months. Calculation of charr harvest should be based on fish production per unit of time and not on the biomass temporarily present in a lake.

Common fishing gear and strategies

Gillnets, seines, traps, rods and lines, and trolling with baited line are common fishing gear and methods. Aboriginal people harvest spawning populations of anadromous charr at spawning sites in a rivers, lakes and estuaries using nets.

Harvesting in Norway is commonly a combination of gillnets and sport fishing using different gear. A lower mesh size is set for gillnets to protect young fish. In the 1950's, monofilament gillnets were introduced and greatly increased gillnet efficiency on specific sizes of fish, depending on the mesh size in use. However, this seriously affected larger mature charr which were fished to extinction. In such lakes, intense gillnet fishing does not permit the survival of larger piscivorous charr. A popular recreational activity during winter is icefishing. Fishing is carried out through a hole in the ice using a lure and hook coverd with live bait. This type of tackle catches most sizes of charr and is not as selective as other gear.

In the Cambridge Bay fishery of anadromous charr, nylon gillnets are used in estuaries and river mouths during the downstream migratory runs in early July and on upstream migratory runs in August and September (Kristofferson et al. 1984). Before gillnets came into use, the Inuit in Labrador used different types of leisters, spears and stone weirs in the rivers (LeDrew 1984).

The Sameh-people of northern Scandinavia fished the lakes in a rotational way which became a system of letting lakes lie fallow for periods of several years. This periodical harvest was basically due to their nomadic behaviour, moving with their reindeer herds from place to place to avoid overgrazing of lichens. The effects on the charr populations were usually positive and stunted charr populations rarely developed (Filipsson and Svärdson 1976).

Interactions with other fish species

The most important competitors and predators of charr seem to be whitefish, cisco, three-spined and nine-spined stickleback, brown trout, burbot, pike, and lake trout.

The strongest competitor of charr is the whitefish. This is due to both species having very similar habitat and niche requirements. Both species are able to utilize different food resources in littoral, pelagic and profundal areas. According to Svärdson (1976), whitefish is clearly dominant over charr, mainly due to its more efficient feeding on zooplankton. If charr are to survive sympatrically with whitefish, they must adapt as a deep-living population (Svärdson 1976). Intense fishing on whitefish is assumed to benefit sympatric charr populations.

Three-spined sticklebacks are able to utilize food in both littoral and pelagic habitats and can feed on small prey like zooplankton. Sticklebacks are able to live in populations with high densities. Therefore, they are considered a strong competitor of charr. In a fertilization experiment in Lake Langvatn, three-spined sticklebacks fed on similar prey to charr (Langeland 1982). Due to a strong reduction of zooplankton, the charr disappeared from the pelagic zone and decreased in density. Simultaneously, sticklebacks were recorded in pelagic waters feeding on smaller zooplankton. The results from this study indicate that the stickleback is a stronger competitor in exploitative competition than the charr due to higher feeding efficiency (Persson 1985). The utilization of pelagic habitat by sticklebach, however, is dependent on charr due to predator avoidance.

In the Northwest Territories, Canada, sympatric stocks of charr and lake trout occur in small lakes (Johnson 1976,1980). In Northern Quebec sympatric stocks occur more frequently (Benoit and Power 1978, Power and Gregoire 1978, Martin 1955). Johnson (1980) claimed that interactions between lake trout and charr are of great importance in determining present distribution of charr in North America. There, however, is considerable uncertainty as to whether predatory lake trout can drive charr to extinction in small arctic lakes. Lake trout is an aggresive fish predator, feeding on most fish species including charr and may greatly affect the population structure of charr stocks.

In Norwegian lakes, burbot seem to be an important regulator of charr density. Information from local fishermen indicates that lakes containing charr in sympatry with burbot, feature large individuals of charr. According to Filipsson and Svärdson (1976) burbot is an effective predator on charr and thus prevent stunting of charr stocks. This is well known by the Sameh-people of Scandinavia which introduced burbot in some lakes to improve charr size. These authors refer to several lakes with charr and burbot where the charr stocks attain a large individual size. The Lakes Snåsavatn and Selbusjøen were well known for their high quality charr a few decades ago. Both of these lakes have stocks of charr, brown trout and burbot. In Lake Selbusjøen, gillnet fishing of charr at spawning sites in autumn yielded high catches of burbot with stomachs full of charr roe. I suggest that predation by burbot is one important reason why stunted stocks of charr rarely have been reported in lakes containing burbot.

In addition to lake trout and burbot, brown trout are well known predators of charr. In several lakes investigated by L'Abée-Lund et al. (1992) the number of brown trout with fish in their stomachs ranged from 0 to 30.1 % (mean 5%). One exception was Lake Tunhovdfjord with

30% piscivorous individuals. According to Aass (1990), the piscivorous brown trout in this lake consume annually a charr biomass of 3-4 kg ha^{-1}, which is more than the average charr annual yield of 2.7 kg ha^{-1}. Brown trout are also an important charr competitor. Langeland et al. (1991) showed that the habitat and resource utilization of Arctic charr and brown trout was a result of selective differences and asymmetric competition, where brown trout are the dominant species in summer in contrast to the superiority of Arctic charr at low temperatures.

Piscivorous pike are commonly distributed in lakes in Arctic and temperate areas and coexist with charr in large and deep lakes. Huitfeldt-Kaas (1918) reported that charr disappeared from Lake Vaalmangen after the introduction of pike, and therefore considered pike the charr's worst enemy in shallow lakes. The same situation occurred in four lakes in Sweden reported by Filipsson and Svärdson (1976). Studies in lakes on the Kola Peninsula in 1993 revealed that charr were able to coexist with pike in deep lakes, but not in shallow lakes with maximum depth of 3 m (Langeland et al. 1994). The availability of refuges and morphometry of lakes are assumed to be of great importance for coexistence between charr and piscivorous fish like pike, burbot, lake trout and brown trout.

Recommended fishing strategy

As interactions between different forms seem to be predominantly environmentally determined (Hindar et al. 1986, Hindar and Jonsson 1993), it is necessary to know the basic mechanisms of intraspecific population structuring for the shift from one form to another. The ontogenetic shift from benthic habitat to pelagic seems to depend on the availability of zooplankton and the presence of predators. Therefore, it is necessary to decide which form is to be fished. One uncertainty is the management of mixed stocks of resident and anadromous charr. According to the literature, partial migration seems to be determined by environmental conditions,and growth rate has been identified as the most important factor (Jonsson and Jonsson 1993). In sockeye salmon, both fast and slow growers may become resident while medium growers migrate to the sea (Ricker 1938). Smoltification and migration may be an alternative strategy that depends on age at maturity and growth rate. Thus, there seems to be no simple solution to the management of anadromous/resident stocks.

The effects of fishing on charr will affect several important population dynamic processes. According to the dynamic pool model, four main processes have to be considered: recruitment, growth, natural mortality and fishing mortality (Pitcher and Hart 1993). In the following, the effects of four scenarios of management (Fig. 1) on these processes are discussed. The basic regime is the age structure of a population in steady state without year-class fluctuations (Fig. 1 A). These scenarios are based on an age-distribution following the cohort from birth to extinction in accordance with cohort-analyses used in modern dynamic pool models (Pitcher and Hart 1993). The main problem in managing charr, however, is the great variation in size due to density dependence and food choice. According to Ebenman and Persson (1988), size is probably the most important population characteristic of any organism. This certainly holds true for charr. Charr size will affect the type of prey it can eat, what predators will attack it, its physiology and energetics and its reproductive success. A challenge would be to develop a size-dependent tool for managing freshwater fish. So far, we need to look for relationships between size and age.

Sustainable harvest

Removal of individual charr from landlocked stocks by fishing implies population density changes. This is predicted to affect population regulating mechanisms which are density-dependent. Backiel and LeCren (1978) concluded that there are two main density effects operating on fish populations: mortality and growth. Mortality will be strongest in early life, particularly the larval and immediate post-larval stages. Density-dependent mortality may operate through intraspecific competition for a limited resource, such as food or space. Indirect effects of competition for food operate by lengthening the time taken for the fish to grow through a stage, making them vulnerable to predation. Stunting of charr may make them vulnerable to piscivorous fish or cannibals for a longer period. Johnson (1976) hypothesized that recruitment in some unexploited fish populations is regulated by older fish within the population. Older fish may suppress recruitment through predation or intraspecific competition for food or space. Removal of older and dominant age-classes of brown trout (Jensen 1977), brook trout (Donald and Alger 1989), whitefish (Healey 1980) and charr (Langeland 1986, Amundsen et al. 1993) have been associated with an increase in recruitment of younger year classes, supporting Johnson's hypothesis. Power (1978) challenged Johnson's hypothesis suggesting that the number of young fish and the ages in northern fish stocks are underestimated.

The second density effect, growth, becomes increasingly important as the fish ages (Backiel and LeCren 1978). Several exploitation experiments with brown trout (Jensen 1977), brook trout (Donald and Alger 1989), whitefish (Healey 1980) and charr (Langeland 1986, Amundsen et al. 1993) resulted in increased growth and a shift in the age-freguency distributions towards younger fish. The degree of increase in size at-age in whitefish from exploited lakes was proportional to the intensity of exploitation (Healey 1980). Thus, it is reasonable to expect that exploitation of older fish in a charr population will result in increased growth, and survival, particularly of younger fish, and a shift in age-distribution towards younger fish. Density-dependent effects on mortality are evident from shifts in a standard age-distribution (Fig.1 A, D b) towards younger charr (Fig. 1 C). This fishing strategy may be defined as **sustainable harvest** and emphasizes the removal of both immature and mature fish. I propose that a permissible upper bar mesh size of gillnet intended to protect larger charr from extinction should be adopted according to the conditions prevailing in different lakes. Experience from low productive Norwegian lakes indicates that an upper mesh size of 29 mm would be advisable (Langeland 1986, Langeland and Jonsson 1990). This mesh size is related to a fish size of about 29 cm (Jensen 1986).

Most charr populations have a high reproductive potential. The many stunted charr stocks indicate that reproduction is not limiting charr density in most lakes. There is little evidence for a relationship between spawning stock and recruits in freshwater fish similar to the models developed by Beverton and Holt and Ricker (Pitcher and Hart 1993). In the case of charr stocks, this is probably due to the excess of spawners satisfying the asymptotic level of recruitment.

Extensive studies by Johnson (1976, 1983, 1987) in the Canadian Arctic concluded that the landlocked undisturbed populations of Arctic charr had reached a **climax condition** characterized by large individual size, a high degree of uniformity, high accumulated total biomass, great mean age, indeterminate age-at-death and low incidence of replacement stock. After severe perturbation by fishing, it was shown that charr stocks returned to their state of least dissipation of energy without oscillation. The absence of oscilliation indicated an effective dampening mechanism in the population. Johnson's description of charr stocks seems to apply to other dense slow-growing populations with low production relative to biomass, e.g. the stocks prior to intensive fishing in Lake Stavåtjønn (Langeland 1986) and Lake Takvatn (Amundsen et al.1993). Amundsen et al. (1993) discuss the possibility that more than one steady state may develop within a lake if the initial conditions are sufficiently different, which is regarded as an expansion of Johnson's hypotheses. A consequence of Johnson's original hypothesis would be that the stock would return to the original configuration relatively quickly after cessation of fishing.

A management strategy of sustainable harvest has been proposed by Langeland (1986) for charr populations with high recruitment potential. Similar proposals have been made for brown trout by Langeland and Jonsson (1990) and Borgstrøm (1993). The strategy is based on the same causal population mechanisms experienced during experimental studies of stunted charr and brown trout stocks. Sustainable harvest of the smaller fish size in Lake Stavåtjønn substantially reduced population density and greatly increased the fraction of larger fish (Langeland 1986). The Lake Songsjøen experiment using gillnets of larger mesh sizes (Fig. 1D b), increased the stunting stage of both brown trout and charr populations throughout a 17 year harvesting experiment (Langeland and Jonsson 1990). The result was a population consisting of younger and smaller fish (Fig. 1D a). A further consequence of fishing with gillnets of large mesh size may be an accumulated stock of small and older fish. In the experiment by Borgstrøm (1993), reduction of the mature segment of the brown trout population caused increased recruitment of younger fish and no growth increase in mature fish. The intensive fishing program in Lake Takvatn using funnel traps caused a substantial increase in growth of charr >5 year, and a strong 1983-year class (Amundsen et al. 1993). The fraction of charr >250 g in Lake Takvatn increased from only one fish out of 1,133 recorded in 1980 to 22% in 1989.

Changes in growth rates caused by changes in food supply are also expected to influence age and/or size at maturity. Generally, fast growers mature younger and smaller than slow-growing individuals (Alm 1959). Grainer (1953) found that faster growing charr matured at an earlier age, but at approximately the same size as slower growing fish. Several other studies both experimentally (Nordeng 1983 for charr, Scott 1962 for rainbow trout, Bagenal 1969 for brown trout) and by field observation (Miller 1956, Healey 1975 and Donald and Alger 1989 all for whitefish) have reported that as food supply increased and fish grew faster, age at maturity decreased. However, Huitfeldt-Kaas (1927) proposed that hunger, which causes slow growth results in early maturation in salmonids (Arctic charr, brown trout, whitefish). In fish stocks where anadromous or cannibalistic behaviour results in substantial growth increase, maturity seems to be delayed. This has been shown for both charr (Nordeng 1961, Skreslet 1973 b) and brown trout (Jonsson 1989). Also in sympatric populations of charr, it has been recorded that fast-growing morphs may mature at older ages and larger sizes than the slow-growing morphs (Klemetsen and Grotnes 1980, Jonsson and Hindar 1982, Sparholt 1985, Jonsson et al. 1988). After removal of charr in Lake Takvatn (Amundsen et al 1993), maturation occurred at an older age and larger size (Svenning 1993). According to Svenning (1993), increasing growth rates for young fish would probably lead to early maturation, while growth increase for older fish may induce a delay in maturity. According to Jonsson and Jonsson (1993), slow growers may delay maturity until their growth levels off, or mature earlier if their fitness is thereby maximized (mature at the growth inflexion). Thus, changes in maturation caused by increased growth as a consequence of fishing can be expected. Changes in age-at-of first maturation may occur at either an earlier or later age, depending on the fishing strategy and resulting individual growth changes. Increased piscivory or cannibalism may likely increase the range in age-at-first maturation (Fig. 1 B).

This fishing strategy is in contrast with practical implementation and historical behaviour of fishermen who only want larger fish. Management practices today have adapted to this opinion by setting a lower limit of mesh size for gillnets and a lower limit of fish size. This practice is mainly based on management of brown trout, where recruitment is assumed to be a limiting factor for population density.

Sport fishery of predatory fish

As previously mentioned, cannibalistic or piscivorous behaviour of charr commonly occurs in most northern regions. Such lakes are characterized by a wide range of length- frequency distributions. Most of the lakes in northern Norway with large charr are in remote areas and are normally fished by handheld gear (Amundsen et al. 1993). They state that such lakes may be as stable as the stunted ones and concludes that more than one steady state may develop in the same lake if the initial conditions are sufficiently different and influenced by management. Use of coarse-mesh monofilament gillnets in easily accessible charr lakes will probably wipe out large charr, which in turn promotes the stunting stage of charr stocks (Nyman 1984, Filipsson 1987, Amundsen et al. 1993). Johnson (1983) mentioned that the removal of large, cannibalistic charr may create greater uniformity in the remaining stock. The results from the Swedish Lake Västansjön supports this theory (Filipsson 1987). Test fishing in 1983-86 indicated that total catch weight and average individual weight and length had increased after the ban of gill net fishing in 1983. In recent experiments with stocked piscivorous brown trout, positive results were achieved as predicted. Stocking a lake of stunted charr with piscivorous brown trout resulted in reduced population density and increased growth and mean length of charr after 63 weeks (Damsgård and Langeland 1994). In another stocking experiment with piscivorous brown trout, individual charr increased in length and condition, the population density was reduced, and the habitat use shifted to safer areas (Sandlund and Forseth 1995). L'Abée-Lund et al. (1993) found that segregation by size and age between pelagic and epibenthic charr appeared to be a result of a trade-off between feeding possibility and risk of predation. Introduction of piscivory fish in charr lakes will probably also induce changes in feeding behaviour. This may force prey to hide in less profitable habitats resulting in reduced growth rate. The prey size available for the predator is mainly determined by suitable refuges for prey and gape limitation of the predator (Damsgård 1993).

Based on laboratory and field studies, Amundsen (1994 a, b) concluded that cannibalism can play a significant role in population regulation of charr. The experiments showed strong individual specialization for cannibalism. Estimations from Lake Takvatn suggested that cannibalism could account for all the natural mortality among 1-4 year-old charr. Based on studies from Svalbard, Svenning (1993) also discussed the possible importance of cannibalism in population regulation and speciation in charr. Yet, quantitative evidence from nature that cannibalism plays a significant role in regulation of recruitment, population structure and density of natural charr stocks, is lacking.

Based on previous considerations a fishing strategy relying on **piscivory** as alternative to sustainable harvest is recommended (Fig. 1 B). Probably the most efficient way to harvest charr on a higher trphic level is to utilize the energy by other piscivorous species like the aforementioned brown trout and lake trout. However, the use of species not naturally present in the lakes may conflict with other purposes of nature conservation. Obviously, the annual yield will be lower in such lakes where piscivory is utilized rather than sustainable harvest directly aimed on the lower trophic level. Lakes with cannibalistic charr or other piscivory species have not been well studied. More knowlede about the stability of charr stocks is required before a proper management practice is established. At present, it is difficult to predict how many piscivorous fishes can be harvested to maintain a stable state within charr stocks. Yield of piscivorous fish eating charr is scarce. According to Martin and Olver (1980), the productivity of piscivorous lake trout is low (0.25-0.75 kg ha^{-1}). Expected yield of piscivorous fish eating charr would probably be less than 1 kg ha^{-1}.

Piscivorous or cannibalistic charr may be recruited from the entire population depending on the availability of suitable fish prey or larger invertebrate prey and critical size of niche shift to piscivory. These fish are very vulnerable to being removed by selective fishing gear. Measures should be taken to ensure the survival of piscivorous charr. A prerequsite for maintaining a stock with cannibalistic charr seems to be complete prohibition of using gillnets. Protecting predatory fish or cannibalistic charr will increase the capability to control recruitment and population density. Larger fish are stronger competitors in interference competition, however, smaller fish may be superior in exploitative competition (Persson 1985). I consider the presence of larger fish and a wide heterogeneous size structure important for benficial harvest of charr and a guarantee against stunting.

Summary management recommendations

Sustainable harvest

- sport fishing and commercial fishery using gillnets and funnel traps: an upper permissible mesh size for gillnets should be adopted according to the specific conditions in the lake
- give highest maximum sustainable yield relative to harvest of piscivorous fish
- fishing of immature fish is important
- intense fishing on resource competitors like whitefish
- protection of larger charr and piscivorous brown trout
- gillnet fishing on spawning grounds is selective on charr
- ice and sport fishing may be encouraged throughout all seasons
- fishing of resident charr probably increases the frequency of anadromous charr

Sport fishery of predatory fish

- sport fishing of piscivorous and cannibalistic charr
- gives low yield due to fishing at the tertiary consumption level
- protection of predatory fish and cannibalistic charr
- prohibition of gillnet fishing in small lakes
- bag limits of 1-2 large fish per person per day
- change fishing areas

Decisions regarding which strategy or combination of strategies to implement should be based on population size and age structure and potential lake productivity.

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Patterns of Diversity and Processes of Speciation in Arctic Char

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Abstract

The following questions are discussed: disputable questions of Arctic char systematics and speciation; phenomena of ecological variability; sympatric groupings - the level of divergence, the ways of their origin; the species boundaries; a complex species as a population system of the highest hierarchic level. Divergence levels in the genus *Salvelinus* and the structure of endemic species; the rate of speciation in Arctic char; the patterns of modern diversity. General conclusion is: the majority of Arctic char forms are not species in *statu nascendi*. The complicated structure does not necessarily reflect the process of speciation and represents a quasistationary state of the interrupted divergence that is able to reverse. For the classification of such a structure, the concept of a species-complex is more applicable.

Keywords: speciation, microevolution, species structure, char taxonomy, biodiversity.

Disputable questions of Arctic chars' systematics and speciation. Historical aspects, and the modern condition

The study of the systematics of char of the genus *Salvelinus* in Europe and North America began a very long time ago. It is possible to single out two main points of view which were prevailing over the entire period of study.

In the first approach, numerous char forms are considered as separate species. 29 species have been described in Europe, 15 in North America and 12 in Siberia and the Far East (Günther 1866, Jordan and Evermann 1896, Regan 1911, Kendall 1914, Berg 1948). The other approach is to view the diversity of forms as a reflection of the great plasticity of the genus and intraspecific variability. The latter point of view prevails in Europe, where the majority of authors reduce all previously described species to a few or even one, represented by diverse intraspecific forms, and in America as well, where 4-5 species only are considered independent (Behnke 1972, 1984).

The taxonomic position of char is the subject of constant ongoing discussions. They have become particularly lively in the last few years. The reason for this lies mainly in the fact that detailed studies revealed the existence of differentiated sympatric forms and the researchers faced the necessity of interpreting these facts. New methods have appeared revealing a high level of polymorphism and allowing ambiguous conclusions to be made. At the same time, the study of populations was continued from typological positions. All of this led to the revival of viewpoints of splitters. The number of species started to increase again (Viktorovsky 1978, Glubokovsky and Chereshnev 1981, Glubokovsky et al 1992).

The status of char populations in Russia is the subject of a controversy, which goes beyond the purely taxonomic issues and touches upon the problems of microevolution and systematics in a broad sense.

Some Russian ichthyologists consider that Arctic char are represented by many species (Viktorovsky 1978, Glubokovsky and Chereshnev 1981), up to 23. They claim that differences between species are very consistent and there are no intermediate phenotypes.

These views are in contradiction with the data on high variability and plasticity of char. In nearly all populations, intermediate phenotypes are present and it is often difficult to determine the status of concrete groupings (Savvaitova 1989).

Therefore, to understand the situation, it is necessary to look through the next main questions and, first of all, the phenomenon of ecological variability.

Ecological variability of Arctic char

The absolute majority of char species (for example in Siberia and in the Far East) has been described in violation of the taxonomic procedure, that is, regional situations alone have been taken into consideration, but not the overall situation throughout the range (Berg 1948, Viktorovsky et al 1978). For this purpose, the morpho-ecological properties of numerous char populations have been investigated from the whole range inhabited by the genus *Salvelinus* (Savvaitova 1989). The distribution patterns for the mean values of pyloric caeca and gill-rakers, the diagnostic characters most frequently used in the literature, have been analysed (Savvaitova and Volobuev 1978, Savvaitova 1989). Three morphotypes have been discovered and described as "malmoid", "alpinoid" and "arctoid" with minimum, medium and maximum values. The same morphotypes have been discovered and discriminated with the help of multivariate statistical analysis for 29 measures and 8 meristic characters (Michailova 1981). It turns out that all the variation within the char's phenons (in sense of Mayr 1969) can be reduced to these morphotypes. The char of each morphotype are ubiquitous, but they predominate in definite parts of the area where corresponding habitats are found. Thus the "alpinoid" morphotype is circumpolar but its predominant habitat is in Europe; the "malmoid" morphotype is found in the Pacific Ocean basin and prevails in streams and the "arctoid" morphotype is found on the Arctic coast of Siberia, North America, in the Alpine lakes of Europe and in the Baikal area - in deep water lakes with extreme conditions.

Morphotypes of Arctic char may be determined rather well on the basis of morphological characters. But individual variability in certain populations is so great that it is possible to find individuals with character values of all detected groups. Even in cases when obvious differences exist between morphotypes, they overlap in all characters. The char populations of one morphotype can apparently have different origins and ages. In some cases their ancestors are char of the same morphotype to which they belong themselves and in other cases these are char of another morphotype. Irrespective of the origin, the resulting phenotype can be similar (Savvaitova and Volobuev 1978, Savvaitova 1989).

Therefore, in different areas of the natural range under similar conditions, as a result of the manifestation of a homologous parallel variability, char phenotypes are formed that are similar in respect to individual features but not identical.

Char morphotypes should be viewed as non-taxonomic "adaptive types" analogous to those in humans (highland type, Arctic type, etc. Alexeeva 1986). They are predominant in certain habitats and can be found in different parts of the range where there are suitable conditions. They are manifestations of biological plasticity in response to the environment and provide balance between populations and the environment which is reflected in their morphology. Thus char morphotypes are phenomena of ecological variability.

Each morphotype includes different ecological forms. Ecological forms differing in their life history can be distinguished among them (anadromous, lacustrine, fluvial). Each includes groups differing in preferred habitats, spawning periods, spawning grounds, growth rates, time of maturation, colour patterns etc. The sympatric groupings confuse the picture even more (Savvaitova, 1976).

Sympatric groupings of Arctic char, and the level of divergence

Throughout the whole circumpolar range, one can find sympatric groupings characterized by different degrees of isolation. However, their interrelationships vary depending on different conditions.

In streams the isolation among groupings as a rule is not absolute and they are all part of the same population systems. For example in anadromous char flocks of the Kamchatka peninsula, dwarf freshwater males occur that reproduce together with anadromous fishes. These males retain throughout their life the morphology and colouring of young fish. They are benthophagous and occupy a niche similar to that of young fish (Savvaitova 1960, 1989). In certain situations (the rivers of the Kommandor Islands) a river grouping is part of the spawning flocks of the anadromous forms as well as the dwarf males. This river grouping is represented both by males and females. Anadromous form, dwarf males, riverine females and males reproduce at the same time on the very same spawning grounds (Savvaitova and Maximov 1975). The absence of absolute reproductive isolation among river groupings ensures survival in changing environmental conditions (Savvaitova 1976).

But other examples of more profound differentiation are known. Although no genetic differences were revealed, it was demonstrated that anadromous and resident char in Vårflusjøen (Svalbard) had established two discrete life-history strategies (Svenning 1993). The char from this lake seem to illustrate a case of an advanced split between resident and anadromous life history strategies in sympatry. This may be related to the long post-glacial period (45,000 years) that has existed in Spitsbergen.

The degree of isolation of sympatric groups in lakes varies. It depends on the size and depth of the waterbody, its age, trophic conditions, presence of spawning grounds. All these determine the evolutionary and taxonomic status of different char populations. In thermokarst lakes with their temporary links, conditions do not favour speciation; in isolated mountain lakes where conditions are much more stable, speciation usually leads to the emergence of comparatively stable groupings and some of them achieve a rather high degree of divergence.

Closely related sympatric small slow-growing forms and large relatively fast-growing cannibals can be observed in Lake Nordlaguna on Jan Mayen (Skreslet 1973). These groups are formed in the ontogeny of one generation.

Genetic divergence is absent between small and large sympatric forms in four unexploited lakes in Greenland (Sparholt, 1985). The two groups differed in feeding habits, growth rates, age of maturation and spawning periodicity. But they did not differ in the frequencies of the F- and S-serum esterase alleles. Small char recruit to the large char by entering a period of fast growth.

The char population in Tasersuaq (Greenland) is divided into three rather separate groups but there is evidence of transformation between them (Riget et al. 1986).

In Lake Thingvallavatn (Iceland) pronounced phenotypic and ecological differences exist between morphotypes of *S. alpinus*. There are no signs of interbreeding between pelagic and benthic morphotypes, which suggests reproductive isolation between them. Insignificant genetic distance between the morphs, however, indicates that segregation must have taken place recently, within the lake basin itself and is not yet completed (Sandlund et al. 1992).

The two morphs within each morphotype differ in life history characteristics. Planktivorous and piscivorous forms appear to develop from one morphologically homogenous group of juvenile fishes. These two morphs have practically identical allele frequencies. These morphs are two trophically specialized groupings but both can develop from each of the two parental types.

The relationship between the two benthic morphs appears to be of a different nature. They differ significantly in allele frequencies in polymorphic loci and in spawning behaviour and also in coloration and gill-raker number. The benthic morphs can be reproductively isolated because of differences in spawning time and assortative mating.

Specialization towards cannibalism can be a force creating and sustaining the two ecological morphs of char from Lake Arresjøen (Svalbard). The char in Arresjøen have different life history strategies, and due to long postglacial isolation, they have evolved into genetically distinct morphs. The two char morphs from this lake are reproductively isolated, which is also in accordance with the observed differences in S-serum esterase alleles and Mdh 4,5 (Svenning's presentation at the symposium). The observed genetic differentiation between the two morphs can even represent an early stage of sympatric speciation (Svenning 1993).

In some lakes of Norway and Sweden, sympatric groups of Arctic char are reproductively isolated and may be considered as sibling species (Nyman 1972, Klemetsen and Grotnes 1975, Nyman et al. 1981, Hammar 1984, Klemetsen 1984). But two distinct spawning groups of char from Ellasjøen, Bear Island, could not be separated by serum esterase analyses. And in this case, according to the authors, the first step of sympatric divergence is observed (Klemetsen et al. 1985).

Pelagic and benthic char from Loch Rannoch, Scotland are genetically distinct (Gardner et al. 1988, Walker and Greer 1988).

There are at least four races of char in Windermere, the largest natural lake in England. The North and South basins of the lake each contain two distinct races that spawn in autumn and spring respectively. In addition to genetic differences and differences in growth rates, the two races differ in some morphological characters (Frost 1965, Child 1984, Partington and Mills 1988, see also Elliott and Baroudy 1995).

Different stages of sympatric divergence are observed in char of the Kola Peninsula, Taimyr Peninsula, Lena River delta, in Lake Labynkyr (East Siberia), in waterbodies of Chukotka, Kamchatka, Okotsk Sea coast (Savvaitova 1989).

Four endemic species of char were described in the waters of the Taimyr Peninsula: *S. tolmachoffi*, *S. boganidae*, *S. drjagini* and *S. taimyricus*. Two other forms live in the Norilo-Pjasina lakes-deepwater char and black lake char. In lake Ayan lives another dwarf char form. As a rule, many forms are sympatric. In different lakes, they usually appear independently. It is likely that the following are the base of the processes for the emergence of char forms in Taimyr: extended spawning season, differences in growth rate and time of sexual maturity. The divergence in type of food from the short vegetation period is revealed here to a lesser degree. Genetic divergence is observed between deepwater and large forms in some lakes of Taimyr in the frequencies of the Est-2 alleles.

In Lake Forelevoe (Lena River delta) two sympatric groupings differing in growth rate and time of maturity were discovered. There are lateral parr marks on the body of the small form. The large and small chars of Lake Forelevoe represent a single population. The process of the emergence of forms in this lake is in the early phase (Savvaitova 1989).

In Lake Labynkyr (Eastern Siberia) we found three forms of Arctic char classified as small, medium and large. These forms differed in various morphological and meristic characters as well as food habits and other ecological characters. When we evaluated the whole complex of characters together, we found a closer relationship between the small and medium forms than between each of them and the large form. Thus the three sympatric forms showed different levels of relationships. Maybe, the result of prolonged spawning activities and differentiation in growth rate are caused by a trophic polymorphism. The three forms of char are probably not reproductively isolated. Their spawning periods overlap and there were no great differences in meristic characters (Savvaitova, 1989).

In the Pegtymel Lakes (Chukotka) we also found three char groupings. The differentiation of the forms was made on the basis of a combination of external morphological characters and coloration. They were called the "long-headed", the "deep-bodied", and the "deepwater" char. The "deepwater" char was planktophagous, the "deep-bodied" char benthophagous, and the "long-headed" char carnivorous. As a consequence of different food, all forms demonstrated different levels of infestation rates of *Diphyllobothrium* spp. and different growth rates.

When comparing the sympatric char forms, we observe that they differ in a number of characters and they are probably reproductively isolated, especially the deepwater char. The long-headed and the deep-bodied char seem to be closer to each other and they possibly hybridize.

We may assume that all forms from this lake have had different anadromous or resident freshwater ancestors. We can also presume two ancestral populations - one which gave rise to the small deepwater char with a high number of gill rakers, the other to a large char with a low number of gill rakers. The latter population diverged into the long-headed and the deep-bodied forms in the lake itself. This divergence is not yet completed. It is also quite possible that all the char forms diverged sympatrically in the lake from one ancestral population on the basis of trophic polymorphism, different growth rates, spawning periods and spawning grounds. The last hypotheses is supported by the fact that the Lake Pegtymel char forms do not correspond diagnostically to any char form described previously by the main diagnostic characters (gill rakers, pyloric caeca and vertebrae) (Savvaitova 1991).

In Ueginskoje Lake (the continental coast of the Sea Okhotsk) the structure of the char population is represented by large and small dwarf groupings. The females dominate among the former and the males dominate among the latter. Both groupings complement one another and reproduce jointly. The differentiation of *S. neiva* into large and small dwarf groupings is probably due to insufficient food in this water body, the dwarf grouping occupied a niche of planktophagy and the large grouping became a benthophage and predator.

Two different forms live in Lake Nashikinskoe (Kamchatka) where they occupy completely different niches. Lake char live exclusivly in the lake, the small lacustrine-riverine char form prefers small rivers flowing into the lake. Besides morphological and ecological differences, these forms differ from each other in karyotype and in the results of hybridization of the thermostable fraction of DNA (Savvaitova 1989). The results obtained by different methods are evidence of reproductive isolation between char forms in this lake.

But the degree of divergence of different forms and populations of char on the Kamchatka peninsula may be different. It is possible to observe morphological differences of varying degree. There are no clear breaks in these populations where it would be possible to draw a natural boundary. A divergence in food, in spawning places and times are prerequisites for the emergence of forms.

There exist two approaches to the explanation of coexistence of sympatric char forms. Some authors believe that each of the now sympatric groups from one water body had a different ancestor and postulate repeated invasions separated by periods of allopatry. After invasion, each new grouping occupied a free ecological niche. Differences of now sympatric groups stem from the differences of ancestral populations (Svärdson 1979, Hammar 1984, Nyman et al. 1981, Viktorovsky 1978, Glubokovsky et al. 1992). The opinion of some other investigators is that the leading role in the divergence of sympatric groups belongs to ecological factors such as differentiation in feeding, growth rate, spawning grounds and spawning time (Frost 1965, Savvaitova 1976, 1989, Grotnes 1980, Klemetsen et al. 1985, Riget et al. 1986, Sandlund et al. 1992, Svenning 1993).

But isolation of sympatric forms in fishes does not necessarily lead to the emergence of new species. As Kondrashov and Mina (1986) demonstrated by computer simulations at early stages of speciation, it is nearly panmictic and dominated by morphologically intermediate specimens. Later on, extremes become more abundant and the distribution of specimens in the space of morphological (or other) characters becomes bi- or polymodal. Such structure, that is linked phenons which are distinguished on the basis of characters controlled by natural selection, can give rise to new species, but in other conditions can remain evolutionary stable for an indefinite time. There is evidence that structures consisting of two or more components are rather abundant.

It should be stressed that such structures are more often found in an unstable environment, for instance in Arctic or Subarctic regions, in mountain lakes or in temporary water bodies of deserts where fish communities are poor and there are vacant ecological niches.

Special attention should be paid to horizontal sequences of intermediate stages of speciation, as their study can help to reconstruct patterns of microevolutionary processes (Mina 1986).

We observed successive stages of sympatric speciation in two anadromous char forms from Chukotka. As the degree of their divergence is different in different parts of the range, it is impossible to determine their status precisely. Greater morphological distances between allopatric populations of the same form than between sympatric populations of the two forms is evidence of their sympatric origin (Savvaitova 1989).

One of the most interesting examples is represented by large and small char from Transbaikalian lakes. Small char feed on plankton, large ones are partly piscivorous (so differentiation of the two forms here depends on the presence of the niche of planktophagy). In different lakes of this region, different stages of speciation can be observed from groups emerging in the ontogeny of one generation and groups spawning together - to reproductively isolated groups (Savvaitova 1989).

Nevertheless, throughout the range of the whole group, reproductively isolated forms are the most frequent. They differ from one another and from analogous groups from other regions. Some of these forms can probably be considered as separate species. Such are sibling species from some Kamchatka lakes, melanistic stone char from Kamchatka river, *Salvelinus elgyticus* from Lake Elgygytgyn in Chukotka. Sometimes divergence can be more profound. Not long ago in Lake Elgygytgyn another char was found and described as representative of a new genus *Salvethymus svetovidovi* (Chereshnev and Skopetz 1990).

Thus regarding various examples of interrelated sympatric ecological groups of char in nature, it is possible to find different stages of speciation which, when properly ranked, parallel the temporal sequence of stages of phenetic divergence during sympatric speciation.

When the probability of assortative mating increases (shifts in spawning time and spawning grounds, growth rate, maturation, behaviour etc.), sympatric forms can give birth to new species. In other words, the main role in sympatric speciation is played by reproductive isolation which follows displacement in ecologically important characters subjected to disruptive selection. The latter leads to polymorphism in natural populations. Assortative mating on the one hand reinforces the effect of selection, on the other, it itself can give impetus to divergence and speciation, though notin every case are new species formed. I would like to stress that not every case of sympatry should be treated as the result of sympatric speciation. Processes of sympatric and allopatric divergence complement each other.

The problem of the criteria of species boundaries and the evaluation of taxonomic rank of Arctic char

Each time the researcher comes across sympatric populations of char there is a question of how to interpret the differences observed and how to assess the taxonomic rank of these groupings?

The problem is really complicated. Groupings that are similar in ecology, coloration and morphology exist in many parts of the range. At the same time there are no absolutely identical populations. They can certainly differ from one another and are often reproductively isolated from neighbouring groupings.

This is situation which was depicted by E. Mayr as "nightmare for systematics, paradise for the evolutionary biologist" (Mayr 1947).

In this situation, the description of new species can result in a classification of char that will be impossible to use. This will be a return to those days when a new species was described from each water body. Such an approach to the solution of the char problem is incompatible with the biological concept of species. With all its merits, the biological concept of species also has faults. In particular the criteria for interbreeding and reproductive isolation are not comprehensive. There are a number of known cases when interbreeding between good fish species results in viable offspring (Gritzenko 1970, Berst et al. 1980).

One should agree with Mayr (1969) that many populations may be found in nature that have passed only part of the way leading to species status. It can be difficult to apply the biological species concept to them. An objective definition of species boundaries is impossible in a multivariate system. Natural populations in contact zones often behave with respect to one another as good species, until their habitats are destroyed. Isolating mechanisms for species in *statu nascendi* are not yet completely formed. Species level is reached after the speciation process becomes irreversible. However it is often impossible to determine whether a species has reached the irreversible stage. Refinement of isolating mechanisms in different populations may occur at varying rates. Therefore when their natural habitats overlap, species can be isolated in some regions, but cross easily in others. Species are populations divided by gaps, but not every gap gives the right to give an isolated population species rank. Cases are known when most diverged populations reach the species level. They do not breed in sympatry but are connected by a chain of populations overlapping in all characters. *S. alpinus sensu stricto-S. malma* could be an example of such a distribution if one could prove species isolation of the extreme members of the series. In the case of sympatry, the situation becomes even more complicated. Separation of species, as a rule, becomes impossible and not even necessary since in not all cases can the various forms of adaptive polymorphism be viewed as the initial stages of sympatric divergence.

Besides, different systems of characters evolving at a different rate are used for identification of char. It is well known that differentiation in life history precedes morphological differentiation, the latter preceding genetic differentiation. There can be no strict correspondence between the degree of phenotypic and genetic divergence as phenotypic variability includes both genotypic and paratypic components.

This situation points to a lack of clear species criteria. The boundaries between species and forms prove to be blurred in a number of cases and this reflects the situation in nature. Arctic char is a complicated complex of forms of different levels of isolation, beginning with groupings that appear each time in the ontogeny of a single generation and ending with sibling species or phenothpically well distinguished species. Besides, zones of intergradation can exist between different forms.

Bearing in mind the evolutionary taxonomic situation described above, we tried to determine the status of Arctic char.

A complex species as a population system of the highest hierarchical level

Regarding high variability of Arctic char groupings, their complex interrelations, and the presence of intermediate phenons, we propose to unite all Arctic char in one superspecies - *Salvelinus alpinus* complex. My point of view is that the complex of Arctic char from various Holarctic water bodies is a population system of the highest hierarchical level. Moreover, it can be viewed as both a superspecies and a syngameon since it unites allopatric and sympatric semispecies and species. Such systems were called by Mina (1986) full species.

This complex is represented by three morphotypes, each of them being characterized by a certain set of adaptive traits. Representatives of one morphotype can include groupings varying in the degree of differentiation. Within the boundaries of the *S. alpinus* complex one can find groups of any level: 1) intraspecific level within the limit of one morphotype or intermediate between two morphotypes, 2) semispecific level and 3) specific level.

Beyond its boundaries are *S. leucomaenis*, *S. fontinalis*, *S. namaycuch* and possibly *Salvethymus svetovidovi*.

Groups of different levels have different degrees of isolation. In some cases continuous variability was found and hiatuses between phenotypes lacking; in other cases sympatric forms were reproductively isolated. Depending on the point of view of the researcher, they can be regarded as species or ecological races.

This scheme of population structure of the "*S. alpinus* complex" can be defined more precisely, as newly examined char groups of any level can be included in it.

Such complex species can be also found in other groups of fishes inhabiting non-stable environments, mainly in high latitudes, for example in the genera: *Brachymystax*, *Coregonus*, *Gasterosteus*, *Oreoleuciscus* and others (Reshetnikov 1980, Mina 1986, Zuganov 1991). It seems probable that such hierarchical systems of groupings are characteristic of extreme environmental conditions.

Divergence levels in the genus *Salvelinus* and the structure of endemic species

A group of char species exists in the genus *Salvelinus* where a different stage of subdivision is observed. The following are included in this group: the western Pacific *S. leucomaenis*, a predominantly anadromous form, the western Atlantic anadromous, riverine and riverine-lacustrine *S. fontinalis* and the American lake char *S. namaycush*. No one doubts their specific status and the definition of separate individuals is not difficult.

The structure of endemic species is much simpler. Throughout most of its range, *S. leucomaenis* is monomorphic and represented by an anadromous form, though one population of a resident form is known in Lake Chuktcha (Tauj River basin near Magadan). Towards the south of the natural habitat, the occurrence of dwarf freshwater males increases in populations of anadromous forms. They are noted on Sakhalin Island and in the Southern Kuril Islands (Savvaitova 1989).

In some waterbodies of Kuril Islands, the differentiation into two seasonal groups is observed. These groups differ in growth rate and spawning periods. A freshwater form of *S. leucomaenis* lives in the south of the area in Japan and apparently in the lower reaches of the Amur river and Primor'ye (Loftus 1958, Savvaitova 1989).

S. fontinalis has freshwater and anadromous forms that are characterized by a significant variability in their morphological features.

S. namaycush is a lake form. A deepwater lake grouping *S. namaycush siscowet* occurs rarely. Lacustrine-riverine populations are also known (Savvaitova, 1989).

The structure of endemic ancient char forms from Elgygytgyn Lake (the age of the lake is over one million years) in Chukotka is likely to be much simpler. This species is adapted to definite narrow niches in the lake (Chereshnev and Skopetz 1992).

So the genus *Salvelinus* is represented by species differing in their size and composition that are on different levels of their evolution.

The rate of speciation in Arctic char

According to Cavender (1980), the oldest known fossil *Salvelinus* found in northern Nevada is at least ten million years old. The affinity with recent North American taxa indicates that at that point, divergence and dispersal of the major evolutionary groups of char had already taken place. Thus, at least the basic distributional pattern of *Salvelinus* that we see today over the North Pacific basin had probably taken place millions of years prior to the first glaciation (Cavender 1980). This is likely to be the case even though the distribution of modern taxa such as *S. malma* and *S. alpinus* was greatly influenced by glaciation.

According to Benke (1972) the divergence of the common ancestor of American *S. alpinus* and *S. malma* took place not later than the Pliocene. Perhaps the divergence of *S. leucomaenis* also took place at that time. It is suggested by their highest chromosomal number among chars (2n 84-86).

The recently described *S. svetovidovi* from lake Elgygytgyn in Chukotka is also considered to have a remote origin close to the Pliocene origin of the lake itself (Chereshnev and Skopetz, 1992, Glubokovsky et al. 1992). On the other hand, this species has the lowest chromosomal number among salmonids (2n 56) which according to Glubokowsky et al (1992) is inoculation of a high rate of evolution of its high karyotype.

However Alekseyev and Power (1995) consider *S. svetovidovi* to be a paedomorphic form, many of its unique features being the result of retardation of somatic development. Other manifestations of this phenomenon are low growth rate and long life span (up to 30 years). Thus, the paedomorphic nature of *S. svetovidovi* indicates that this cannot be a very primitive form, but a derived form which is in concordance with karyological data.

Primitive char species are as a rule characterized by monomorphism and low rate of speciation. Dispersal of Arctic char and formation of their present population structure took place mainly in the Holocene and was strongly influenced by glaciations. This process was characterized by a high speciation rate, however only in a few cases, it resulted in the formation of new species.

Conclusions

1. It is difficult to put in stable formula of the eternally changing essence of a species.
2. The modern evolutionary taxonomic concept (concept of biological species, subspecies, syngameon, taxonomic species) cannot explain convincingly the situation in the *S. alpinus* complex.
3. Arctic char as a whole is a population system of the highest hierarchical level. Different populations of this system are found at different stages of genetical and phenotypical isolation.
4. Most of the Arctic char forms are not species in *statu nascendi*. Often the complicated species structure does not necessarily reflect processes of speciation and represents a quasi-stationary state of an interrupted divergence that is able to reverse.
5. Such complex structure of species has an adaptive significance and it enhances their homeostasis in the oscillating environment under extreme conditions. It is rather common in other groups of fishes at high latitudes.
6. Various factors can lead to the formation of complicated intraspecific systems, especially trophic polymorphism and also a discrepancy in spawning grounds and spawning seasons.
7. The conception of the species-complex is more applicable for the classification of such a structure.

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The Ecological Parasitology of Charrs: Relationships Between Parasites and Food Web Structure in Northern Lakes

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Abstract

Research on the ecological parasitology of charrs requires information from the fields of fisheries biology, limnology and parasitology. This paper illustrates how parasitological studies on *Salvelinus* species can contribute to the understanding of northern lake ecology and fish foraging behavior. Charrs occupy a central position in the food webs of northern lake ecosystems, functioning as predators on other fish (e.g. *Salvelinus namaycush*), as benthic foragers (e.g. *S. fontinalis*) or as pelagic feeders and opportunists (e.g. *S. alpinus*), niches which shift in response to intraspecific and interspecific competition. Data on charr parasites reflect food web interactions and provide better long term measures of niche relationships than do stomach content analyses. In lakes where *S. alpinus* occurs at the top of the food web, long-lived parasites may accumulate in host fish and cause morbidity and mortality. Occurrence and abundance of charr parasites can be related to factors such as lake morphology, physicochemical characteristics and the composition of fish and invertebrate communities. Experimental stock depletions in densely populated charr lakes can alter invertebrate prey populations and parasite infection rates, yielding new information on the regulation of charr foraging behavior and parasite transmission.

Keywords: Arctic charr, *Salvelinus alpinus,* parasites, food webs, northern lakes.

Introduction

It is of fundamental importance to understand ecological factors influencing the transmission of parasites to northern fishes. To achieve progress in such research, it has been informative to place the quantitative observations of parasitologists together with detailed studies on fish populations and their habitats. Such an endeavor ideally represents a synthesis of analytical work in limnology, fisheries biology and parasitology, but there are few instances where findings from these interrelated fields have been put to use to convincingly account for patterns in fish parasite abundance. Some of the progress achieved is covered in this selective review on parasites of charrs in northern lakes.

A primary objective of this paper is to describe how the occurrence and abundance of parasites in Arctic charr (*Salvelinus alpinus*) and brook charr (*S. fontinalis*) can be related to structural features of lake food webs. This begins with an overview of the factors which shape parasite transmission in northern lakes, using examples based on *Salvelinus* species, followed by three "case studies" from northern Canada. The first delineates basic food web relationships between the fish and their parasites, the second describes changes in parasite transmission following fish stock depletion, and the third indicates how data on charr parasites can measure the extent of specialized feeding behavior within a population. A concluding section suggests some new areas for investigation.

Lake characteristics in relation to parasite transmission

General trends for northern lakes

There are considerable differences in the occurrence and abundance of helminth parasites found in charr populations living in lakes throughout the circumpolar north. However, there are broadly recognizable patterns within this heterogeneity, based on quantifiable factors such as the physicochemical and biological properties of the lakes.

A number of features of northern lake ecosystems directly affect parasite transmission to charrs (Table 1). The food webs of northern salmonid lakes generally contain fewer species than do lakes at lower latitudes, and exhibit a higher degree of seasonality. Fish population structures tend to remain stable over time if not disturbed by human activities, and the lakes exist as relatively closed systems with few bird and mammal predators. The small number of fish species, predominantly charrs and other salmonids, display opportunistic feeding behaviors and live for a comparatively long time. Their parasites are primarily transmitted by the food web and most are capable of infecting a variety of northern fishes. Because charrs function as top predators in many such lakes and exhibit low mortality rates, they can accumulate parasites in much the same manner as mercury and other heavy metals are concentrated by the food chain.

Table 1. Characteristics of northern lake ecosystems and their fish and parasite faunas (source: Curtis 1988).

1. Food Web Characteristics
    - Simplicity (few species)
    - High degree of seasonality
    - High degree of stability
    - Relatively closed system

2. Fish Host Characteristics
    - Few, closely related species
    - Opportunistic feeding behaviours
    - Low natural mortalities

3. Parasite Characteristics
    - Transmission predominantly via food web
    - Low host specificity
    - Low mortality in fish host

Previous authors have attributed a number of additional factors as being important to the formation of fish parasite faunas in aquatic ecosystems. Among these are zoogeographic considerations such as the ranges of host fish (Price and Clancy 1983), the relative isolation of lakes (Kennedy 1977) and the presence and abundance of intermediate hosts (Dogiel 1961). Other suggested factors include physical and chemical characteristics (Kennedy 1978) as well as the mix of co-occurring fishes within the lakes (Leong and Holmes 1981). All such variables can be relevant for northern charr lakes, in which food web interactions among fish species can also play a dominant role in altering parasite transmission (Curtis 1982).

Temperature, calcium ion concentrations and digeneans

Restrictions in intermediate host occurrences provide some of the most obvious examples of physical factors affecting parasite transmission to charrs. In Arctic Canada, this point is clearly illustrated by the limits to mollusc distributions imposed by low temperature, even where calcium concentrations remain adequate for shell formation. No digenean trematodes are found in the Canadian Arctic Archipelago above the Northwest Passage. On southern Baffin Island Arctic charr are infected by *Crepidostomum farionis*, for which the fingernail clam (*Pisidium*) serves as an intermediate host, and on the continental mainland the eye fluke (*Diplostomum spathaceum*) hosted by Lynmaeid snails, appears together with *Crepidostomum* in many populations of Arctic charr, Lake charr (*S. namaycush*) and brook charr. Among the lakes of northern Quebec *Diplostomum* exhibits a patchy distribution in brook charr and other susceptible fish. Charrs from lakes associated with drainage basins overlying calcareous rock (dolomite) characteristically are infected by the parasite, while fish from other lakes overlying noncalcareous strata (e.g. Canadian Shield) are typically uninfected. Thus the occurrence of the parasite from lake to lake can be determined by examining detailed geological maps (Curtis and Rau 1980).

Intermediate host presence and parasite occurrence

In addition to the examples cited above are other cases where the presence or absence of charr parasites depends upon intermediate host occurrence. For example, Arctic charr feeding upon *Mysis relicta* acquire the swimbladder nematode *Cystidicola stidmatura*, but *Mysis* and therefore *Cystidicola* are limited in Arctic Canada to lakes comparatively near sea level. Similarly, the acanthocephalan *Echinorhynchus lateralis,* which requires amphipods as intermediates, is not found in areas of the Canadian Arctic Archipelago and Greenland where amphipods are rare or absent (Due and Curtis 1995).

In each instance the presence of parasites in charr from a given lake demonstrates the existence of the required invertebrate intermediate hosts, even through the invertebrate may not have been otherwise sampled or detected in fish stomach contents. Such major differences in intermediate host occurrences profoundly affect parasite faunas in charrs throughout the Canadian Arctic (Table 2). In far northern lakes such as Char Lake on Cornwallis Island and Lake Hazen on Ellesmere, Arctic charr are infected by a depauperate fauna containing only parasites which have copepods as intermediate hosts (e.g. cestodes of the genera *Diphyllobothrium*, *Eubothrium*, *Cyathocephalus*, and *Proteocephalus*, and the nematode *Philonema*), or parasites having direct life cycles (e.g. the monogenean *Tetraonchus*, and the parasitic copepod *Salmincola*). These two lakes lie beyond the northernmost range of molluscs, and contain no digeneans (*Diplostomum, Crepidostomum, Phyllodistomum*). Arctic charr from southern Baffin Island are infected by the digenean *Crepidostomum,* transmitted by bivalve molluscs, while charr from northern Quebec, situated within the range of other molluscan intermediate hosts, are additionally infected by *Diplostomum* and *Phyllodistomum*. The northern Quebec charr are also parasitized by *Echinorhynchus lateralis* due to

Table 2. Occurrences of some common parasites in Arctic charr from lakes at various locations in northern Canada. Sampling sites are as follows: Lac Kitturiak in northern Quebec (Bérubé and Curtis 1986), Shona Lake on Baffin Island (Curtis 1980), Char Lake on Cornwallis Island (Beverley-Burton 1978, Curtis, unpublished data), Lake Hazen on Ellesmere Island (Curtis, unpublished data).

Parasite	Northern Quebec	Baffin Island	Cornwallis Island	Ellesmere Island
Diplostomum spathaceum	*			
Phyllodistomum limnosa	*			
Crepidostomum farionis	*	*		
Cyathocephalus truncatus	*			*
Diphyllobothrium ditremum	*	*	*	*
Diphyllobothrium dendriticum	*	*	*	*
Eubothrium salvelini	*	*	*	*
Proteocephalus sp.	*	*	*	*
Cystidicola stigmatura			*	
Echinorhynchus lateralis	*			
Philonema agubernaculum	*	*	*	*
Salmonicola edwardsii	*	*	*	*
Tetraonchus alaskensis		*		

the presence of suitable amphipod intermediate hosts.

The geographic range of host fishes

It has been reported that fish species having a large geographic range tend to harbor more parasites than fish with more limited distributions (Price and Clancy 1983). However, when we test this relationship with data for charrs occurring in North America it is evident that an inverse pattern occurs, with the charr species having the largest geographic range (Arctic charr) exhibiting the most restricted parasite fauna while the charr species with the smallest range (brook charr) having the richest parasite fauna (Table 3). Clearly, in the case of these charrs the latitude is more important than distribution range. Arctic charr, with the most extensive geographic distribution, occupy comparatively simple northern ecosystems containing fewer fish parasites. Brook charr, which extend into lower latitudes than the other *Salvelinus* species, inhabit lakes with many parasite species that they may share with other coexisting fishes, as elaborated below.

Efects of the other members of the fish community

Work by Leong and Holmes (1981) on fishes of Cold Lake, Alberta, demonstrated how parasite populations can be maintained by several coexisting fish species. Taxonomic affinities and the relative population sizes of coexisting fish are important in establishing the magnitude of this exchange. As an example one may consider parasites of three charr species from northern Canada (*S. alpinus*, *S. fontinalis*, *S. namaycush*) plus lake whitefish (*Coregonus clupeaformis*), three-spine sticklebacks (*Gasterosteus aculeatus*) and nine-spine sticklebacks (*Pungitius pungitius*). Jaccard indicies (Table 4) indicate a high degree of parasite sharing among the charrs, and even some degree of sharing among phylogenetically unrelated fishes (e.g. sticklebacks and charrs).

How feeding interactions affect parasite transmission

A fish feeding study in northern Quebec (Fraser and Power 1984) is highly informative in illustrating how food web partitioning can affect parasite transmission among charr species. The investigators compared two Arctic charr populations, one coexisting with *Gasterosteus* while the other occurred with lake charr and brook charr. In the first population the Arctic charr fed predominantly on zooplankton and insects when small and then switched to feeding on *Gasterosteus* when larger. As a result, these fish were highly infected by the larval cestodes *Diphyllobothrium ditremum* and *D. dendriticum*, which are transmitted to fish which consume copepods or *Gasterosteus*. Charrs which lived

Table 3. Numbers of metazoan parasite species found in charr species from northern North America in inverse relation to their ranges of distribution, with Arctic charr (*S. alpinus*) ranked as having the broadest geographic range and brook charr (*S. fontinalis*) ranked as having the most restricted range (Source: Margolis and Arthur 1979).

Species of fish	Geographic distribution	Number of parasite species
Salvelinus alpinus	Circumpolar	23
Salvelinus namaycush	Northern North America	39
Coregonus clupeaformis	Northern North America	44
Salvelinus fontinalis	Northeastern North America	55

Table 4. Jaccard similarity coefficients comparing parasite faunas of northern Canadian charrs with one another and with coexisting fishes. Jaccard index=100 x c/a + b - c, where a=number of parasite species in one fish species (e.g. *S. alpinus*), b=number of parasite species in another fish species (e.g. *S. namaycush*), and c=number of parasite species common to both.

	Salvelinus namaycush	*Salvelinus fontinalis*	*Coregonus clupeaformis*	*Gasterosteus aculeatus*	*Pungitius pungitius*
Salvelinus alpinus	40.9	30.0	30.6	25.7	16.6
Salvelinus namaycush		32.4	29.0	17.6	18.8
Salvelinus fontinalis			21.5	20.6	16.1
Coregonus clupeaformis				11.8	9.1
Gasterosteus aculeatus					40.7

together exhibited interactive segregation such that the lake charr functioned almost exclusively as piscivores, while the brook charr fed on adult and larval insects and the Arctic charr mainly consumed gastropods, amphipods and zooplankton. Under these circumstances the Arctic charr were rarely infected by *Diphyllobothrium* spp., the presence of lake charr functioning to reduce their acquisition of the parasite. In turn, the lake charr appeared less susceptible to infection by *Diphyllobothrium* than Arctic charr, and rarely became heavily infected.

Relationships between parasites and food web structure

Case study 1 - Parasite transmission and lake morphology

In northern Quebec we studied two small lakes where fish and invertebrate faunas were the same but parasite transmission was strikingly different (Bérubé and Curtis 1986). The lakes contained Arctic charr and threespine sticklebacks as the only fish species. Both lakes have a surface area of less than 10 ha and are situated 1 km apart. Information from stomach content analyses indicated that the Arctic charr of one lake (Milugiak) had better feeding conditions than those of the other (Kitturiak). After ice breakup in spring, fish in both lakes predominantly consumed insect lavae and pupae, but by late summer charr in Milugiak concentrated on benthic foods (insect larvae, amphipods, molluscs) while those in Kitturiak fed limnetically upon insect adults and pupae at the water surface, copepods and sticklebacks. The better feeding conditions in Milugiak were reflected by higher growth rates for its Arctic charr population.

Because of the differences in prey consumption patterns, *Diphyllobothrium ditremum* infections were much higher in Kitturiak (prevalence=78%, abundance=27.7) than in Milugiak (prevalence=18%, abundance=1.2). We were drawn to the conclusion that the contrasting diets of Arctic charr in the two lakes could be satisfactorily explained by reference to lake morphometrics. Shoreline development is much higher in Milugiak (2.42) than Kitturiak (1.61), a feature which allows a greater development of the littoral invertebrate fauna in Milugiak, to the apparent advantage of its Arctic charr population. In Kitturiak, the littoral benthos appears to become depleted in summer such that Arctic charr must increase their levels of limnetic feeding and diminish benthic feeding, resulting in increased *Diphyllobothrium* transmission.

Case study 2 - Regulating parasite transmission by fish stock depletion

To further investigate relationships between charr parasite transmission and food web structure the population size of any component involved may be altered, thus perturbing the system and observing its response. We considered that intensive depletion of a brook charr population would enable us to gain insight into how food web structure regulates fish feeding behavior and parasite transmission. The working hypothesis was that benthic invertebrate populations would respond to fish stock depletion by increased production, and the residual brook charr stock would then exploit preferred benthic food items, causing a shift in the prevalence and abundance of parasites.

For the study we selected a 5 hectare lake in northern Quebec containing a dense population of brook charr (Albert and Curtis 1991). The only other fish species in the lake, lake chubb (*Couesius plombeus*), was comparatively rare. The first year of the four-year program involved a baseline assessment of the brook charr population and its parasites, at which time the stock was partially depleted by the removal of about 550 fish. From the end of the second sampling season and for the following two years, the entire catchable brook charr stock of approximately 1,200 individuals was annually removed from the lake, leaving at the end of each season a brook charr population in which very few fish were older than 3+ (Wright 1991, see Fig. 1).

As early as the first year of the experiment after the brook charr stock had only been partially depleted, there was a distinct shift in fish feeding and parasite acquisition (Albert and Curtis 1991). Increased *per capita* food consumption was indicated by higher growth rates and higher levels of parasite acquisition. Both the cestode *Eubothrium salvelini*, and the digenean *Phyllodistomum umblae*, became significantly more abundant. *Eubothrium* is transmitted by zooplanktonic copepods while *Phyllodistomum* is transmitted by benthic insect larvae (Odonata). We interpreted this to mean that the residual stock experienced enhanced feeding conditions in both the benthic and limnetic zones of the lake.

In subsequent years the residual stock experienced further growth enhancement (Wright 1991) and fed more on large benthic insect larvae (Odonata, Trichoptera, Ephemeroptera) and less on zooplankton. Consequently, *Eubothrium* decreased, while the abundance of parasites transmitted through the benthos (*Phyllodistomum, Crepidostomum*) remained high. Although planktonic crustaceans continued to be available as prey for the residual charr stock, the fish clearly preferred to feed upon the large larval insects which became available to them after a time lag of two years from the initial stock depletion (Fig. 2).

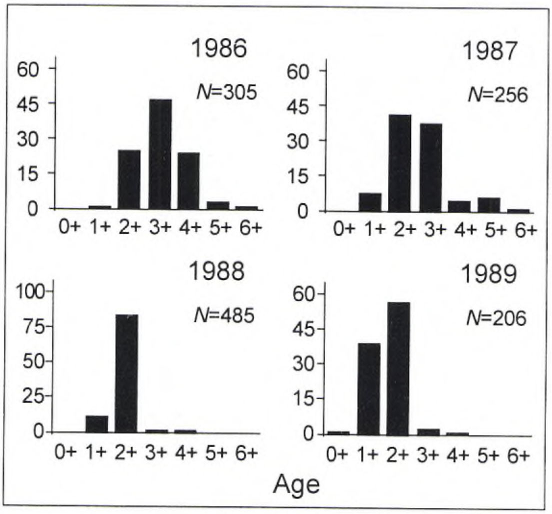

Fig. 1. Age frequency distributions for brook charr sampled from Matimaco Lake in northern Quebec during an experimental gill net depletion study in 1986-89 (Source: Wright 1991).

Our study showed the extent to which invertebrate prey populations and fish feeding patterns could be altered, and also gave evidence of the robustness of the parasite transmission links in the system. Parasite community changes and improvements in fish growth were clearly linked to the brook charr diets and patterns of intermediate host consumption.

Case study 3 - Parasite evidence for individual fish feeding behavior

In Arctic charr samples from the Kitturiak study site (Case study 1 above), we found interesting statistical associations between the fish stomach contents and helminth parasites (Curtis, in

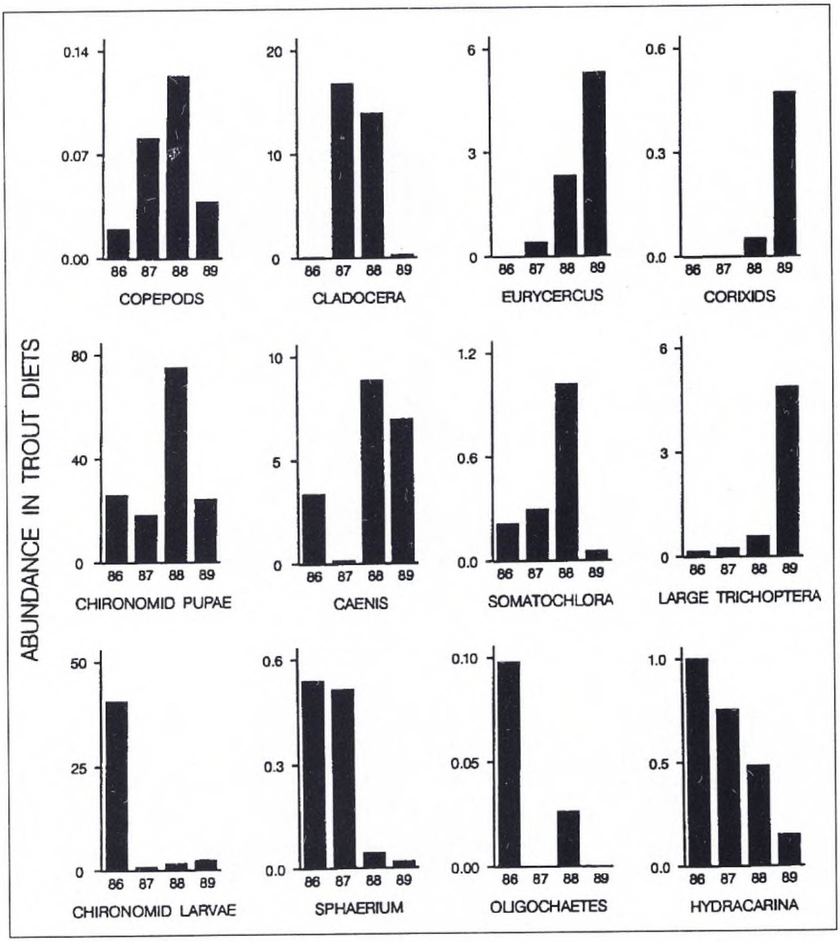

Fig. 2. Changes in the occurrence of invertebrate prey items in brook charr stomach contents during the 1986-89 stock reduction experiment at Matimaco Lake (Source: Wright 1991).

press). When a presence/absence matrix of food types *vs*. helminth parasites was analysed, a number of significant positive associations were found linking parasites to their intermediate hosts and, conversely, negative associations were evident between parasites and prey organisms which did not serve as intermediate hosts. Statistically significant "nonsense associations" were absent.

The data was further analysed to test the extent to which individualized feeding behavior might occur within the Arctic charr population. This was predicated on the view that if individual fish fed sporadically on a variety of prey items, depending only on chance and seasonal availability, these individuals would randomly acquire parasites and there would be no significant relationships between their stomach contents, which reflect feeding just prior to capture, and their parasites. Alternately, if individual fish tended to specialize on certain prey types, or specialize in limnetic or benthic feeding, one would expect there to be strong statistical associations between data on stomach contents and parasites. For the Arctic charr of Kitturiak, this latter explanation appears to coincide remarkably well with the true field situation.

For example, the occurrence and abundance of *Diphyllobothrium ditremum* is considerably higher in charr containing threespined sticklebacks (*Gasterosteus*) in their stomachs than is the case for charr with food in their stomachs but no evidence of sticklebacks remains (Fig. 3). There are similarly striking associations between fish feeding on copepods and the occurrence of *Eubothrium salvelini* and between fish feeding on amphipods and the occurrence of *Echinorhynchus lateralis* (Fig. 3).

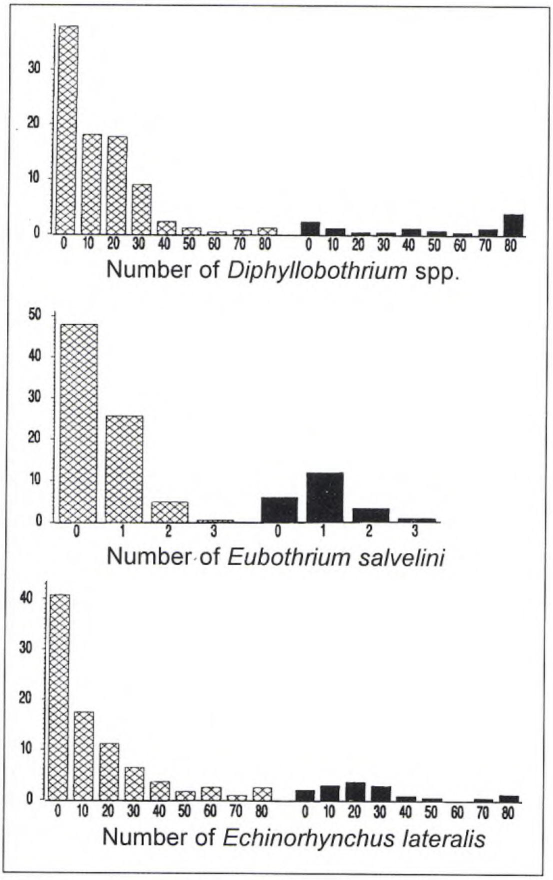

Fig. 3. Frequency percent distributions of parasites from Arctic charr of Lac Kitturiak which are feeding or not feeding upon various prey items serving as intermediate hosts. Cross-hatched histogram bars denote fish not feeding on the particular food item whereas solid black histogram bars denote fish feeding on the particular food item as follows: For *Diphyllobothrium ditremum* - copepods; for *Eubothrium salvelini* - copepods, for *Echinorhynchus lateralis* - amphipods. *Eubothrium salvelini* numbers were grouped into categories as follows: 0=0, 1=1-5, 2=6-10, 3=>10.

This approach of using parasites to indicate long term trends in feeding behavior may be seen as generally useful, because the residence time of parasites in their hosts can be measured in months and years whereas the persistence of prey items in fish stomachs is typically in the order of hours. Yet, on the basis of analyses of parasite and fish food data sets for sampling sites other than Kitturiak, I have found little additional evidence for the phenomenon observed. It is possible that the extremely restricted prey availability in Kitturiak, in concert with a dense Arctic charr population has given rise to rather special conditions that induce a higher degree of individual feeding specialization than is typical for allopatric charr populations. We must continue to seek and analyse data from other areas to determine the extent of this interesting phenomenon (see also Knudsen 1995).

Conclusion - perspectives on future research

While the research results described above lead to a better understanding of certain factors determining the occurrence of parasites in Arctic charr populations, a great deal yet remains unknown. Here I will consider some areas which require particular attention.

Even through parasite transmission to charrs is mediated through interactions with intermediate hosts, susceptibility of various charr species to infection may differ. For example, Arctic charr seem to be particularly suitable hosts for *Diphyllobothrium* species, as evidenced by the abundance of these parasites in many lake resident Arctic charr populations. Moreover, although *Diphyllobothrium* larvae in Arctic charr become encapsulated by a fish host immune response, in most cases the parasites are not killed but instead appear to live indefinitely, possibly even for the life of the host (Curtis 1984). In contrast, lake charr are generally less frequently infected by *Diphyllobothrium* than are Arctic charr, despite the fact that the piscivorous feeding habits of lake charr must expose them to high numbers of potentially infective larvae. In lake charr we have observed most *Diphyllobothrium* larvae to be encapsulated and dead, possible evidence of an effective immune response. Brook charr are also infected by *Diphyllobothrium*, but in our observations we have never witnessed the high levels of infection attained in Arctic charr. Bylund (1972) witnessed a similar diversity of responses to *Diphyllobothrium* infections in coregonids. Although the immune response to *Diphyllobothrium* has been studied in rainbow trout, *Onchorhynchus mykiss*, (Sharp et al. 1992) similar studies on this and other parasites have yet to be conducted on the charrs.

While it is now possible to account for the presence or absence of certain charr parasites in various lake habitats, factors regulating parasite abundance are still little known. Further observations are necessary to better understand the variables controlling parasite transmission.

Another relevant area for additional research entails determining the potential of charr parasites for regulating fish populations by causing morbitity and mortality. Field data alone generally seems inadequate to resolve questions of this nature, perhaps because only a comparatively small portion of the charr population at any given time is heavily infected and, given the heterogeneities in natural lake populations, statistical tests of parasite impacts are generally inconclusive. Only well designed field and laboratory experiments with appropriate controls are likely to address such issues. Work carried out by Bristow and Berland (1991) on the nature of growth inhibition in farmed salmon (*Salmo salar*) by the fish tapeworm *Eubothrium* stands out as a good example of such research.

Finally, there is the question of how parasites may indirectly mediate food web interactions. It is evident that parasites can alter intermediate host behavior in order to increase the probability that higher level hosts will become infected. This is demonstrable both for charr as predators (Poulin et al. 1990) as well as charr as prey (Brassard et al. 1982). Yet, it remains to be seen to what extent parasites may serve as "catalysts" in altering energy flow within natural food webs. Perhaps one way to test this will be to concentrate upon interactions such as those between Arctic charr and *Gasterosteus*. The *Gasterosteus* preyed upon by Arctic charr in many northern lakes are commonly infected by the large larval cestode *Schistocephalus*, which renders its hosts more susceptible to predation (Giles 1983). It seems likely that Arctic charr would not feed extensively upon *Gasterosteus* if they were not partly immobilized by *Schistocephalus solidus*, but both field and laboratory work is needed to evaluate the implications for energy flow in affected lakes.

The answers to these and other challenging problems will require effort on the part of a variety of biologists with experience in fisheries and related fields. The result may be a greater awareness of the role of parasitological studies in finding the answers to questions of fundamental significance to northern lake biology and fisheries ecology.

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Feeding of Charr in Relation to Aquaculture

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Abstract

It is a prerequisite for the achievement of rapid and homogeneous rates of growth, and uniform size at harvest, that the feed supply be evenly distributed amongst the fish making up the rearing group. Consequently, inequalities in feed acquisition among individuals result in increased size disparity and leads to sub-maximal rates of biomass gain. Disparate feed acquisition may arise because of the behavioural interactions that result from high levels of competition for limited food resources, or inequalities in feeding may be a consequence of the formation of dominance hierarchies. Changes in social behaviour of charrs can be induced by manipulating the rearing environment, with both increasing stocking densities and exposure of the fish to water currents leading to the incidence of agonistic interactions being markedly reduced. It is suggested that these behavioural changes have a pronounced influence on social environment, thereby affecting feeding conditions, growth performance and production efficiency.

Keywords: Charr, feeding behaviour, feed intake, growth.

Introduction

The farming of salmonids in Northern Europe, Canada and USA is largely concentrated upon Atlantic salmon, *Salmo salar,* rainbow trout, *Oncorhynchus mykiss,* and various species of Pacific salmon, *Oncorhynchus* spp. Other species of salmonids have, however, been produced for stock enhancement and sport fishery purposes, with several species within the genus *Salvelinus* having been reared for release. During the 1970s and 80s interest in the farming of a number of charr species increased, both for restocking and to supply fish for the table. The development of Arctic charr, *Salvelinus alpinus,* farming has been reviewed recently (Jobling et al. 1993b), and it is not the intention to repeat information here. Consequently, the main emphasis in this paper will be directed towards feeding and feed management.

Within fish farming it is the desire of the commercial producer that the fish grow rapidly, efficient use is made of the feed provided and wastage is kept to a minimum. From the marketing viewpoint it is also desirable that the harvested fish are of uniform size and the nutritional value of the saleable product is maintained within clearly defined limits. Whilst this requires that the fish be provided with correctly formulated feeds, it will be impossible to achieve these goals if feeding and management practices are suboptimal. There will, for example, be little benefit to be gained by feeding highly palatable diets that are known to fulfil all the nutritional requirements of the fish, if feed presentation is inadequate or the propensity of the fish to feed is reduced due to a poor rearing environment.

Thus, nutritional information is required if feeds are to be manufactured to meet the needs of a particular species or ontogenetic stage. Furthermore, if the fish are to be provided with a rearing environment that ensures optimal growth and effective production, information must also be available about the ways in which feeding behaviour, feed intake and growth performance are influenced by changes in various biotic and abiotic factors.

The purpose of the current paper is, therefore, to provide examples of how various manipulations of the rearing environment affect feeding conditions, and thereby influence fish growth and production efficiency.

Feed particle sizes

The size of the food particles offered can affect both the willingness of the fish to accept the feed and the efficiency with which it is utilized for growth. Consequently, effective production requires that information be available about the sizes of food particles to be fed to the different ontogenetic stages of the fish. For example, Linnér and Brännäs (1994) reported that Arctic charr of 20 cm fork length (FL) responded more rapidly to the presentation of large pellets (over 2% FL) than to small pellets, but handling time increased with increasing size of the pellets. Consequently, the shortest sum of reaction and handling times was recorded for pellets of intermediate size (2.25% FL), and pellets of intermediate sizes were those that were least often missed or rejected. Thus, the fish failed to consume over 30% of the pellets within the largest and smallest size categories offered, rejected 10-15% of the pellets within the size range 2-3% FL, but only 5% of pellets with a diameter of 2.25% FL were lost or rejected.

Tabachek (1988) investigated the effects of feed particle size on acceptance and growth in juvenile Arctic charr (3-20 g). Growth of small fish (7-11 cm) was best when feed pellets corresponding to 1.5-1.8% FL were offered, but feed particle sizes promoting best growth of 12-13 cm charr were approximately 2.4% FL (Tabachek 1988). For larger charr (20-40 cm) feed particles having a diameter corresponding to 2-2.5% of the fork length of the fish promote good growth, and pellets of this size can be considered as being close to the optimum.

Daily rations

The amounts of feed consumed by Arctic charr of different sizes (year-classes) held under a variety of rearing conditions have been monitored in several studies (e.g. Jørgensen and Jobling 1989, 1990, Christiansen and Jobling 1990, Pálsson et al. 1992, Jobling et al. 1993a), and these data have formed the basis for the calculation of feed allowances (Jobling et al. 1993b). Whilst much of the variability in food intake by fish can be explained by taking into consideration the two factors fish size and water temperature, many other factors also influence consumption (Brett 1979, Jobling 1994). Fish of a given size held under conditions of constant water temperature may, for example, show quite marked day-to-day variations in feeding behaviour, and five- to tenfold differences in daily feeding activity have been observed in Arctic charr allowed to feed by operating on-demand feeders (Brännäs and Alanärä 1993, Linnér and Brännäs 1994). There may also be marked temporal variations in food consumption related to seasonal changes in photoperiod, the salinity of the surrounding medium, or the stage of the reproductive cycle of the fish (Higgins and Talbot 1985, Pálsson et al. 1992, Arnesen et al. 1993, Jobling et al. 1993a,b). One additional, but relatively little studied, factor that may be expected to have a major influence on feed intake and growth is the social environment existing within a group of fish (Brännäs and Alanärä 1993).

Feed acquisition and growth - influence of rearing environment

The rearing of salmonids in small groups can lead to territory defence and the establishment of dominance hierarchies. This can, in turn, lead to marked disparity in feeding activity and food acquisition, with the consequence that the growth of subordinate individuals may be suppressed (Yamagishi 1962, Li and Brocksen 1977, Metcalfe et al. 1992, Thorpe et al. 1992, Grant 1993, Brännäs and Alanärä 1993, Alanärä 1994). Charrs are often overtly aggressive, displaying quite high rates of agonistic encounters even after a hierarchy has been established (Noakes 1980, East and Magnan 1987, Winberg 1993). Consequently, social rank has an important influence on food acquisition and growth of individual fish. It has, for example, been demonstrated that when Arctic charr are fed using demand feeders, relatively few of the fish within a group use the feeder (Brännäs and Alanärä 1993). This has been attributed to the establishment of dominance hierarchies rather than to differences among fish in learning abilities. Further, there was found to be a close correlation between the use of the demand feeder ('bite-activity') by a fish and the growth performance of that individual (Alanärä 1994).

The large influence that hierarchy formation can have on the growth of Arctic charr was demonstrated by Winberg et al. (1992), who examined the behaviour and growth of individual charr held in small groups. Dominant individuals, assessed on the basis of the numbers of aggressive acts initiated, displayed positive rates of growth, whilst many of the lower ranking fish within each group lost weight. Thus, there were marked differences in rates of weight gain among individuals within each group, with coefficients of variation (CV = [SD/mean] • 100) ranging from 448 to 2,164 (Table 1). Overall rates of growth were very poor (-0.14 to 0.02% b.wt.d^{-1}) compared to those predicted using data presented by Jobling et al. (1993b) (approx. 1% b.wt.d^{-1} for 100 g charr at 10°C) despite the fact that the fish were provided with sufficient feed (1-2% b.wt.d^{-1} commercial trout pellets) to promote good rates of weight gain. In addition to poor overall growth and considerable inter-individual variability, there was also a lack of consistency among tanks in growth performance.

Thus, hierarchy formation may lead to growth performance that would be considered most undesirable under farming conditions - low rates of biomass gain, inconsistency of growth performance among groups, and marked heterogeneity in rates of weight gain among individuals within a group. Consequently, there would appear to be considerable scope for improving total biomass gain and production efficiency by making manipulations to the rearing environment of the fish.

An even distribution of feed among the fish within the group (i.e. low inter-individual variability in feed intake) would be expected to be a prerequisite for the achievement of homogeneous growth (i.e. low CVs for feed intake would be expected to be linked to low CVs for both growth rates and harvest weight). Thus, the challenge is to manipulate the rearing environment in such a manner that all the fish within the group are provided with feeding conditions that enable them to grow at rates approaching their physiological potential.

Table 1. Growth performances of Arctic charr held in small groups: influences of social status (dominance rank) on growth (SGR), and the consequences of the formation of dominance hierarchies on average rates of growth and heterogeneity (CV_{SGR}) within groups. Specific growth rate, $SGR = [\ln W_2 - \ln W_1] \cdot 100/(t_2-t_1)$, where W_1 and W_2 are fish weights at times t_1 and t_2, and (t_2-t_1) is the time between weighings. Coefficient of variation, CV=(SD/mean) • 100. (Data from Winberg et al. 1992.)

Fish rank	SGR	SGR	CV_{SGR}%
A1	0.62		
A2	-0.18		
A3	-0.43		
A4	-0.39	-0.09	459
B1	0.76		
B2	-0.17		
B3	-0.04		
B4	-0.47	0.02	2,164
C1	0.55		
C2	0.33		
C3	-1.05		
C4	-0.40	-0.14	448
D1	0.56		
D2	-0.01		
D3	-0.12		
D4	-0.34	0.02	1,589

Restricted feeding - feed acquisition and growth performance

Competition will often be found to increase under conditions of resource restriction (Grant 1993), so provision of food at sub-maximum levels would be expected to lead to both growth depression and increased competition among individuals for the limited resource. The provision of food at several fixed levels would allow both the study of the effects of resource restriction on inter-individual competition, and the examination of the growth-rations relationship (Brett 1979, Elliott 1982, Jobling 1994).

Traditionally, the growth-rations relationship has been considered to be highly curvilinear in form. Starting at zero ration, where the fish are starving and losing weight, the curve rises steeply to cross the point of zero growth rate at the maintenance ration. With increasing food supply the curve begins to flex, and it plateaus at the point of maximum rations and maximum growth rate (Brett 1979, Elliott 1982, Jobling 1994). One problem with studies in which growth-rations relationships have been investigated is that the amounts of food supplied to the fish have been recorded, but there has often been considerable uncertainty as to whether or not all the food provided was eaten. Thus, whilst there are a number of factors that may influence the shape of the growth-rations relationship (Elliott 1982, Hogendoorn et al. 1983), there must remain some doubt as to whether many of the growth-rations relationships reported hitherto are accurate. In other words, the high degree of curvilinearity apparent in some of the published growth-rations relationships may be artefactual, being the result of considerable food waste at high feeding levels.

Problems associated with varying amounts of feed waste at different feeding levels can be overcome by employing X-radiographic techniques that enable consumption to be monitored accurately (Talbot and Higgins 1983, Talbot 1985, Jobling et al. 1990, 1993a). By combining use of the X-radiographic technique with the study of individually-tagged fish, inter-individual differences in food consumption under different feeding and rearing conditions can also be examined (Jobling et al. 1993a). In other words, repeated measurement of feed intake by individual fish enables inter-individual variability (designated CV_G) to be examined, and also permits the study of the ways in which such variability may influence growth performance.

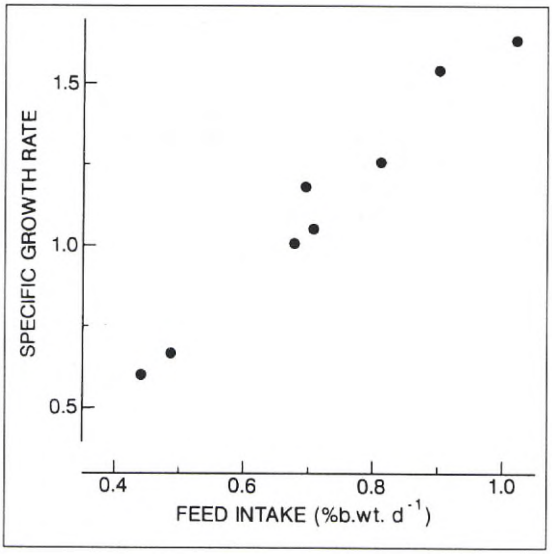

Fig. 1. Relationship between feed intake and growth for groups of Arctic charr fed various daily feed allowances at 8°C. Feed intake was calculated from group consumption based upon three feed intake measurements made using radiography. Growth rates are given as group mean specific growth rates. Specific growth rate, SGR = $[\ln W_2 - \ln W_1] \cdot 100/(t_2-t_1)$, where W_1 and W_2 are fish weights at times t_1 and t_2, and (t_2-t_1) is the time between weighings.

Groups of Arctic charr were held on a range of fixed rations, ranging between a highly restricted ration and excess feeding. Food consumption, by both the groups and each individual fish, was monitored on three occasions using radiography. Growth performance was also recorded, permitting examination of the growth-rations relationship. There was little evidence of curvilinearity in the relationship between feed intake and growth (Fig. 1). Thus, the marked bowing of the curve reported in many previous studies of growth-rations relationships was not observed. Consequently, it would seem that the conclusion to be drawn is: in several previous studies of the growth-rations relationship the extent of the bowing of the curve may have been exaggerated due to increasing amounts of unregistered feed waste at high levels of feed supply.

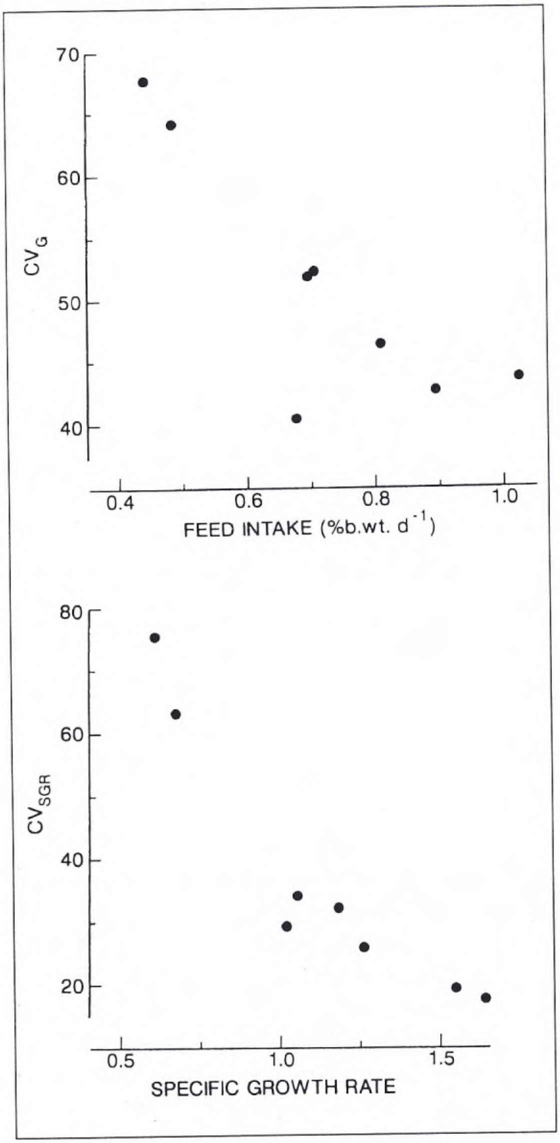

Fig. 2. The influence of restricting daily feed allowance upon average feed intake and inter-individual variability in feed consumption (CV_G) (upper figure), and rates of weight gain and inter-individual variability in growth rates (CV_{SGR}) (lower figure) of Arctic charr. Coefficient of variation, CV=(SD/mean) • 100. Spearman Rank Correlation Coefficient for the relationship between average feed intake and inter-individual variability in feed consumption: R=-0.619 ($P<0.05$). Spearman Rank Correlation Coefficient for the relationship between rates of growth and inter-individual variability in growth rates: R=-0.929 ($P<0.01$).

Restricting the supply of food not only led to reduced consumption and growth (Fig. 1), but also resulted in an increase in inter-individual differences in feed intake and growth (Fig. 2). In other words, inter-individual differences in feed intake were lowest (i.e. lowest CV_G) among the charr held in the groups that consumed the greatest quantities of food, and CV_G increased as food supply became increasingly restricted. These differences in feed intake were reflected in the growth responses displayed by the fish - as food supply decreased not only did the average rate of weight gain decrease, but there was also an increase in heterogeneity (i.e. CV_{SGR} increased) (Fig. 2). Taken together, these results clearly suggest that restricting the food supply led to increased competition among individuals for the limited resource. This, in turn, was reflected in a significant correlation between inter-individual variability in feed intake (CV_G) and the heterogeneity of the growth rates of fish making up the group (CV_{SGR}) (Fig. 3).

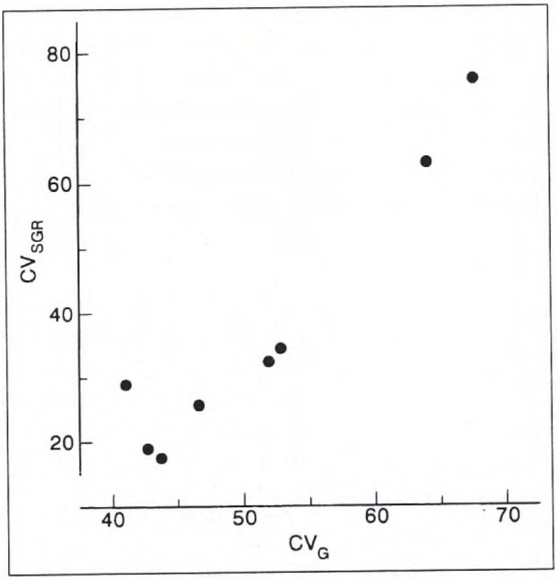

Fig. 3. The influence of restricting daily feed allowance upon inter-individual variability in feed consumption (CV_G) and growth rates (CV_{SGR}) of Arctic charr. Coefficient of variation, CV=(SD/mean) • 100. Spearman Rank Correlation Coefficient for the relationship between CV_{SGR} and CV_G: R=0.833 ($P<0.01$).

Inter-individual and intra-individual variability in feed acquisition

Repeated measurement of feed intake by individual fish not only enables inter-individual variability (CV_G) to be examined, but also provides the information required for the study of the day-to-day variations in feed intake shown by each individual (designated CV_I). It has been suggested that information of this type can be used to provide an indirect assessment of the social environment existing within a group of fish with respect to the establishment of feeding hierarchies (Carter et al. 1992, McCarthy et al. 1992).

In making assessments of this kind it is assumed that dominant fish gain preferential access to the food resources and, therefore, have higher overall rates of consumption than subordinates (i.e. dominants consume a greater proportion of the group feed intake [%GFI]). This assumption has been borne out by direct observations on several salmonid species (e.g. Thorpe et al. 1990, 1992, Gotceitas and Godin 1992, Thorpe and Huntingford 1992), including Arctic charr (Winberg 1993). It is further assumed that by securing access to the food resources the dominants will be able to feed to satiation each day and will, therefore, display little day-to-day variation in feed intake (i.e. dominants will have a low CV_I). Subordinates, on the other hand, may be prevented from feeding to satiation each day by the activities of the dominant individuals, resulting in more sporadic feeding and greater variability in daily feed intake (i.e. subordinates may have a high CV_I). With this as a basis, a number of predictions can be made.

Firstly, under conditions where there is little competition, the fish would be expected to have equal access to food, resulting in only small inter-individual differences in feed intake (i.e. CV_G will be low). Furthermore, since all fish gain access to food and can feed to satiation, all individuals would be expected to show relatively little day-to-day variability in feed intake (i.e. all fish will have low CV_Is).

Data relating to food consumption by juvenile Arctic charr in the absence of interference from conspecifics are available (Miglavs and Jobling 1989). Analyses performed on these data give information about both intra-individual and inter-individual variabilities in food intake under base-line conditions. Intra-individual variation in food intake (CV_I) was found to range between 1-62%, with the majority of values being 20-35%. Inter-individual variation, expressed as CV_G, was within the range 25-40% (Jobling and Baardvik 1994). Thus, in the absence of interference from conspecifics both intra-individual (CV_I 1-62%) and inter-individual (CV_G 25-40%) variabilities in food intake are relatively low, and this leads to correspondingly low variability in growth rates (CV_{SGR} 15%).

When there is competition for food, or a hierarchy develops, some fish may monopolise the food supplies leading to increased differences amongst individuals in feed intake (i.e. dominants consume larger proportions of the feed and have higher %GFIs than subordinates). This, in turn, would result in an increase in the CV_G of feed intake over base-line values. When intra-individual variability in feed intake is considered, the CV_I should be low for those fish which secure regular access to the food supplies and thereby exhibit little day-to-day variation in feed intake. On the other hand, those fish that feed more sporadically will display greater day-to-day variability in feed intake (i.e. have higher CV_Is).

From this it follows that it should be possible to test whether or not competition for food exists by an examination of intra-individual and inter-individual variabilities in feed intake recorded for groups of fish. For example, the presence of a strong feeding hierarchy would be indicated by a highly significant negative correlation between the %GFIs of given individuals and the CV_Is of the same fish (Carter et al. 1992, McCarthy et al. 1992). On the other hand, under conditions where there is competition for food in the absence of resource monopolisation a general increase in CV_I might be expected, but there would not be any significant correlations between CV_I and %GFI.

Using this as a starting point, examinations of the effects of different rearing environments on feed intake and growth rates of individual Arctic charr have been undertaken (Jobling and

Baardvik 1994). A summary of the findings is presented below, and the implications of the results are discussed within the context of manipulations that can be expected to increase overall rates of biomass gain and improve production efficiency under farming conditions.

Stocking density, feed acquisition and growth

Many of the growth trials conducted with charrs have been carried out at stocking densities within the range 5-25 kg m^{-3} but rearing at these densities has resulted in large disparities in size among individuals (Wandsvik and Jobling 1982, Jobling 1983, Jobling and Wandsvik 1983, Papst and Hopky 1983, East and Magnan 1987, Papst et al. 1992). In addition, charrs reared at low stocking densities often engage in aggressive encounters (Noakes 1980, East and Magnan 1987, Christiansen and Jobling 1990, Brown et al. 1992, Winberg 1993).

One way in which changes in social behaviour can be affected is via the manipulation of stocking densities. When Arctic charr are held at stocking densities in excess of 20 kg m^{-3} the fish tend to form distinct schools in the water column, rather than congregate in a loose group close to the tank bottom (Wallace et al. 1988, Jørgensen et al. 1993). There also appears to be a marked decrease in the incidence of agonistic interactions as stocking density is increased (Brown et al. 1992).

Jørgensen et al. (1993) studied the effects of stocking density on feed intake and growth in juvenile Arctic charr. They reported that rates of both feed intake and growth were higher in groups of fish held at high stocking density than in those reared at low density. Examination of the data also suggests that the groups of fish reared at the two higher stocking densities were more homogeneous than those held at the lowest density. Thus, not only were growth rates lower for the fish held at low density, but there were also marked differences in average performance among groups of fish held in different tanks (Table 2A). This inconsistency of performance between tanks of charr held at low stocking density has also been observed in another recent study (Table 2B) (Jørgensen and Jobling 1993).

In addition to unpredictable group performances at low stocking density, rates of growth displayed by individual charr held at low stocking density were also very heterogeneous (CV_{SGR}: Table 2). This is, in turn, a reflection of inequalities in feeding, with large inter-individual differences in feed intake being recorded (CV_G: Table 2). This suggests that social interactions may have had the greatest negative consequences for feed acquisition by individual fish in the groups of charr stocked at low density.

Table 2. Rates of weight gain (SGR), and inter-individual variations in feed intake (CV_G) and growth (CV_{SGR}) displayed by Arctic charr reared at different stocking densities. Variability is expressed as the coefficient of variation (CV=[SD/mean] • 100). (Data are from (A) Jørgensen et al., 1993; (B) Jørgensen and Jobling, 1993.)

A

Stocking density	*N*	SGR	CV_{SGR}	CV_G
15 kg/m^3	18	0.45	151	136
	20	0.07	704	212
	19	-0.13	350	202
60 kg/m^3	69	0.94	56	62
	77	1.08	46	61
	78	0.99	47	63
120 kg/m^3	136	1.12	41	65
	127	1.14	32	71
	144	0.96	54	77

B

Stocking density	*N*	SGR	CV_{SGR}	CV_G
10 kg/m^3	24	0.88	66	106
	23	0.32	205	125
36 kg/m^3	98	1.10	39	109
	97	0.98	62	74

Thus, growth rates of Arctic charr tend to be poor, and highly variable, when fish are held at stocking densities of 5-15 kg m^{-3}. Overall rates of gain improve markedly as stocking density is increased from 15 to approximately 40 kg m^{-3} (Baker and Ayles 1990), and high rates of weight gain may be achieved at stocking densities in excess of 100 kg m^{-3} (Wallace et al. 1988, Baardvik and Jobling 1990, Pálsson et al. 1992, Jørgensen et al. 1993) provided that good water quality is maintained. Available evidence suggests that the increased rates of weight gain observed in groups of charr stocked at high density may arise as a consequence of a decrease in levels of agonistic interactions (Brown et al. 1992). These improvements in the social environment are suggested to result in increased rates of feed intake (Jørgensen et al. 1993), leading to both less heterogeneity of growth among individuals within a group, and a greater consistency of performance among rearing groups.

Sustained exercise and growth performance

There is a large body of evidence indicating that growth rates of salmonids can be improved by forcing the fish to swim against moderate water currents for prolonged periods (reviewed by Davison 1989, Jobling et al. 1993c). The beneficial effects of sustained exercise may be the result of the fish displaying a range of both behavioural and physiological changes.

Charr exposed to water currents may exhibit schooling behaviour, distribute themselves evenly in the water column and show much lower levels of agonistic behaviour than fish held in standing water (East and Magnan 1987, Christiansen and Jobling 1990). This leads to the possibility that feed acquisition by individual fish may be less influenced by social interactions in exercised than in unexercised groups. When held at low stocking density (12 kg m^{-3}), exercised Arctic charr juveniles may display lower inter-individual variabilities in feed intake and growth rates than unexercised fish (Table 3), lending support to the idea that exercise regimes may improve the chances of individual fish to acquire food, and thereby show increased growth. It should, however, be noted that not all groups of charr held in standing water, or exposed to low water currents, displayed highly heterogeneous feed intake and growth (Table 3). Consequently, there is generally found to be a low level of precision in the growth data among tanks of charr held in standing water at low stocking density (Tables 2 and 3).

Table 3. Rates of weight gain (SGR), and inter-individual variations in feed intake (CV_G) and growth (CV_{SGR}) displayed by Arctic charr exposed to different water current regimes. Fish were held in groups of 50 (stocking density 12 kg m^{-3}), but analyses were carried out using data collected from fish for which complete records of feed intake (5 intake measurements) and growth were available. (Data are from Christiansen and Jobling, 1990.)

Exercise regime cm s^{-1}	N	SGR	CV_{SGR}	CV_G
0	20	0.631	98	63
	19	0.175	394	120
6.5	22	0.848	56	45
	23	0.371	174	80
13	12	0.863	63	59
	24	0.825	67	76
19.5	24	0.994	63	69
	8	0.721	63	57
26	22	1.623	39	65
	23	1.263	45	42

More in-depth analysis of the data obtained in the Arctic charr study conducted by Christiansen and Jobling (1990) revealed negative relationships between %GFIs and CV_Is for the fish held in static water (Fig. 4). This suggests that feeding hierarchies had been established in these groups. Since not all correlations were found to be significant for the groups exercised at higher speed (Fig. 4) it is suggested that hierarchy development may have been weaker in the fish exposed to the stronger water currents (Jobling and Baardvik 1994). Thus, the

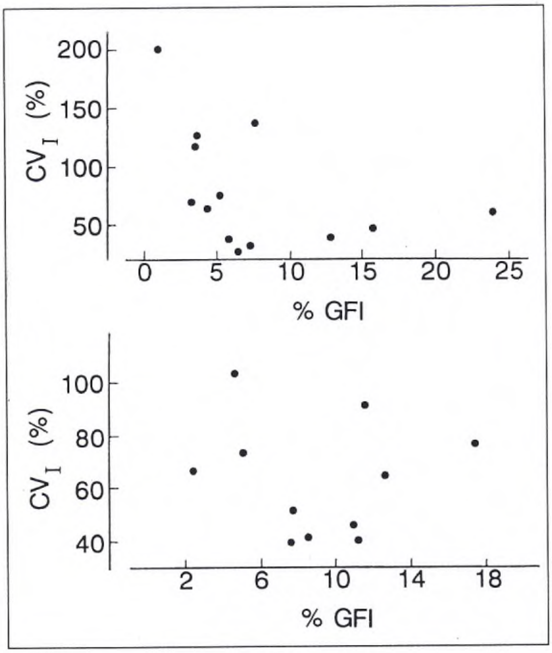

Fig. 4. Scattergrams showing the relationships between intra-individual variability in feed intake (CV_I) and proportion of group feed intake (%GFI) consumed by juvenile Arctic charr reared either in standing water (upper figure) or exposed to a water current of 13 cm s^{-1} (lower figure). The establishment of a feeding hierarchy is assessed by the examination of the relationship between CV_I and %GFI, a highly significant negative correlation being indicative of hierarchy formation. Spearman Rank Correlation Coefficients (*R*) were -0.852 ($P<0.01$) and -0.559 (*P* NS) for the groups of charr held in standing water and exposed to water currents, respectively. (Data from Christiansen and Jobling, 1990.)

greater homogeneity in both feed intake and growth observed in the exercised groups of charr (Table 3) may have arisen due to a hindrance of hierarchy formation following exposure to water currents.

The results of a number of other studies suggest that exercised salmonids may be more uniform in body size (East and Magnan 1987, Christiansen et al. 1991) and display more homogeneous rates of growth (Houlihan and Laurent 1987) than do unexercised controls. This lends further support to the idea that the increased growth observed in fish held in flowing water may, at least in part, result from improvements in social environment and a weakening of feeding hierarchies.

In this context it is of particular interest to note that exposure to water currents had little influence on the homogeneity of rates of growth displayed by Arctic charr held at high stocking density (Christiansen et al. 1992). Examination of the feed intake data collected by Christiansen et al. (1992) revealed that there were no marked differences between exercised and unexercised groups in either CV_Gs (Unexercised: 35-67%; Exercised: 37-67%) or CV_Is (Unexercised: 60-66%; Exercised: 30-77%), and in no instance was a significant negative correlation found between CV_I and %GFI (Jobling and Baardvik 1994). Thus, when held at high stocking density, there did not appear to be pronounced differences between exercised and unexercised fish in equality of feed distribution, nor was there any evidence indicating the formation of distinct feeding hierarchies within any group.

Since it is suggested that high stocking density *per se* may lead to improved growth via influences on social behaviour, it is possible that both stocking density and water current manipulations exert their effects via reductions in agonistic behaviour and hierarchy disruption. The net result: exercise regimes are of reduced efficacy in promoting higher rates of growth in groups of charr stocked at high density.

Concluding comments

Much of the research conducted in connection with salmonid aquaculture has been directed towards the investigation of the effects of different dietary formulations and feed ingredients upon growth performance. This work has resulted in the production of feeds that give good growth performance under commercial conditions, and charr generally grow well when fed diets produced for other salmonid species.

Whilst the prospects for the promotion of increased growth by making changes to dietary formulations may be limited, it appears that there is considerable scope for improving production via manipulating the rearing environment of the fish. The benefits gained would seem to be linked to the effects of different types of manipulation upon the social environment existing within the group. Thus, any manipulation that led to a more even distribution of feed among individual fish within a group would be predicted to result in increased rates of weight gain, improved efficiency of feed utilization and a greater homogeneity of fish sizes at harvest. Manipulations to stocking density and the exposure of the fish to water currents seem to be simple methods by which growth and production efficiency of charr may be improved in a commercial context.

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World Status and Conservation of the Arctic Charr *Salvelinus alpinus* (L.)

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Abstract

The Arctic Charr *Salvelinus alpinus* (L.) is the most northerly freshwater fish and occurs in many countries in the northern hemisphere - in Asia, Europe and North America. Worldwide, the status of the species is satisfactory but in a number of countries, especially those on the southern fringe of its distribution, many individual populations have been lost. The main threats to Arctic Charr are from acidification, eutrophication, pollution, hydropower developments, overfishing, genetic degradation from alien translocated *Salvelinus*, introductions of other, disruptive, fish species and possibly global warming. The Arctic Charr is an important species in the northern hemisphere and merits serious international conservation efforts to maintain its integrity and status. It is well known in some countries, but less well known in others. It is important to many native peoples in the arctic and more generally of value to anglers, to commercial netsmen and, more recently, to fish farmers. Conservation management for this species varies widely and more programmes are needed at both national and international levels. Reliable inventories of individual populations in each geographic area are highly desirable. The main methods proposed for conservation include improved legislation, habitat management and restoration, and in some cases, careful translocation, captive breeding and cryopreservation. Improved education is also greatly needed in order to increase public awareness of this most attractive and valuable fish species.

Keywords: Arctic Charr, *Salvelinus alpinus*, world status, conservation.

Introduction

The Arctic Charr, *Salvelinus alpinus* (L.), is a holarctic salmonid fish with numerous isolated freshwater populations in North America, Europe and Asia - occurring naturally in 16 countries altogether (Table 1). Worldwide, its natural distribution is the most extensive of any salmonid.

In southern areas the species is confined to fresh water and is found chiefly in lakes except at spawning time when some populations migrate into running water. North of about 65°N, however, many of the stocks are anadromous and here the adult fish, which rarely reach a kilogram in fresh water further south (with a few exceptions), may reach a large size (sometimes over 10 kg) and can be of considerable economic importance.

Although neglected for many years by scientists, the last two decades have seen an upsurge of research on this species and there is now an extensive literature available within the normal scientific journals (Marshall 1977 and subsequent bibliographies), the proceedings of several recent symposia (Balon 1980, Johnson and Burns 1984, Kawanabe et al. 1989).

The basis for the information contained in this paper is a questionnaire sent out in December 1993 to charr experts in all the charr countries of the world. Those people who provided information are acknowledged individually below. In some of the larger, or more complex, states (e.g. Canada, Great Britain and the United States) data were obtained individually for each relevant area and then summarised for this paper.

Table 1. National data on populations of Arctic Charr: (a) number of lakes with indigenous Arctic Charr, (b) number of lakes with indigenous Arctic Charr plus introduced stocks from elsewhere, (c) number of new lakes with introduced Arctic Charr, (d) number of lakes with sympatric Arctic Charr, (e) number of stocks of anadromous Arctic Charr, (f) number of lakes where Arctic Charr are now extinct.

Country	(a)	(b)	(c)	(d)	(e)	(f)
Austria	15	13	150	15	0	2
Canada	3,449	5	18	422	423	0
Faroes	1	0	4	0	0	0
Finland	100	3	7	3	1	8
France	2	2	135	0	0	29
Germany	14	12	51	0	0	0
Great Britain	191	0	10	2	0	9
Greenland	1,001	0	0	501	500	0
Iceland	1,000	50	100	50	200	0
Ireland	31	0	1	0	0	25
Italy	30	3	2	0	0	5
Norway	30,000	49	400	50	140	228
Russia	1,000	0	10	100	250	0
Sweden	13,000	350	118	101	0	75
Switzerland	12	12	10	2	0	0
United States	461	0	66	101	20	6
Totals	50,307	499	1,082	1,347	1,534	387

It was realised at the outset, that some types of information would be difficult to obtain accurately but scientists were urged to supply their best estimates of the numbers involved, with written provisos concerning the accuracy of information. Thus many of the data given in the tables should be treated with caution and in most cases regarded as minimum, order of magnitude, figures. The objective has been to give a broad overview of the status of Arctic Charr throughout the world and, hopefully, to stimulate workers in some countries to produce more accurate figures than are available at the moment. For some of the more remote regions, for example Arctic Canada and northern Russia, very few statistics are available.

World status of Arctic Charr

This paper deals mainly with countries in which the Arctic Charr is a native species. As noted above, there are 16 such countries (Table 1) and the only one of these where there is some doubt as to whether this species is native or not is Italy. However, there is some documentary evidence to support it as an indigenous species there (Yoichi Machino, personal communication), notably the Italian word 'salmerino' (=*Salvelinus alpinus*) and the reference to this fish by Duhamel du Monceau (1777) from Trente in Italy.

It is apparent, from the review initiated by the questionnaires on which this paper is based, that *Salvelinus alpinus* also occurs now in several other countries where it has been introduced successfully this century. These are: Slovenia (two populations), Croatia (one population) and Montenegro (one population) (Meta Povz, personal communication).

Number of populations

The exact status of many individual populations is a matter of considerable debate. In many wilderness areas the stocks are almost certainly pristine but in other parts, humans have introduced stocks of Arctic Charr from other waters and the degree of mixing is usually quite uncertain. Arctic Charr have also been introduced to many new waters where they have established self-sustaining populations. Sympatry is a common feature of Arctic Charr populations and two, sometimes three or even more, separate stocks can inhabit the same water. Many of the more northerly waters have anadromous stocks. Finally a significant number of indigenous stocks have become extinct over the last century, due to a variety of causes, which are discussed below.

The total number of indigenous populations of Arctic Charr worldwide is unknown, but probably well over 50,000 (Table 1a). The most accurate data are from those countries where the species is least common and where, in some cases, there is a current database of existing stocks - for example in Finland (Kallio-Nyberg and Koljonen 1991) and Great Britain (Maitland 1972, 1992). However, the overall numbers are dominated by the most northerly countries, notably Norway (with apparently over half of the world stocks), Sweden, Greenland and Iceland.

In several countries (e.g. Great Britain, Greenland, Ireland and the United States), the existing populations appear never to have been subject to the introduction of alien stocks (Table 1b). However, elsewhere (e.g. Austria, Germany, Iceland, Norway, Sweden and Switzerland) many of the waters with indigenous stocks have had introductions of stocks from other waters and the total number of lakes involved is probably over 500 worldwide.

Stocking of Arctic Charr into waters in which they did not occur naturally has also been a widespread practice and there are now many established populations in new waters (Table 1c). In several countries there are now many more 'new' populations than indigenous ones - notably in Austria, France and Germany.

Sympatry has been recorded for many lakes with stocks of Arctic Charr (e.g. Walker et al. 1988) and it is likely that there are many other lakes where sympatric populations have yet to be discovered. Examples of well documented lakes are Salangen (Nordeng 1983) and Thingvallavatn (Jonasson 1992). As might be expected, sympatry is high in northerly areas (Table 1d) where anadromous stocks are present and usually exist alongside resident lake forms (e.g. Canada, Greenland, Iceland and Norway). However, there are also significant numbers of lakes with sympatric freshwater resident populations both north and south.

Anadromous populations, as already noted, occur only in the most northerly areas (Table 1e) and, apart from a single stock in Finland, are found only in Canada, Greenland, Iceland, Norway and the United States (Alaska).

Extinctions of native populations are known to have taken place in many areas (Table 1f), perhaps most notably in France (which has lost 29 out of 31 of its original introduced stocks) and Ireland (25 out of 56), but also significantly in Norway (80 out of 30,080) and Sweden (75 out of 13,075) (where the species is common), as well as Austria (2 out of 17), Finland (8 out of 108), Great Britain (9 out of 200), Italy (5 out of 35) and the United States (6 out of 467).

Economic value

The Arctic Charr has a significant economic and sporting value in many countries and the total sums of money and people involved, both directly and indirectly, are large (Table 2).

Angling for Arctic Charr takes place, to a greater or lesser extent, in all 16 countries in which this fish is found and the total annual catch, worldwide, is several million fish (Table 2a). In some countries, it is regarded as a useful sport fish and is popular with anglers (e.g. in France); in other areas it is more the quarry of specialist fishermen (e.g. England (Great Britain)). In several countries it is caught incidentally during general angling or in the hunt for other species (e.g. Scotland (Great Britain)). The species is also important to anglers indirectly as a food base for large 'specimen' ferox trout (Hardie 1940, Campbell 1979).

The Arctic Charr is an important commercial fish in several countries (Table 2b), especially those where anadromous stocks are found (e.g. Canada, Greenland and Iceland). It is also important to commercial fishermen in the lakes of

Table 2. World usage of Arctic Charr: (a) numbers angled annually, (b) tonnes in annual commercial catch, (c) tonnes in annual subsistence catch, (d) tonnes farmed annually.

Country	(a) Angling	(b) Commercial	(c) Subsistence	(d) Farmed
Austria	30,000	35	0	0
Canada	21,300	209	690	75
Faroes	550	0	0	0
Finland	30,850	6	13	30
France	220,000	14	0	0
Germany	1,000	7	0	50
Great Britain	10,500	0	0	2
Greenland	100,000	1,000	100	100
Iceland	50,000	50	0	500
Ireland	300	0	0	0
Italy	10,000	20	0	0
Norway	2,500,000	5	10	300
Russia	10,000	30	30	0
Sweden	183,000	1,290	79	150
Switzerland	500,000	31	0	0
United States	4,000	0	1	1
Totals	3,671,500	2,697	923	1,208

the Alpine region - in Austria, France, Italy and Switzerland. In several countries (Faroes, Great Britain and Ireland) there is no commercial fishery. The total annual commercial catch, worldwide, is probably about 3,000 tonnes.

In a few of the most northerly countries where Arctic Charr occurs, the species is very important to the subsistence fisheries of native people (e.g. in northern Canada, Finland, Greenland, Norway and Sweden). Statistics for such fisheries are notoriously difficult to obtain but it appears that the annual total catch, worldwide, is over 500 tonnes (Table 2c).

The farming of Arctic Charr, like that of Atlantic Salmon *Salmo salar*, is a relatively new practice, but one which is proving successful in a few countries (e.g. Canada, Greenland, Iceland and Sweden). There is also interest in other countries (e.g. Great Britain and Ireland) where some fish farmers are experimenting with this species. The total annual production, worldwide, in recent years is over 1,000 tonnes (Table 2d).

Major threats

A number of human activities pose serious threats to populations of Arctic Charr in many areas (Hesthagen and Sandlund 1994) and indeed, as pointed out above, many stocks have become extinct over the last century. As might be expected, the situation varies among the 16 countries in which the species occurs - some threats being more serious in some countries than others. In addition, there is considerable interaction among some of the threats discussed (e.g. agriculture and eutrophication, angling and fish introductions, etc.). Respondents to questionnaires were asked to indicate which, of a list of 14 named potential threats, were important in their areas and also to list any other threats which they felt were of significance. The results, indicated in Table 3, are listed in order of importance as perceived on a worldwide basis and discussed further below in that order.

Table 3. The principal threats to Arctic Charr and the number of countries in which each has been identified.

Threat	Countries
Fish introductions	12
Eutrophication	12
Hydropower schemes	10
Agriculture	10
Angling	10
Commercial fishing	10
Domestic pollution	8
Acid deposition	8
Forestry	8
Industrial pollution	7
Water abstraction	7
Lake drainage	6
Fish farming	6
Global warming	5
Other threats	3

Fish introductions

The ways in which introduced fish can interact with native fish have been analysed by Nilsson (1985); he suggests four options. The introduced species could: **1**) be rejected because there is no 'vacant niche' or because predators graze down the population at an early stage (e.g. the unsuccessful introductions of Rainbow Trout *Oncorhynchus mykiss* and Danube Salmon *Hucho hucho* into Scandinavia), **2**) hybridise with very closely related stocks formerly adapted to the ecosystem (e.g. the introduction of various whitefish (*Coregonus*) into lakes in Italy where they have hybridised with native stocks and with each other), **3**) eradicate or suppress (Lemly 1985) a stock that is either an 'ecological homologue' or a very available prey (e.g. the introduction of *Coregonus lavaretus* to *Salvelinus alpinus* populations), **4**) find a 'vacant niche' within the community, which means that it adapts to resources that are not fully exploited by native species and thus enable it to survive in the community (e.g. Ruffe *Gymnocephalus cernuus* (Maitland et al. 1983)).

The great majority of the fish introductions and fish transfers have been related to angling and it is important that the national angling bodies adopt a more responsible and rational attitude to their activities. There are also dangers from new fish species and diseases introduced with ornamental fish. The bulk of these fish are of tropical origin and destined for private aquaria and there is probably very little risk here. However, with temperate species there are definite disease and parasite risks associated with their introduction to the country. Even if the host fish with which a disease or parasite was introduced was unable to establish itself in the wild, the parasite might well do so by transferring to native species (Kennedy 1975).

Arctic Charr are certainly vulnerable to a variety of diseases and parasites (Curtis 1985) and though relatively little is known about the incidence of infection in individual stocks, some may be very vulnerable to the introduction of a new pest because of their previous isolation. To take one example, the crustacean gill parasite *Salmincola edwardsii* occurs commonly on Arctic Charr in five lochs in Scotland, but not, so far as is known in any others. We have no idea of the impact of this or any other parasite if it were introduced to virgin populations (cf. *Gyrodactylus* introduced to Norway from Sweden).

Some years ago, the International Council for the Exploration of the Sea adopted a code of practice to reduce the risks of adverse effects arising from the introduction of non-indigenous marine species (ICES 1973). A similar code was adopted for inland waters by the European Inland Fisheries Advisory Commission and recently the American Fisheries Society and the International Council for the Conservation of Nature and Natural Resources have issued positive statements on the question of introductions and transfers. There have also been a number of positive proposals from individual scientists (e.g. Ryder and Kerr 1984).

Eutrophication

Eutrophication from increased nutrient levels due to phosphorus, nitrogen and other nutrients being washed into lakes from agricultural activities (including afforestation) and organic sewage has changed the nature of many lakes.

The effects of eutrophication are various and include increased algal growths, potential deoxygenation of the lower cooler layer of water during stratification in summer and under ice in winter, and a tendency for the fish community to change from one dominated by salmonids to one where coarse fish predominate (Maitland 1984). Eutrophication is likely to be the main cause of the extinction of many fish in lakes.

Hydropower schemes

Hydro-electric schemes can have deleterious effects on local fisheries and this is certainly the case with Atlantic Salmon in some waters. However, Arctic Charr seem to be less affected than other salmonids, and there is evidence that some stocks (which are mainly plankton feeders) may be favoured by the fluctuating water levels, which adversely affect Brown Trout *Salmo trutta*. It is believed that, because the fluctuating levels often devastate the littoral flora and fauna (Smith et al. 1987), the trout population, which mainly feeds in the littoral area, is also adversely affected. The plankton, on the other hand, is not affected and so charr still have their main food source. Certainly many hydro-electric reservoirs have large populations of Arctic Charr and indeed new populations have developed in some reservoirs (e.g. Cruachan Reservoir above Loch Awe in Scotland) where water (and charr) have been pumped up from an established charr loch).

Agriculture

The clearing of forests for agriculture also increases the run-off of surface water and the rate of soil erosion with subsequent silting and nutrient increase in the waters draining such areas. Most types of cultivation lead to loss of soil and nutrients; deficiency of the latter is commonly overcome by the regular addition of agricultural fertilisers. These too tend to be washed off and affect the nutrient status and ecology of waters into which they drain thus causing eutrophication. There are also serious problems from pesticides, herbicides, silage and other agricultural activities.

Angling

There has been increasing controversy in recent years concerning the impact of angling on aquatic wildlife (Maitland and Turner 1987). In general, the management of fresh waters for angling poses various problems for fish. Apart from the direct effect of angling itself, fishery management practices have included the following: the complete elimination of native fish stocks using piscicides, the removal of predators (e.g. Pike *Esox lucius*) using gill nets and other means, the application of lime and occasionally fertilisers to 'improve' water quality, the regular introduction of non-native stocks of salmonids (including Salmon, Brown Trout and Sea Trout - some of foreign origin), the development of put-and-take fisheries (mainly for Brown and Rainbow Trout) where farmed fish are released at catchable size to be caught at any time thereafter (sometimes the day after release), the transfer of coarse fish (sometimes being used as livebait) from one water (sometimes one country) to another, the wholesale removal of riparian vegetation of importance to wildlife.

The main conservation concerns in relation to angling for Arctic Charr include overfishing which is certainly a potential threat, especially in very small lochs where the stocks are likely to be small. It is a characteristic feature of catch records of Arctic Charr in Scotland that on occasion huge bags may be obtained; hundreds may be taken in a single day and small stocks are thus vulnerable. It is a common feature of angling management that when catches are low, stocking is suggested as the panacea. Apart from the possible introduction of disease, stocking is often a very bad policy, especially where alien stocks are used, because of possible damage to genetic integrity of local stocks. Although relatively few anglers fish actively for Arctic Charr at the moment and none are known to use fish as livebait, its use is a very real threat to sensitive native fish such as Arctic Charr if any of the livebait species escape or are released - as has happened on several occasions at Loch Lomond (Maitland and East 1989).

Commercial fishing

Intensive commercial fishing on vulnerable migratory stocks or using modern gill nets indiscriminately can lead to stocks declining to such a point that they never recover. This is believed to have happened at St. Mary's Loch in Scotland many decades ago where the annual run of fish into a local burn was overfished by local shepherds.

Domestic pollution

The influence of polluting substances on natural waters is variable according to local conditions and organisms within the water concerned. Pollutants can act in three main ways: by settling out on the substrate and smothering life there, by being acutely toxic and killing organisms directly, or by reducing the oxygen supply so much as to kill organisms indirectly. Since even clean cold water holds only about 12 mg l^{-1} oxygen, there is never a great deal available compared to air, and many fish populations have already been eliminated through deoxygenation.

Acid deposition

Acid precipitation has caused major damage to fish stocks in various parts of the world including North America, Scandinavia and the British Isles. Salmonid fish are particularly vulnerable, but all fish species have been affected. A survey of fish populations in 50 lakes in south-west Sweden showed that, in acidified lakes, Brown Trout, Arctic Charr, Roach *Rutilus rutilus* and Minnow *Phoxinus Phoxinus* were all affected (Almer et al. 1974). Atlantic Salmon, have been completely eliminated from several Swedish rivers over recent decades (Wright et al. 1977). Acid precipitation has also devastated fish populations in southern Norway where the principal fish species affected are Atlantic Salmon, Brown Trout, Arctic Charr and Brook Charr *Salvelinus fontinalis* (Almer et al. 1974). Several workers have tried to define and classify various levels of acidification and the resultant fish communities. Kelso and Minns (1981) have produced such a scheme which, if applied to recent conditions in charr lochs in southern Scotland fits the disappearance of charr there. In some areas, acidified lakes have been made suitable for Arctic Charr again by liming (Nyberg 1988).

Forestry

The impact of coniferous afforestation and forestry practice on freshwater habitats has caused much concern in recent years. The effects of each stage of the forestry cycle - ground preparation, tree planting to canopy closure, the maturing crop and felling - may all have an impact on local fresh waters (Maitland et al. 1990). The physical aspects of afforestation affect: (i) the hydrology of streams, as shown by (a) increased loss of water through interception and evaporation from the coniferous forest canopy, and (b) a tendency to higher flood peaks and lower water levels during droughts; (ii) the release of sediments to streams because of erosion following ploughing and weathering of exposed soils; (iii) reduced summer water temperatures in afforested streams where the channel is shaded.

The principal chemical changes in fresh waters in afforested catchments include: (i) increased nutrient levels from the leaching of exposed soils and applied fertilisers, and (ii) the acidifying effect of air pollutants (especially sulphates) which are intercepted by conifers (as airborne particles) and then transferred to the ground (by rain - itself often very acid) and eventually to adjacent water courses. The base-richness of local soils and rocks is of major importance here, for it is only in areas lacking basic ions that acidification occurs. Much of the biological damage is due to the high amounts of aluminium (leached from the acid soils).

It seems highly likely that recent extensive afforestation in the catchments of Lochs Grannoch and Dungeon, where Arctic Charr have recently become extinct has exacerbated acidification already taking place in their headwaters.

Industrial pollution

Industrial pollution may be caused in various ways - by the addition of substances which may act as acids, alkalis or as nutrients. Radioactive substances, tainting of domestic water supplies, and alteration of water temperatures are other examples. Effluents with high suspended solids are typical of mining industries, poorly treated domestic sewage, and various washing processes. Most of the solids settle out soon after discharge, at a rate dependent on their size, density and local current conditions. The effect of inorganic particles is mainly a physical one, and plants and invertebrates may be completely covered and destroyed. Fish often die through their gills becoming clogged. If the particles involved are organic, their decay may add the problem of deoxygenation to that of alteration of the substrate.

The impact of toxic substances on organisms in natural waters is complicated by the fact that different species have varying resistance thresholds to poisons (which may act variably at different temperatures) and that some poisons are cumulative in their effect and other are not. Most toxic substances originate from industrial processes, though some arise from mining and agriculture. Organic materials in sewage effluents are a source of major pollution of fresh waters. Though these effluents often contain plant nutrients, these cannot be utilised for some time because of the high oxygen demand of the decomposing organic material. In extreme cases, especially in lakes and slow-flowing rivers, so much oxygen is used up that anaerobic conditions result and no organisms other than bacteria and some fungi can exist.

Water abstraction

Water supply schemes may also have significant effects on fish populations, especially where large volumes of water are transferred from one catchment to another. In England, for instance, large numbers of Arctic Charr and Schelly, *Coregonus lavaretus* are pumped out of Haweswater each year as part of the water supply system supplying Manchester (Maitland 1985a). The impact can be particularly serious where no account is taken of local fish ecology when the engineering works are being designed. This can lead to serious damage to fish stocks as, for example, at Loch Lee where substantial numbers of adult Arctic Charr are washed out of the loch each year at spawning time, due to construction of a spillway near charr spawning grounds.

Lake drainage

The draining of lakes and marshlands and the straightening and canalisation of river courses to prevent flooding is often done in a crude way and often the original habitat may be so altered that it can never return to its original condition. Recolonisation by plants and animals from other areas may still be possible but, because of simplification of the environment, the decrease in microhabitats leads to impoverishment. Piping or ditching land to improve drainage increases the dangers resulting from from higher water levels in wet weather and lower levels in dry weather, both a direct result of the faster run-off of water from the land.

Fish farming

The success of the farming of Atlantic Salmon and Rainbow Trout has led at times to an overproduction of these species with consequent reduction of prices in the market place and many farmers have been looking for possible alternative species which might have a high market value. A number of countries are now rearing Arctic Charr on an experimental basis and are finding that this species has considerable potential.

In Scotland, the recent advent of fish farming in several lochs containing Arctic Charr has led to a number of changes. There is clear evidence that charr learn to aggregate around the fish cages and feed on waste food falling through the meshes. These charr also grow much larger than normal and all the recent rod caught records (the British record weight has trebled in less than five years) have been of fish taken in the vicinity of cages in Scottish lochs. However, many of the Rainbow Trout being reared in these cages escape and grow to a large size, becoming potential predators of Arctic Charr and of Atlantic Salmon smolts.

Perhaps even more worrying than the escape of farmed Rainbow Trout or the effects of waste food and faeces or transfer of disease to Arctic Charr is the potential threat posed by the development of charr farms to the genetic integrity of individual stocks if charr are moved around for commercial purposes.

Global warming

As well as the many current threats to their existence, native salmonids face the prospect of additional problems in the future. The most topical of these is global warming and the present distribution and composition of our freshwater fish communities could be radically altered if there are significant increases in ambient temperatures. Most affected will be the cold-loving species such as virtually all the salmonines, including salmonids, thymallids and coregonids (Maitland 1991).

If the temperature rises at present forecast by some scientists do take place, the southern parts of Europe, North America and Asia may become totally unsuitable for anadromous salmonids - this has already happened historically to Arctic Charr which migrate to the sea only in the extreme north of their range. Consequently Salmon and Sea Trout could be restricted to northern waters and even Brown Trout could be rare in the south. Many populations of Arctic Charr may also disappear, especially those in the south and at low altitudes. Conservation policies for salmonid fish and fisheries must make provision for such radical possibilities as the 21st Century approaches.

Other threats

Apart from the above, few other human activities are felt to be threats to populations of Arctic Charr at the moment. However, respondents to the questionnaire did list the following as potential threats,now or in the future: subsistence fisheries (in parts of Canada), the introduction of invertebrates, such as *Mysis*, (in Sweden) and the use of dynamite for geological inspection (as has happened already in at least three lakes in Italy).

Extent of protection

Freshwater fish are protected in a variety of ways (Table 4) which vary considerably among the sixteen Arctic Charr countries. The two main forms of protection are through the creation of protected sites of one kind or another (usually

Table 4. The protection given to Arctic Charr in different countries.

Country	(a) Fishery legislation	(b) Nature legislation	(c) Nature reserves	(d) Active conservation	(e) Other controls
Austria	+	+	-	+	-
Canada	+	+	+	+	+
Faroes	+	+	+	-	-
Finland	+	-	+	+	+
France	+	+	-	+	-
Germany	+	-	-	+	-
Great Britain	+	-	+	+	-
Greenland	+	+	-	+	-
Iceland	+	-	-	-	-
Ireland	-	-	-	-	-
Italy	+	+	+	+	-
Norway	+	-	-	+	-
Russia	+	-	-	-	-
Sweden	+	-	-	+	+
Switzerland	+	-	-	+	-
United States	+	-	+	+	+
Totals	15	6	6	12	4

known as nature reserves or national parks) and a number of individual pieces of legislation. Most of the latter are concerned with fish species of sporting or commercial interest but there are notable exceptions, which though essentially fisheries legislation do help to protect other freshwater fish and their environment. However, most of these relate directly to the fishery and farming interests of Atlantic Salmon, Brown and Rainbow Trout and other important commercial species and may only incidentally help other species such as Arctic Charr.

Public perception of Arctic Charr

The public perception of Arctic Charr varies enormously around the world. In some countries, where it is important as a commercial species, it is well known among the public in general. In other countries it is often poorly known and this is true even in some where there are quite large numbers of populations (e.g. Scotland).

Accordingly, the artefacts and publicity surrounding Arctic Charr vary widely. Only one postage stamp is known (from Sweden) and it never seems to have appeared on a calendar, though some postcards have been produced. However, articles on Arctic Charr in angling journals and in natural history magazines are not uncommon. There are many paintings and a number of good illustrations of Arctic Charr in general books about fish. A few ornaments are known and some pottery featuring charr - e.g. the charr pots made to hold 'potted charr' from the Lake District of England (Kipling 1991) - is now very valuable.

Conservation

One of the desirable preliminary objectives of any conservation programme for Arctic Charr are comprehensive database/registers of all important stocks, in much greater detail than has been available before (Maitland 1972). The author already has such a database for all known populations of Arctic Charr in Great Britain. Special attention must be given to 'unique' stocks, either locally (Maitland 1985b) or on a national or international basis (Maitland et al. 1984). With existing knowledge, an exact definition of which populations would come into this category is not easy, but certainly stocks which showed unusual features of morphology (e.g. the two distinct stocks of Arctic Charr in Loch Rannoch: Walker et al. 1988) or behaviour, or where there seemed to be good evidence that the stock was aboriginal, would qualify here (Stephen 1984). In addition, stocks which were part of unusual or unique communities would also merit conservation listing, for obvious reasons - as would the stocks held in fish farms in each country (Nyman and Henricson 1991). Considerable research remains to be carried out before any definitive list for Arctic Charr can be produced.

Such stocks merit special conservation treatment, including strict measures to control land use in their catchments and to avoid genetic contamination from other stocks. In addition it would be ideal to avoid charr farms within the catchments of important stocks. It is important also to persuade fishery managers to distinguish between 'wild' fisheries (in unstocked natural waters) and artificial 'put-and-take' fisheries (in stocked reservoirs). Ideally, each fishery authority should compile a register declaring which waters come into each category. This would afford some protection to the integrity of wild stocks, allow consistent management over the years and offer a clear choice to anglers of wild fish or farmed fish.

Thus the Arctic Charr is under threat in various parts of the world and has disappeared from a number of waters. It is clear that active conservation measures are necessary now if vulnerable stocks are to be saved and the genetic integrity of others preserved. The main future options for the conservation of this (and many other fish species around the world) are habitat management and restoration, stock transfer to new sites, captive breeding and cryopreservation (Maitland and Lyle 1992). The first two of these are the most useful for the long-term conservation of threatened species. Improved legislation would also help, especially in relation to preventing the import and transfer of potentially harmful species - including stocks of Arctic Charr from other countries.

Habitat management and restoration

Habitat management and restoration should be a major goal in the conservation of most species and communities. Obviously enormous damage has been done to many fish habitats and the situation is often not easy to reverse - especially in the short term where fish species or communities are severely threatened. In many cases, potentially unique stocks have completely disappeared. Even where habitat restoration is contemplated, stock transfer (discussed below) could be an important interim measure. However, there are a number of important examples of habitat restoration in temperate areas and it should be emphasised that habitat restoration, protection and management are the principal long-term means through which successful fish conservation will be achieved.

Many fresh waters in Scandinavia, North America and the British Isles have lost their fish populations over the last three decades because of acidification, and altogether many thousands of individual stocks have disappeared (Maitland et al. 1987, Steinberg and Wright 1994)). Various ways of ameliorating the impact of acid precipitation have been investigated, most of them involving the addition of calcium in some form, either directly to the water body or to the catchment of the system involved. Most of the pioneering work in this form of habitat restoration has been carried out in Scandinavia.

Translocation

One of the most positive areas of management for endangered stocks of fish lies in the establishment of new populations - either to replace those which have become extinct or to provide an additional safeguard for valuable stocks in threatened waters (Maitland 1985b). Any species which is found in only a few waters could be in potential danger and the creation of additional independent stocks is an urgent and worthwhile conservation activity.

This can be done without any threat to the existing stocks. It is possible to obtain substantial numbers of fertilised eggs by catching and stripping adult fish during their spawning period. They can then be returned safely to the water to spawn in future. Most fish produce a considerable excess of eggs and so substantial numbers can be taken at this time without threat to the parent population. Having identified an appropriate water in which to create a new population this can be initiated by placing the eggs there, or hatching the eggs in a hatchery and introducing the young at various stages of development. Depending on the state of the parent stock, adults may also be moved in some cases.

As well as promoting the importance of habitat management and conservation at specific sites, the author has implemented trial programmes of translocation for Arctic Charr (as well as Powan *Coregonus lavaretus* and Vendace *Coregonus albula*) to create new safeguard populations (Maitland and Lyle 1990). Specific criteria have been developed in planning such translocations. For example, the translocation activities must pose no threat to the parent stock, nor to the ecology or scientific interest of the introduction site, which clearly must be ecologically suitable. In general, sites from which the species concerned has disappeared should be considered unsuitable unless the causal factors have been identified and removed. Ideally, the introduction site should be in the same catchment, or the same geographic region as the parent stock; or in the same geographic region as a former stock, now extinct. Permission must be obtained from riparian owners, relevant statutory authorities, or conservation agencies in the case of nature reserves. Stock may be transferred as eggs, fry, juveniles or adults, but the removal of adults could pose a threat to the parent stock. Special consideration should be given to the genetic integrity of the stock to be translocated. Once the stock has been defined, maximum genetic diversity should be sought by selecting material widely in space and time. The transfer of undesirable diseases or parasites can be achieved by taking eggs only from the parent stock and checking for disease. Notes of each translocation experiment should be kept and details published where relevant. Finally, it is important that the fate of the translocated stock is monitored.

In Scotland, the stock of Arctic Charr in Loch Doon (Maitland et al. 1991) seemed clearly to be a case where the creation of new stocks is valid (and indeed urgent) in view of the disappearance of the populations in other lochs in southwest Scotland and the threat to the stock in Loch Doon itself. In the autumns of 1986, 1987, 1988, 1989 and 1990 fertilised eggs were obtained in early October. These eggs were hatched under controlled conditions and numbers of young fish (and some adults) have been introduced to two large waters in the Scottish Borders - Megget and Talla Reservoirs. It is believed that these will provide ideal conditions for new populations. Megget Reservoir is linked to St. Mary's Loch where Arctic Charr are now extinct. Already, there is evidence that the adult charr in Talla Reservoir have bred successfully over two spawning seasons and in 1991 an adult charr was caught by an angler in Megget Reservoir.

Captive breeding

Captive breeding is widely used throughout the world for a variety of endangered animals, including fish (Maitland and Evans 1986). However, for most animals it can really only be regarded as a short term emergency measure, for a variety of genetic and other difficulties are likely to arise if small numbers of animals are kept in captivity over several generations or more. Captive breeding in the long-term does not seem appropriate for most of the larger northern freshwater fish species at present under threat, worldwide, including Arctic Charr.

However, short-term captive breeding involving only one generation does have some advantages for a number of species and has already been carried out in the present project with Arctic Charr. It is especially relevant where translocations are desirable but it is difficult to obtain reasonable numbers of eggs or young because of ecological or logistic constraints. In such cases there are considerable advantages to be gained in rearing small numbers of stock in captivity and then stripping them to obtain much larger numbers of young for release in the wild. Because of genetic problems related to inbreeding and loss of genetic diversity it should not be carried out for more than one generation from the wild stock.

Cryopreservation

Modern techniques for rapid freezing of gametes to very low temperatures have proved successful for a variety of animals, including fish. After freezing for many years and then thawing the material is still viable. However, the technique is successful only for sperm and though much research is at present being carried out on eggs, no successful method of cryopreservation has yet been developed. The technique is thus at the moment only of limited value in relation to the conservation of fish species.

However, where a particular stock seemed in imminent danger of dying out it would be worthwhile giving consideration to saving at least some of its genetic material through the cryopreservation of sperm. At the very least these sperm can be used to help maintain the genetic diversity of captive stocks of arctic Charr which are being kept over more than one generation. When it is possible to preserve female gametes in a similar way, the technique will have obvious possibilities in relation to the long-term conservation of a wide variety of fish species.

Discussion

There have been previous reviews of the status of Arctic Charr populations in certain geographic areas (Went 1971, Maitland 1983, McCart 1980, Clements 1988, Hammar 1989, Kallio-Nyberg and Koljonen 1991) and these will prove to be valuable baseline studies in the future. However, although there have also been some worldwide reviews of fisheries for Arctic Charr (MacCrimmon and Gots 1980), the present study is believed to be the first attempt at an international synthesis of the overall status of this species. Although the Arctic Charr is not threatened on a worldwide basis and therefore not listed internationally as a Red Data Book species (IUCN 1990), it does now appear in some national Red Data Books (e.g. Keith et al. 1992, Whilde 1993).

Internationally, relatively little attention has been paid to the conservation of freshwater fish, including Arctic Charr, but fortunately, this attitude has changed in recent years and there is now an increasing interest in this topic in most parts of the world (e.g. McDowall 1983, Pollard et al. 1990. Nyman 1991). In North America in particular, there have been several important initiatives (Johnson and Rinne 1982, Williams and Miller 1990) including the creation of a facility devoted entirely to the captive breeding and rearing of rare species. The present review of the world status and conservation needs of Arctic Charr will hopefully provide a foundation for the conservation of this important northern species and it is hoped that at least some of the proposals emanating from it will be implemented in future years.

As well as the implementation of conservation management programmes for Arctic Charr, research and monitoring studies are also needed to aid such management and to maintain an awareness of the status of important species. Practical conservation measures of this kind, coupled with further studies of charr distribution and ecology in more countries, are essential if the future of this attractive and potentially valuable fish is to be secured for the future.

The recognition of especially important sites for Arctic Charr, even in areas where the species is common and thus complete databases are difficult, is important. For example, in Scotland, Loch Meallt is the only site where Arctic Charr and Three-spined Stickleback occur together in the absence of other species (Campbell 1984); Loch Eck is unique in the British Isles in the composition of its fish community which includes Arctic Charr (Maitland 1985b). Included in the development of regional databases should be relevant information from systematic studies (e.g. Nyman 1972, Ferguson 1981, Gardner et al. 1988, Hartley 1990).

The general conclusion from the review is that, although there has previously been some legislation and management in relation to both fish and various general aspects of conservation (such as the establishment of nature reserves), little of this has been aimed directly at the protection of threatened fish species. This situation must be improved if further valuable stocks of native species, such as Arctic Charr, are not to be lost. However, there is every reason to hope that, given adequate support, Arctic Charr and other valuable native species can be managed more positively, thereby saving for posterity this valuable and renewable resource, so important for scientific, recreational, commercial and aesthetic purposes.

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Ontogenetic Changes in Skull Morphology of *Salvelinus fontinalis* and *S. namaycush* with Comments on Heterochronies in Evolution of Salmonids

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Abstract

Ontogenetic changes of diagnostically important osteological characters from hatching to adulthood were studied in *Salvelinus fontinalis* and *S. namaycush* in order to evaluate the role of developmental factors (heterochronies) in morphological evolution of these species and some other salmonids. The divergence of *S. namaycush* and *S. fontinalis* is a case of "dissociated heterochrony", each species displaying both paedomorphic and peramorphic character states. *S. namaycush*, in comparison with most representatives of the *S. alpinus* complex, has a juvenilized skull morphology. Within the *S. alpinus* complex, chars from the Taimyr Peninsula are most juvenilized. *Salvethymus svetovidovi* is a paedomorphic taxon characterized by reductions in skeletal elements appearing late in the ontogeny and by juvenilized shapes of bones. *Brachymystax lenok* has juvenilized skull morphology in comparison with *Salvelinus*. Shapes of some bones diagnostic to the two genera (e.g. vomer) differ from the moment of their appearance in the ontogeny. A number of morphological parallelisms exist between *S. namaycush* and sharp-snouted lenok, *S. fontinalis* and blunt-snouted lenok. Progressive ontogenetic acceleration of skull morphology is observed in the family Salmonidae, *Brachymystax* being the most juvenilized, *Oncorhynchus* the most ontogenetically advanced genus.

Keywords: *Salvelinus*, Salmonidae, skull morphology, ontogeny, heterochrony.

Introduction

Studies of the systematics and evolution of char traditionally concentrate on adult specimens (Vladykov 1953; Morton and Miller 1954; Qadri 1964; Behnke 1980, 1989; Cavender 1980; Glubokovsky 1977, 1980; Savvaitova 1989). However, adult morphology is only the final episode in the chain of ontogenetic changes taking place in a fish throughout its life. Subtle shifts in rate and timing of ontogenetic processes known as heterochronies (Gould 1977; Alberch et al. 1979; McNamara 1986) can lead to pronounced coordinated changes in adult characters. Ontogenetic data can thus add much to our understanding of patterns and mechanisms of morphological evolution in chars.

Insights into the problems of heterochronies, paedomorphosis and juvenilization in chars can be found in Mina (1962), Vasil'yeva (1977, 1980b), Balon (1979, 1980a, 1981, 1984), Barbour (1984), Maekawa (1984) and Skulason et al. (1989). Despite these works, the role of heterochronies in char evolution is poorly understood and there is little information about the patterns of ontogenetic changes of most characters important for the systematics of char, especially in early ontogeny.

The aim of this paper was to evaluate the possible role of ontogenetic factors (heterochronies) in the morphological evolution of some diagnostically important, primarily osteological, characters of *Salvelinus namaycush* and *S. fontinalis.* Changes in form were studied from the moment close to the appearance of recognisable structures in ontogeny to adulthood. The data obtained were then used to analyse, from a developmental viewpoint, the morphological peculiarities of some other salmonids. Lake and brook chars were chosen because they exhibit distinct differences in morphology and life history. They also show little intraspecific variability in comparison to *S. alpinus.* Traditionally, *S. namaycush* and S. *fontinalis* are assigned to different subgenera (Behnke 1980, 1989; see also Grewe et al. 1990 for molecular evidence). The latest karyological (Cavender and Kimura 1989) and molecular (Phillips and Pleyte 1991, cited after Pleyte et al. 1992; Phillips et al. 1992; Pleyte et al. 1992) data indicate the possibility of a sister-group relationship between them. Our results were used to evaluate the role of ontogenetic factors in the divergence of these two species and some other salmonids.

Materials and Methods

The ontogenetic series of chars used in this study were obtained from Hills Lake and Chatsworth hatcheries, Ontario, Canada. The series from Hills Lake hatchery included young-of-the-year of the 1991 generation: *S. namaycush* sampled at the age of 24, 61, 70, 88, 104, 116, 130, 151, 165 and 180 days after peak of hatching (samples 1-10 of *S. namaycush* 0+), and *S. fontinalis,* age 38, 61, 84, 102, 116, 130, 144, 165, 179, 194 days after peak of hatching (samples 1-10 of *S. fontinalis* 0+); yearlings of both species (age about 400 days) of the 1990 year class and older fish: *S. fontinalis* - 35 months (*S. fontinalis,* adults), *S. namaycush* - 59 months (*S. namaycush*, adults - 1). The series from Chatsworth hatchery was represented by *S. namaycush* only, age 14, 21, 26, 28, 30, 33, 40, 44, 47, 56, 65, 72, 79, 86, 100, 114 (young-of-the-year, 1991 year class) and about 400 days (yearlings of the previous year). At Hills Lake hatchery mean water temperature during most of incubation and the first month after hatching was +4.0 - 4.5°C. At Chatsworth hatchery, incubation temperature was + 7.0 - 7.3°C. The series of 0+ -fish from these hatcheries will be referred to as the +4°C-series and the +7°-series, respectively. Samples of juveniles included 5-25 specimens each, half of them fixed in 4% formalin and half fresh-frozen, although five samples were represented by fixed and one by frozen fish only. Each sample of adults included three fresh-frozen heads.

Additional series of the two species were reared from fertilized eggs obtained from Finnish hatcheries by courtesy of M. Kaukkoranta. Incubation of these eggs, rearing, and sampling of larvae and juveniles was carried out at the Department of Ichthyology of the Moscow State University at + 2.1°C by M. Pichugin. The material kindly provided by him included formalin-fixed samples of *S. namaycush* (age 0, 5, 10, 44, 58, 65, 80, 87, 93, 106, 114, 119, 135, 151, 185 days) and *S. fontinalis* (age 0, 6, 10, 68, 73, 75, 80, 86, 90, 97, 120 days and an older young-of-the-year for which age was not recorded). There were 1-5 specimens in each sample referred to as the + 2°-series. Five frozen heads of adult *S. namaycush* from lake Travaillant, Mackenzie drainage, Canada, (*S. namaycush*, adults-2) were obtained through the kindness of J. Reist and J. Johnson (Freshwater Institute, Department of Fisheries and Oceans, Winnipeg, Manitoba). Because of prolonged hatching (about a week in the +4°-series), the "age" of fish in samples is only approximate for each individual.

Formalin-fixed fish were cleared and stained (Jakubowsky 1970) or double-stained (Balon and Flegler-Balon 1985). Fresh-frozen fish were used for making disarticulated osteological preparations as described in Savvaitova et al. (1977) (adults) or prepared using 3-5% KOH with alizarin to remove flesh and stain bones (0+, 1+ -fish). Cleared preparations were used for determining the sequence of ossification, measuring chondrocraniums of 0+ fish and measuring bones in samples represented by formalin-fixed specimens only. All other measurements were performed on disarticulated preparations.

The scheme of osteological measurements included: Lbas - length of skull base from the anterior edge of vomer to the posterior edge of basioccipital; in % of Lbas: Ch.H - maximal chondrocranium depth (at the level of supraoccipitale), Ch.S - maximal chondrocranium width (at the level of sphaenotica), DF - size (maximal length) of dorsal (postpineal) fontanelle; Lch - length of dorsal surface of chondrocranium; in % of Lch: L.eth - length of ethmoidal region; in % of maximal chondrocranium width: S.eth - width of ethmoidal region; in % of the length of corresponding bone: Op.W - operculum width, Pop.W - praeoperculum width, Seth.W - supraethmoideum width, Seth.Wh - width of shaft of supraethmoideum (measured only in *S. namaycush* 1+ and *S. namaycush* adults-2), F.W - frontale width, F.W1 - width of the anterior part of frontale (next to the tapered anterior end); Pm.H - praemaxillare depth, Mx.W -maxillare width, D.H - dentale depth (width), D.S - "length of the notch" in dentale, D.R - position of the posterior end of the coronoid process, A.R - position of the anterior end of the dorsal process of articulare, P.W - width of the anterior (ethmoidal) part of parasphenoideum, P.Wm - minimal width of parasphenoideum (in the orbital region), V.W - vomer width, G.W - glossohyale width, H.W - hyomandibulare width, V.1 - distance between the bases of anterior and posterior vomerine teeth in % of vomer width; P.W1 - width of anterior part of parasphenoideum in % of the width of its posterior part. In every case, unless indicated, these are maximal widths, depths and lengths of the bones or their parts. Measurements correspond to those illustrated in Savvaitova et al. (1977) and are given the same abbreviations, with the following exceptions: H.W was measured together with the opercular process, Seth.W is maximal supraethmoideum width corresponding either to Seth.Wc (in all specimens studied by us except adults of *S. namaycush*) or to Seth.Wh in Savvaitova et al. (1977). V.1 and P.W1 are new characters, measurements needed for their estimation not illustrated in Savvaitova et al. (1977) are shown in Figs. 1 and 3, respectively.

Measurements of skulls of juveniles were performed with an ocular-micrometer under a dissecting microscope, those of adults with dividers. Fork length (FL) in 0+ fish was measured only in cleared or formalin-fixed specimens because of the poor condition of some frozen specimens. For that reason estimates of minimal, maximal and mean FL of frozen 0+ - fish used for bone measurements are those of 10 cleared and formalin-fixed specimens from the same sample.

When estimating the ossification sequence, the following procedure was used. After determination of presence-absence of all ossifications in all specimens, the number of specimens within the series lacking the ossification was calculated for each of the 100 elements studied. Based on these data, elements were ranked within each series. The element present in all specimens received the loweset rank. Absent in all specimens was given the highest rank. Elements absent in the same number of specimens received the same rank. Mean ranks were calculated over three series for *S. namaycush* and over two series for *S. fontinalis.* These means were used for final ranking of the elements.

Approximate FL of adults was calculated using head length/FL ratios given in Qadri (1964). Nomenclature of skeletal elements corresponds to that in Norden (1961) and Svetovidov (1975).

Results

Morphological differences between *S. namaycush* and *S. fontinalis* were described by Vladykov (1954), Morton and Miller (1954) and in detail by Qadri (1964). Before describing osteology, it should be mentioned that larvae of both species, have a non-forked caudal fin, its shape changing to forked in *S. namaycush* later in ontogeny. Thus, caudal fin shape in adult *S. fontinalis* is juvenilized (paedomorphic) but advanced (peramorphic) in *S. namaycush*. Adult brook chars also deviate less from juveniles in the number of gill rakers, but more in body depth and jaw length (Morton and Miller, 1954; Quadri, 1964; present study). Here and below we shall use the terms "paedomorphic", "paedomorphosis" and "peramorphic", "peramorphosis" as defined in McNamara (1986) with the exception that we compare not descendants and ancestors but related extant species and speak about characters' states being paedomorphic (peramorphic) in one of them compared to the other(s).

Ontogenetic changes in skeletal proportions

Ontogenetic changes in the shapes of several bones are shown in Figs. 1-4. Changes in the supraethmoideum, vomer, glossohyale, praeoperculum, Figs. 1 and 2, are for both species. Changes in the rest of the bones, Figs. 3 and 4, are for *S. namaycush* only. Changes in osteological measurements are given in Tables 1 and 2 and in Figs. 5 and 6. The results of *t*-tests of differences between means of characters in samples of *S. namaycush* and *S. fontinalis* of comparable FL are presented in Table 3. It should be noted that, in a number of cases, the lack of significant differences between species as indicated in Table 3 is due to the low number of specimens in compared samples (e.g. *S. fontinalis*, adults N=3). Ontogenetic changes in the skulls of the two species are summarized in Table 4.

The most important osteological difference between adult *S. namaycush* and *S. fontinalis* is

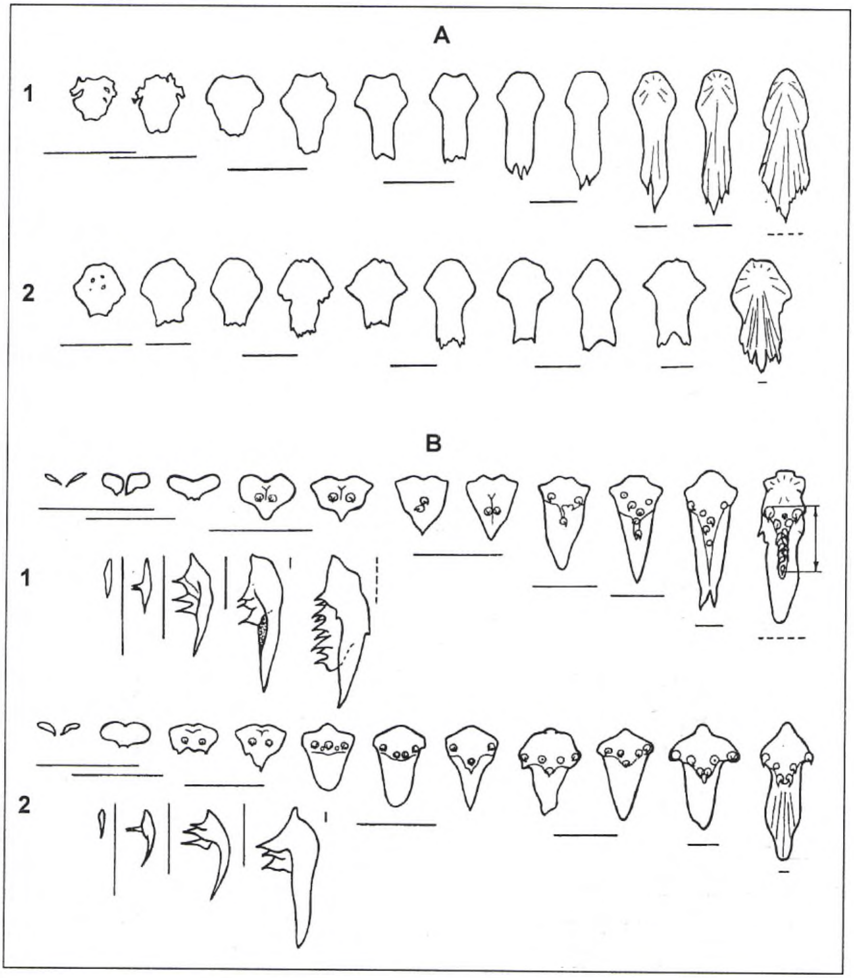

Fig. 1. Ontogenetic changes in shapes of supraethmoideum (A) and vomer (B) in *S. namaycush* (1) and *S. fontinalis* (2). All temperature series combined (mainly +4°-series). Measurement of the distance between the bases of anterior and posterior vomerine teeth shown by arrows. Scale bar: solid line - 1 mm, broken line - 10 mm.

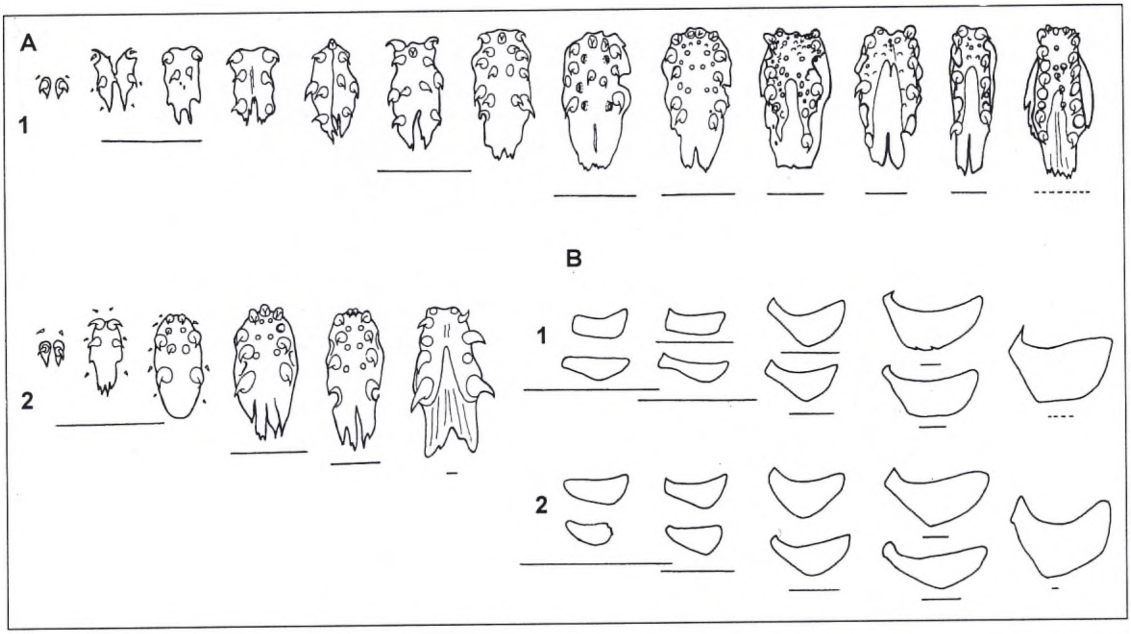

Fig. 2. Ontogenetic changes in shapes of glossohyale (A) and suboperculum (B) in *S. namaycush* (1) and *S. fontinalis* (2). All temperature series combined (mainly +4°-series). Scale bar: solid line - 1 mm, broken line - 10 mm.

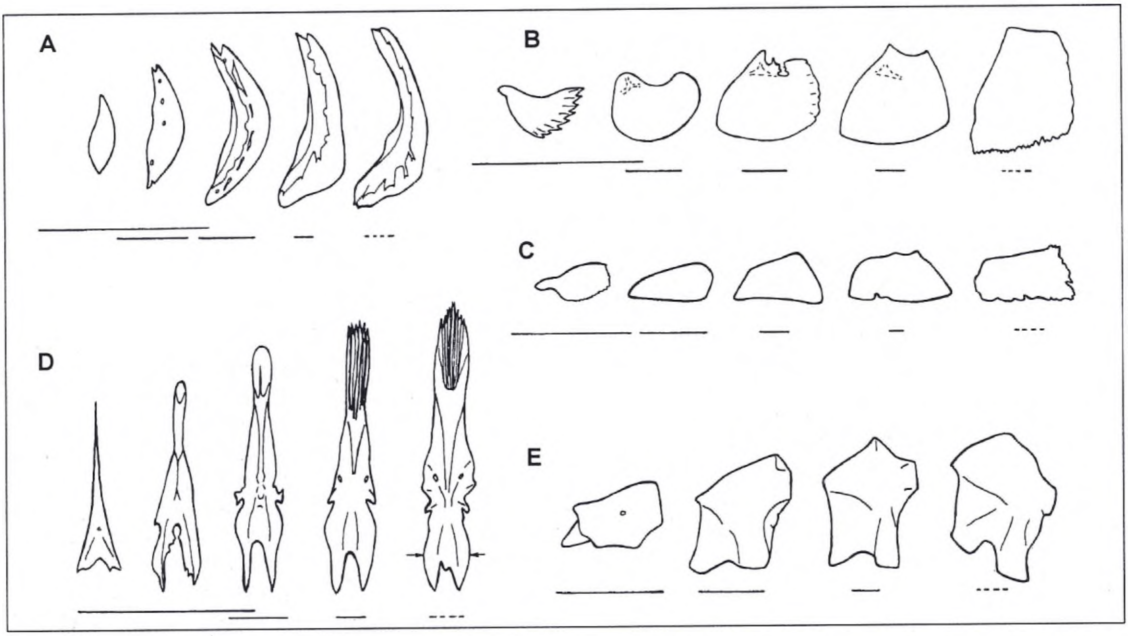

Fig. 3. Ontogenetic changes in shapes of some bones of *S. namaycush:* A - praeoperculum, B - operculum, C - interoperculum, D - parasphenoideum, E - hyomandibulare. All temperature series combined (mainly +4°-series). Measurement of the width of the posterior part of parasphenoideum shown by arrows. Scale bar: solid line - 1 mm, broken line - 10 mm.

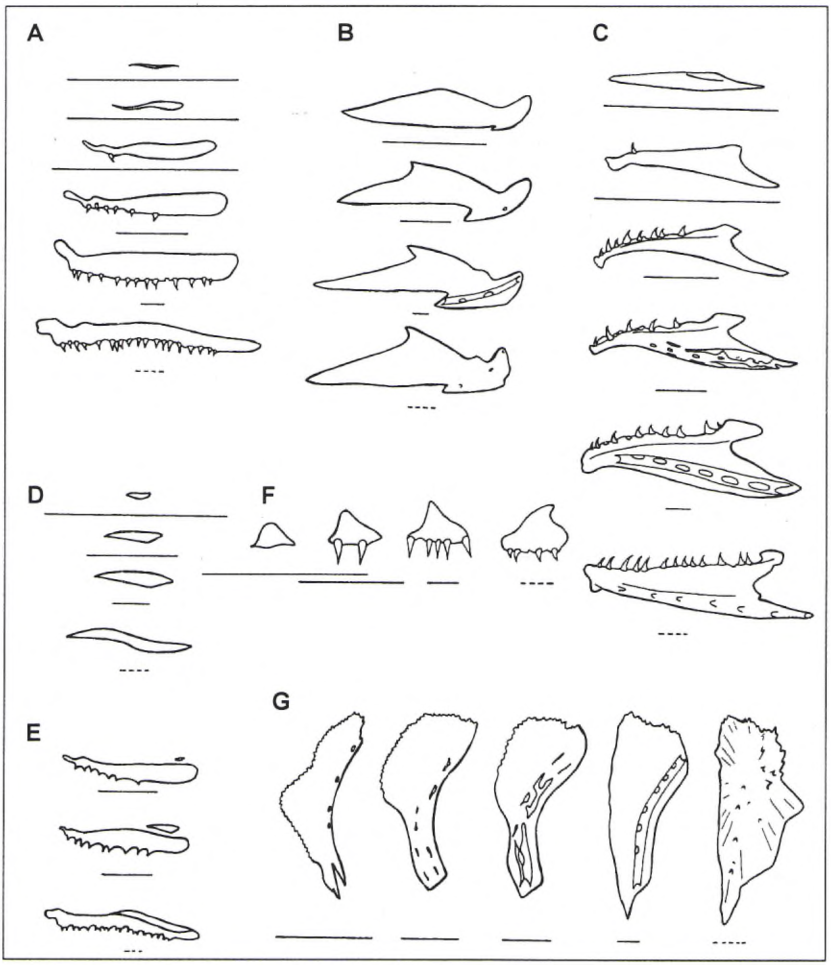

Fig. 4. Ontogenetic changes in shapes of some bones of *S. namaycush:*
A - maxillare,
B - articulare,
C - dentale,
D - supramaxillare,
F - praemaxillare,
G - frontale,
E - changes in the position of supramaxillare in relation to maxillare. All temperature series combined (mainly +4°-series). Scale bar:
solid line - 1 mm,
broken line - 10 mm.

in the shape of the supraethmoideum, which is long and narrow in *S. namaycush*, and shorter and wider in *S. fontinalis* (Kendall, 1919; Qadri, 1964). In both species, the anlage of this bone is short and wide and the bone rapidly elongates backwards during the first year of life (Fig. 1A). Consequently, its width in % of its length (Seth.W) decreases, this decrease proceeding at a higher rate in lake char than in brook char (Figs. 1A, 6A, Table 2). Thus, the unique shape of the supraethmoideum in *S. namaycush* is the result of a heterochrony - acceleration of the bone elongation in comparison with *S. fontinalis*. At late ontogenetic stages, in adults of *S. namaycush*, the direction of Seth.W change is reversed as a slight widening of the bone, shaft in particular, takes place after its elongation stops. This process can be better illustrated by changes in the relative width of the supraethmoideum shaft (Seth.Wh). In *S. namaycush* 1+ Seth.Wh is 13.6-22.2 (19.2±0.83), N=10; in *S. namaycush* adults-2, 29.6-33.9 (31.7±0.93), N=4, and the difference in means is significant (P<0.001).

The shape of the vomer, with an elongated tooth crest attached to the shaft in the lake char, short and non-attached in the brook char, is another diagnostic feature of the two species. In both of them, the vomer appears as a paired structure (Qadri 1964; Alekseyev 1993) which, after fusion of the two halves, elongates posteriorly like the supraethmoideum, V.W rapidly decreasing (Figs. 1B, 6B, Table 2). The tooth

Table 1. Measurements of chondrocranium of *Salvelinus namaycush* and *S.fontinalis* (0+ fish from +4°-series). FL in mm, lim - limits (minimum and maximum), M - mean, m - standard error of M. Refer to text for details of measurements and definition of symbols.

#	Sample	FL	*N*	Ch.H		Ch.S		Df		L.eth		S.eth	
				lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m
I	S.nam.,0+	27.0- 40.0(33.2)	10	27-34	29.7±0.69	47-57	53.1±0.83	29-43	33.2±1.39	21-30	24.2±0.80	60-71	65.7±1.35
II	S.nam.,1+	71.0-134.0(102.9)	10	32-37	34.4±0.55	50-55	52.5±0.45	20-27	22.6±0.69	32-43	36.9±1.18	64-73	69.0±0.84
III	S.nam.,adults1+2	396-689(557)	7	35-41	37.6±0.88	50-65	55.3±1.96	13-17	14.7±0.59	45-52	47.1±0.91	69-82	74.6±1.77
IV	S.font.,0+	25.0-40.5(32.5)	10	31-35	32.9±0.55	56-67	60.4±1.12	30-39	34.9±0.83	24-30	26.3±0.66	51-70	61.8±1.99
V	S.font.,1+	79.0-137.0(101.3)	10	36-42	39.9±0.59	56-64	59.6±0.71	22-26	24.2±0.33	34-41	37.7±0.69	59-67	62.1±0.74
VI	S.font.,adults	301-350(321)	3	42-45	43.9±0.92	58-62	59.1±1.20	16-21	18.9±1.32	44-50	46.4±1.80	71-78	74.8±2.20

crest elongates during ontogeny (increase in V.1 - see Table 2), posterior teeth appearing last. In *S. namaycush,* V.W and V.1 deviate more from the juvenile states (character states observed at the time of the appearance of the structure in the ontogeny and soon after) than in *S. fontinalis*, thus the vomer in this species is ontogenetically more advanced.

Shapes of the subopercle (with narrower anterior part, narrower and more elongated ascending process in *S. namaycush*) and supramaxilla (long and tapered at both ends in *S. namaycush*, widened posteriorly in *S. fontinalis*) were listed by Qadri (1964) among diagnostic characters of the two taxa. These characters can also be considered as deviating more from the juvenile state in *S. namaycush*. Differences in suboperculum shapes are conspicuous at rather early ontogenetic stages, though some intermediate cases were noted. However, at the earliest stages, the bone is often rather wide anteriorly and lacks the ascending process which appears later and is at first short, then elongates (Fig. 2B). The supramaxilla appears over the posterior part of the maxilla and at first is rather short, then grows forward. At this stage the anterior elongating end is more tapered and the posterior wider. Tapering of the posterior part of supramaxilla takes place later and is more obvious in *S. namaycush* (Fig. 4D, E). It should be noted, however, that differences in the shapes of the supramaxilla were not so pronounced in our samples as in those described by Qadri (1964).

Thus the shapes of the supraethmoideum, vomer, suboperculum, and supramaxillare can be interpreted as being relatively juvenilized in *S. fontinalis* and ontogenetically advanced in *S. namaycush.* However, several other characters are more juvenilized in *S. namaycush* than in *S. fontinalis* (Figs. 5, 6 and Table 2). In both species Ch.H, Op.W, F.W1, P.W, P.W1 change unidirectionally, deviating less from the juvenile state in *S. namaycush*. The direction of change of Pop.W in the ontogeny of the two species reverses and, at the point of reversal, this character in adult lake char deviates less from the juvenile form. The same applies to Mx.W and D.H except that the differences between adult lake

Table 2. Measurements of some bones of *Salvelinus namaycush* and *S.fontinalis* (0+ fish from +4°-series) FL in mm, lim - limits (minimum and maximum), M - mean, m -standard error of M. Op.W - operculum width, Pop.W - praeoperculum width, Seth.W -supraethmoideum width, F.W - frontale width, F.W1 - width of the anterior part of frontale, Pm.H - praemaxillare depth, Mx.W -maxillare width, D.H - dentale depth (width), D.S - "length of the notch" in dentale, D.R - position of the posterior end of the coronoid process, A.R - position of the anterior end of the dorsal process of articulare, P.W, P.W1 - width of the anterior part of parasphenoideum, P.Wm - minimal width of parasphenoideum, V.W - vomer width, V.l - distance between the bases of anterior and posterior vomerine teeth, G.W - glossohyale width, H.W -hyomandibulare width. V.l - in % of maximal vomer width, P.W1 -in % of the width of the posterior part of parasphenoideum, others - in % of maximal length of corresponding bone. Refer to text for more details of measurements.

#	sample	FL	n	Op.W		Pop.W		Seth.W		F.W		F.W1		Pm.H		Mx.W		D.H	
				lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m
1	S.nam.0+ (1)	19.3-20.4(19.9)	3	135-173	149±12.2	-	-	-	-	15-17	15.9±0.48	-	-	-	-	12-15	13.8±0.97	16-18	16.9±0.42
2	S.nam.0+ (2)	[about 23]	5	150-167	156±3.06	27-33	29.5±1.17	-	-	23-29	26.4±1.07	12-18	14.5±1.08	63-70	66.0±1.33	13-16	14.2±0.46	19-22	20.5±0.49
3	S.nam.0+ (4)	26.1-29.1(27.6)	5	135-151	140±2.95	25-29	27.2±0.81	80-110	96.1±5.29	26-36	30.4±1.98	16-19	16.4±0.68	57-73	64.8±3.48	14-15	14.1±0.16	19-25	22.6±0.92
4	S.nam.0+ (5)	28.4-33.9(31.3)	5	119-130	125±1.99	23-27	25.5±0.76	64- 85	73.0±3.85	36-39	37.8±0.70	15-19	16.8±0.81	65-71	67.6±1.17	15-16	15.8±0.22	26-29	27.3±0.39
5	S.nam.0+ (6)	34.8-40.0(36.7)	5	114-140	123±4.62	23-26	24.2±0.62	59- 71	63.5±2.14	38-46	40.5±1.35	16-19	17.3±0.55	58-73	64.7±2.96	16-18	16.8±0.29	27-34	29.7±1.27
6	S.nam.0+ (7)	37.0-45.0(40.2)	5	107-113	111±1.00	23-27	24.9±0.73	53- 64	59.2±2.19	32-48	40.4±2.16	17-21	18.6±0.73	61-74	67.7±2.09	15-17	16.0±0.27	28-33	30.1±0.78
7	S.nam.0+ (8)	42.0-48.5(46.0)	5	95-111	105±3.02	23-27	24.9±0.77	43- 53	50.0±1.84	38-40	39.7±0.42	17-19	18.1±0.34	65-71	67.6±1.32	14-17	15.8±0.46	27-31	29.4±0.61
8	S.nam.0+ (9)	49.0-59.0(53.8)	5	98-109	103±2.22	22-25	23.7±0.61	39- 47	42.1±1.30	39-41	40.2±0.49	18-19	18.3±0.24	70-80	74.2±1.79	13-15	14.6±0.37	30-33	31.2±0.57
9	S.nam.0+ (10)	53.0-65.0(57.3)	5	93-108	101±2.58	23-24	23.4±0.22	36- 44	39.2±1.27	36-42	39.6±1.11	18-23	19.5±0.89	65-74	69.7±1.68	15-17	15.2±0.36	30-34	32.2±0.59
10	S.nam.1+	75-134(105.0)	10	79-110	92.2±2.69	23-28	25.3±0.41	28- 35	31.1±0.81	35-41	37.8±0.61	15-22	18.6±0.80	65-84	73.0±1.80	13-17	14.9±0.37	29-38	34.0±0.69
11	S.nam.adu (1)	[396-425(408)]	3	77- 83	78.8±1.90	27-28	27.4±0.55	27- 37,	32.0±2.68,	35-42	38.4±1.90	24-30	26.6±1.61	84-95	90.3±3.21	8-10	9.1±0.56	30-34	32.1±0.88
12	S.nam.adu.(2)	[545-689(644)]	5	80- 86	81.7±1.09	26-29	26.6±0.52	30- 34[1]	32.5±1.07[1]	40-42	41.5±0.35	27-33	29.0±1.05	74-91	81.6±3.20	8-11	9.8±0.59	27-33	30.3±1.19
13	S.font.0+ (2)	19.5-21.8(20.7)	5	120-140	130±3.33	24-33	29.1±1.37	-	-	25-34	29.5±1.79	10-14	11.9±0.88	60-81	70.9±3.68	11-13	12.4±0.37	20-24	22.5±0.76
14	S.font.0+ (3)	23.6-25.5(24.5)	5	92-139	117±8.19	24-29	27.0±0.88	-	-	28-38	34.2±1.86	14-18	16.1±0.72	70-74	72.2±0.89	13-17	14.7±0.65	26-35	28.9±1.54
15	S.font.0+ (4)	25.0-31.1(28.1)	5	100-112	106±2.39	20-25	22.7±0.82	96-124	104.1±6.64	39-44	41.3±0.77	16-21	18.5±0.78	71-84	78.1±2.29	16-21	17.7±0.96	31-36	32.6±1.02
16	S.font.0+ (5)	29.6-34.5(31.7)	5	100-121	107±3.82	23-27	25.1±0.65	78-110	95.6±5.99	36-46	41.7±2.03	15-19	16.3±0.78	62-75	70.1± 2.2	13-19	16.6±1.06	32-38	33.9±1.01
17	S.font.0+ (6)	32.5-41.1(36.3)	5	86-105	95.9±3.38	21-28	24.4±1.10	73-100	86.6±5.71	45-50	46.6±0.91	17-19	17.4±0.36	60-75	65.9±2.61	15-18	15.9±0.69	33-37	34.9±0.62
18	S.font.0+ (8)	40.0-54.0(47.1)	5	78- 98	86.8±3.71	22-31	28.0±1.64	58- 89	74.2±5.52	42-49	45.0±1.29	18-21	19.5±0.52	68-74	71.5±0.97	15-21	18.1±1.01	33-39	35.5±1.00
19	S.font.0+ (9)	45.0-57.5(51.7)	5	76- 91	86.0±2.75	23-28	24.9±0.96	66- 77	70.5±2.35	40-48	44.5±1.27	17-21	18.8±0.74	68-81	72.5±2.29	15-19	17.0±0.62	35-41	37.8±1.01
20	S.font.0+(10)	53.0-65.0(57.7)	5	73- 86	79.9±2.32	26-30	27.6±0.85	56- 72	63.8±3.14	41-46	44.0±1.05	18-22	19.5±0.57	65-78	71.9±2.32	17-19	18.2±0.35	35-37	36.0±0.29
21	S.font.1+	79-137(101.3)	10	67- 81	73.0±1.41	23-33	27.2±1.05	49- 74	60.7±2.96	40-46	43.1±0.77	18-24	21.8±0.47	64-86	70.5±2.11	13-20	15.3±0.65	30-35	33.1±0.48
22	S.font.adu.	[301-350(321)]	3	-	-	28-33	30.8±1.46	46- 56	50.1±3.21	40-44	42.6±1.34	30-35	32.0±1.60	74-88	79.2±4.53	9-8	8.7±0.09	24-31	28.3±1.95

#	D.S		D.R		A.R		P.W		P.Wm		P.W1		V.W		V.1		G.W		H.W	
	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m
1	26-32	28.7±1.91	69-79	73.2±2.91	-	-	6.0- 7.5	6.7±0.40	-	-	34-37	35.1±0.79	-	-	-	-	-	-	-	
2	28-33	30.7±1.04	73-77	75.0±0.78	-	-	8.0-10.0	9.0±0.32	6.0-7.5	6.7±0.31	39-49	44.8±1.77	122-191[3]	156[3]	-	-	-	-	148-167[1]	155±4.57[1]
3	32-39	36.3±1.14	70-77	72.7±1.18	-	-	7.0- 9.0	8.3±0.41	5.5-7.5	6.5±0.39	39-51	44.6±2.38	98-129	114±5.70	20-35[2]	27.4±4.14[2]	39-47	43.5±1.50	108-130	121±3.76
4	32-37	35.0±0.98	74-79	75.4±0.92	38-42	40.0±0.71	7.5- 9.0	8.2±0.25	6.5-7.5	6.7±0.22	43-52	46.9±1.84	70- 96	83.2±4.95	20- 44	27.6±4.41	40-49	44.4±1.81	96-100	98.5±0.90
5	33-38	35.4±0.94	74-78	75.5±0.72	36-39	37.2±0.65	7.5- 8.5	8.1±0.15	6.0-6.5	6.4±0.13	39-46	43.6±1.44	66- 80	71.8±2.76	17- 39	24.7±3.74	44-47	45.6±0.51	91-113	96.8±4.21
6	32-38	33.7±1.09	72-78	74.9±1.10	35-41	38.3±1.03	7.0- 8.0	7.4±0.18	6.0-7.5	6.6±0.24	35-44	40.3±1.69	63- 87	74.4±3.91	19- 54	40.5±6.19	43-52	46.3±2.12	86- 92	89.1±1.09
7	32-38	35.2±1.17	72-78	75.1±0.97	37-42	38.7±1.00	7.0- 8.5	7.9±0.25	5.0-6.5	5.9±0.24	41-48	44.2±1.19	55- 69	60.7±2.47	39- 67	52.4±4.69	39-46	43.5±1.65	83- 90	86.0±1.42
8	33-37	34.2±0.65	72-79	76.7±1.33	37-42	38.9±0.92	8.0- 9.0	8.5±0.21	5.5-7.5	6.6±0.35	44-57	49.1±2.55	49- 54	51.6±0.77	50- 65	55.2±2.62	42-47	44.2±0.82	81- 86	83.4±0.89
9	27-36	32.2±2.18	72-78	74.8±0.91	37-45	40.2±1.35	7.5- 9.0	8.1±0.40	4.5-8.0	6.1±0.72	39-52	45.7±2.52	38- 52	47.8±2.67	57- 87	71.2±4.86	44-56	47.4±2.33	79- 88	82.6±1.52
10	31-43	35.4±1.08	75-86	81.2±1.26	39-47	43.7±0.97	7.5-10.5	9.3±0.30	4.5-7.5	6.3±0.29	46-59	51.8±1.52	31- 48	39.1±2.06	54-148	102±9.10	38-46	40.9±0.74	74- 80	77.0±0.65
11	30-33	32.1±0.88	84-87	85.0±0.87	47-48	47.5±0.32	11- 13.5	12.3±0.76	9.0-9.5	9.3±0.15	85-96	91.3±3.39	33- 36	34.2±0.97	75-108	93.5±9.80	42-47	44.2±1.42	74- 77	75.3±0.84
12	26-31	28.3±1.11	82-86	84.1±0.74	47-51	49.1±0.76	10.5- 13	12.3±0.47	9.0- 14	11.3±0.82	74-91	82.8±3.07	27- 32	29.0±1.01	33-172	152±8.04	39-50	44.1±2.16	76- 81	79.3±1.00
13	28-35	32.2±1.27	72-79	74.1±1.17	-	-	6.0- 9.5	7.7±0.60	4.0-7.0	5.6±0.49	31-48[1]	41.0±3.66[1]	146-222	174±13.0	-	-	37-54	42.7±3.03	96-108	102±2.04
14	31-37	34.4±1.13	73-77	74.8±0.67	-	-	7.5- 9.0	8.1±0.31	4.5-7.0	6.2±0.47	44-46[2]	44.9±0.46[2]	100-139	117±7.76	19- 21	20.0±0.46	36-47	41.9±2.37	88- 97	90.3±1.76
15	35-40	37.5±0.86	70-82	74.8±1.99	-	-	7.5-10.5	8.8±0.60	5.5-9.0	7.0±0.61	43-48[2]	45.5±1.46[2]	81-104	95.0±4.01	16- 40	27.4±5.21	42-56	50.6±2.28	83- 96	87.3±2.42
16	35-39	36.6±0.77	67-75	71.7±1.41	39-42	40.4±0.59	8.5-10.5	9.6±0.41	-	-	-	-	70-100	89.3±6.62	18- 32	25.1±2.81	49-61	52.9±2.10	71- 85	80.4±2.61
17	30-37	33.1±1.10	74-79	76.1±0.97	39-45	41.4±1.10	8.0-11.0	9.9±0.49	6.0-8.0	6.9±0.29	35-55	47.8±3.63	58- 74	64.1±2.90	35- 47	41.1±2.10	45-49	46.0±0.78	74- 82	77.7±1.29
18	33-38	35.1±1.04	72-83	78.6±1.87	44-49	46.5±0.81	9.5-12.5	10.9±0.49	6.0-8.5	7.1±0.37	46-74	55.3±4.83	42- 71	64.1±5.60	30- 58	42.1±4.72	41-49	44.0±1.45	72- 81	75.6±1.55
19	33-39	35.8±0.94	75-82	78.9±1.33	42-46	44.3±0.59	9.0-12.5	10.8±0.57	6.0-8.0	6.9±0.35	47-60	54.0±2.81	53- 64	57.4±2.16	29- 50	44.2±3.88	34-48	41.9±2.58	74- 77	75.7±0.61
20	31-35	33.4±0.78	73-82	79.1±1.70	43-49	45.6±1.29	9.0-13.0	11.3±0.77	6.0-7.0	6.5±0.14	44-70	55.2±4.51	57- 73	62.5±3.25	36- 53	42.1±2.94	41-47	44.0±1.26	71- 77	72.9±1.25
21	30-36	32.9±0.54	79-87	81.9±0.86	46-53	48.2±0.71	10-15.5	13.4±0.50	6.5-8.5	7.5±0.23	52-74	66.2±2.25	44- 64	54.6±1.95	36- 66	50.9±3.25	39-49	44.5±1.06	66- 78	71.9±1.02
22	29-31	30.3±0.74	81-87	83.4±1.78	48-53	51.4±1.56	12-16.5	14.2±1.22	7.0-8.5	7.9±0.41	87-100	95.6±4.44	37- 47	41.6±3.04	61- 67	62.6±2.02	38-41	39.2±1.74	63- 72	66.4±2.91

1) Number of specimens one less than indicated, 2) - two less than indicated, 3) - three less than indicated.

Table 3. The results of t-test of difference between means of osteological measurements in samples of *Salvelinus namaycush* and *S. fontinalis* of comparable mean size (FL). * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$, - -difference insignificant, n.d - no data. Numbers of samples and symbols as in Tables 1,2.

## of compared samples	Ch.H	Ch.S	Df	L.eth	S.eth	Op.W	Pop.W	Seth.W	F.W	F.W1	Pm.H	Mx.W	D.H	D.S	D.R	A.R	P.W	P.Wm	P.W1	V.W	V.l	G.W	H.W
I-IV	**	***	-	-	-	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
1-13	n.d	n.d	n.d	n.d	n.d	-	n.d	n.d	**	n.d	n.d	-	**	-	-	n.d	-	n.d	-	n.d	n.d	n.d	n.d
2-14	n.d	n.d	n.d	n.d	n.d	**	-	n.d	**	-	**	-	***	*	-	n.d	-	-	-	-	n.d	n.d	***
3-15	n.d	n.d	n.d	n.d	n.d	***	**	-	***	-	*	**	***	-	-	n.d	-	-	-	*	-	*	***
4-16	n.d	n.d	n.d	n.d	n.d	**	-	*	-	-	-	-	***	-	-	-	*	n.d	n.d	-	-	**	***
5-17	n.d	n.d	n.d	n.d	n.d	**	-	**	**	-	-	-	**	-	-	*	**	-	-	-	**	-	**
7-18	n.d	n.d	n.d	n.d	n.d	**	-	**	**	-	**	-	***	-	-	***	***	*	-	-	-	-	**
8-19	n.d	n.d	n.d	n.d	n.d	**	-	***	*	-	-	*	***	-	-	**	**	-	-	*	*	-	***
9-20	n.d	n.d	n.d	n.d	n.d	***	**	***	*	-	-	**	***	-	-	*	**	-	-	**	***	-	**
10-21 (=II-IV)	***	***	*	-	***	***	-	***	***	**	-	-	-	-	-	**	***	**	***	***	***	*	***
[11+12]-22 (=III-VI)	**	-	**	-	-	n.d	**	***	-	-	-	-	-	-	-	*	-	*	-	**	*	-	**

and brook char in these characters were insignificant, probably because of the small sample sizes (Table 3). However, the direction of differences is the same as that found by Qadri (1964). The large size of sensory pores in the bones of *S. namaycush* (Qadri, 1964, present study) is also a juvenile character, as the relative size of pores decreases in the ontogeny of salmonids and other fishes.

One more diagnostic character is the shape of the glossohyale - with tooth rows parallel in *S. namaycush* and converging anteriorly in *S. fontinalis* (Vladykov 1954, Qadri 1964). Differences in the shape of this bone are probably not connected with heterochronies but rooted deep in the ontogeny (Fig. 2A). The anlage of the glossohyale is paired, two bony plates ossifying around the bases of the first pair of teeth. The first three tooth pairs form the first two longitudinal tooth rows. Next, teeth are added to the edges of the bone outside the old ones, the latter then falling out. Addition of new outside tooth rows takes place several times. Thus, in the development of the glossohyale, not only addition but also replacement of teeth is taking place rapidly at early stages of development. As a result, the bone in juveniles looks different from that of adults as inside the marginal tooth rows there are older teeth which have not yet been shed and tooth alveoli. In juveniles the glossohyale is also much flatter in sagittal profile and the distance between marginal tooth rows is somewhat larger than in adults. Differences in glossohyale shape between adults of the two species are determined by the distance between the teeth of the second tooth pair, which are the anteriormost teeth of the first juvenile longitudinal tooth rows. This is greater in *S. namaycush* which leads to a wider anterior part and non-converging tooth rows in adults. Small intermediate teeth, found in some adult *S. namaycush,* are probably not juvenile teeth which have not fallen out but later additions, as all yearlings studied lacked them. However, the area between marginal tooth rows probably has some affinity to tooth formation since it bore teeth in juveniles.

Table 4. Ontogenetic changes in the skulls of *S.namaycush* and *S.fontinalis.*

Structure	Main ontogenetic changes
Chondrocranium	Increase in length and width of ethmoidal region, increase in skull depth, decrease in the size of fontanella postpinealis ("dorsal fontanelles") and fontanella praepinealis (fontanelles in the skull roof of the orbital region); the latter become very small and can completely disappear (one or both). Variation in the degree of development of ossifications appearing last (orbitosphenoideum in S.namaycush).
Operculum	Hyomandibular articulatory facet and the adjacent posterior region are first to ossify. Bone at early stages arched, wide and shallow, upper edge concave, lower edge convex (looking like a very deep branchiostegal ray). Decrease of relative width throughout life. Becomes deeper, quadrangular, notch at the upper edge is closed by bone, shape of the upper edge changes from concave to straight or convex, of the anterior edge - from convex to straight.
Praeoperculum	Anlage rather short and wide, tapered at both ends, anterior edge often straight, posterior convex. Elongation of dorsal and ventral limbs and decrease of relative width up to FL 30-40 mm, increase of relative width after 50-100 mm continuing in adults. In juveniles bone more symmetrical, maximal widths closer to its centre; in adults that moves to the ventral limb the latter becoming blunt and conspicuously wider than the dorsal limb.
Suboperculum	Anlage shallow, lacking the ascending process, often looking like a branchiostegal ray. Increase in depth in the ontogeny, development of the process.
Interoperculum	Anlage narrow anteriorly (often tapered in S.namaycush), bone triangular-shaped in juveniles, more quadrangular with blunt anterior end in adults.
Supraethmoideum	Anlage rounded, as wide as long, appearing at the place of supraethmoideum head of adults. Rapid elongation and decrease of relative width up to FL about 100 mm. Increase of width in larger fishes (weak in S.namaycush, not observed in this study in S.fontinalis).
Frontale	Narrow anlage along the upper edge of the orbit, following the course of supraorbital sensory canal. Elongates forward and (mainly) backwards and widens growing in the direction of the midline of the skull, the gap between frontals thus decreasing (remains longer between the anterior parts). Relative width rapidly increases up to FL about 40 mm when two frontals approach each other in the midline, then slightly decreases and remains constant, in S.namaycush increases again after FL about 400 mm. Width of anterior part increases throughout life, especially intensively after FL 100 mm
Praemaxillare	Anlage triangular. Development of the ascending process. The latter straight in juveniles, bending backwards in adults. The next ontogenetic stage ("wing-like" premaxilla as in some large specimens of S.alpinus) not observed.
Maxillare	Elongation throughout life. Relative width increases up to FL 40-50 mm, then decreases.
Supramaxillare	Anlage appears over the posterior part of maxillare and elongates forward. Anterior part in juveniles tapered, posterior more widened.
Dentale	Anlage narrow. Development of the coronoid process. Relative width first increases, decreases after FL 50(S.fontinalis)-100(S.namaycush) mm. Shape of the bone changes from bent downwards to bent upwards. The process moves backwards.
Articulare	At early stages lacking the dorsal process, the latter moves backwards in ontogeny.
Parasphenoideum	Anlage in form of elongated triangle: anterior part narrow, posterior wide. Ascending processes develop later, first attached to the bone by narrow anastomoses, then fusing with it and enclosing foramens of arteria pseudobranchialis efferens. Anterior part widens in the ontogeny.
Vomer	Paired anlage. After fusion wide and short, elongates backwards. Anterior teeth appear earlier than posterior.
Hyomandibulare	Ossification proceeds from the upper part of hyosymplecticum downwards, the bone at early stages wider than deep, relative width decreases in the ontogeny. Opercular and ventral posterior processes move downwards.
Glossohyale	Paired anlage. A complex pattern of teeth addition. New teeth attach to the edges of the bone outside old ones, the latter then falling out. Bone in juveniles flat and rather wide, becomes deeper in sagittal profile in adults.

Table 5. Ossification sequence in *Salvelinus namaycush* and *S. fontinalis*. FL in mm, age in days after peak of hatching. See explanations in text.

Skeletal element	Rank in S.	Rank in S.	S.namaycush						S.fontinalis			
			+2° - series (n=24)		+4° - series (n=32)		+7°-series(n=73)		+2 ° - series (n=34)		+4° - series (n=34)	
	nam.	font.	FL	age	FL	age	FL	age	FL	age	FL	age
cleithrum	4	2	<16.8	<0	<19.3	<24	<17.7	<14	<10.7	<0	<17.9	<38
1-st otolith (sagitta)	4	2	<16.8	<0	<19.3	<24	<17.7	<14	<10.7	<0	<17.9	<38
2-nd otolith (lapillus)	4	2	<16.8	<0	<19.3	<24	<17.7	<14	<10.7	<0	<17.9	<38
maxillare	4	5.5	<16.8	<0	<19.3	<24	<17.7	<14	12.1	0	<17.9	<38
dentale	4	5.5	<16.8	<0	<19.3	<24	<17.7	<14	12.1	0	<17.9	<38
operculum	4	5.5	<16.8	<0	<19.3	<24	<17.7	<14	12.1	0	<17.9	<38
caudal fin rays	4	5.5	<16.8	<0	<19.3	<24	<17.7	<14	12.1	0	<17.9	<38
supracleithrum	8	9	<16.8	<0	<19.3	<24	<17.7	<14	13.4	5	<17.9	<38
parasphenoideum	9.5	9	<16.8	<0	<19.3	<24	<17.7	<14	13.4	5	<17.9	<38
maxillare teeth	9.5	21.5	<16.8	<0	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
dentale teeth	12.5	21.5	<16.8	<0	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
posttemporale	12.5	9	16.8-17.0	<0	<19.3	<24	<17.7	<14	13.4	5	<17.9	<38
pharyngeal plates' teeth	12.5	21.5	17.9	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
branchiostegal rays	12.5	21.5	17.9	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
pectoral fin rays	15	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
interoperculum	17	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
praemaxillare teeth	17	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
dorsal fin rays	17	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
mesopterygoideum	24.5	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
glossohyale teeth	24.5	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
articulare	24.5	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
anal fin rays	24.5	21.5	18.2	6	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
palatinum teeth	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
praemaxillare	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
symplecticum	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
quadratum	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
occipitale laterale	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
hypuralia	24.5	39	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	>13.9<16.6	>10<44	<17.9	<38
pharyngeal plates	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	<17.7	<14	16.6	44	<17.9	<38
neural vertebral arches	24.5	21.5	>19.1<21.1	>10<68	<19.3	<24	17.7	14	>13.9<16.6	>10<44	<17.9	<38
suboperculum	31	21.5	>19.1<21.1	>10<68	<19.3	<24	18.0	14	>13.9<16.6	>10<44	<17.9	<38
frontale	32	39	>19.1<21.1	>10<68	<19.3	<24	18.8	14	16.6-18.2	58	<17.9	<38
haemal vertebral arches	33.5	21.5	>19.1<21.1	>10<68	<19.3	<24	19.6	14	16.6	44	<17.9	<38
angulare	33.5	39	>19.1<21.1	>10<68	<19.3	<24	19.6	14	16.6-18.2	58	<17.9	<38
urohyale	35.5	33	>19.1<21.1	>10<68	<19.3	<24	21.1	21	16.6-18.0	44	<17.9	<38
uroneurale-1	35.5	39	>19.1<21.1	>10<68	<19.3	<24	19.6	21	16.6-18.2	58	<17.9	<38
ceratohyale	37	21.5	21.4-21.6	>10-75	20.4	24	18.0-19.8	14-21	>13.9<16.6	>10<44	<17.9	<38
praeoperculum	38.5	43.5	>19.1<21.1	>10<68	20.4	24	19.6	21	16.6-18.2	65	<17.9	<38
gill rakers	38.5	48	>19.1<21.1	>10<68	20.4	24	19.6	21	16.6-18.2	65	<17.9	<38
glossohyale	40	48	>19.1<21.1	>10<68	20.4	24	21.1	21	16.6-18.2	65	<17.9	<38
basioccipitale	41	34.5	>19.1<21.1	>10<68	20.4	24	21.1	21	16.6-18.2	58	<17.9	<38
palatinum	42	48	>19.1<21.1	>10<68	>20.4<23.0	>24<70	19.6	21	16.6-18.2	65	<17.9	<38
pelvic fin rays	43	39	>19.1<21.1	>10<68	>20.4<23.0	>24<70	21.1	21	16.6-18.2	58	<17.9	<38
ribs	44	39	>19.1<21.1	>10<68	>20.4<23.0	>24<70	21.1	21	16.6-18.2	58	<17.9	<38
ceratobranchialia	45	48	21.1-22.3	73-97	20.4	24	21.1	21	16.6-18.2	80	<17.9	<38
uroneurale-2	46	61	>19.1<21.1	>10<68	>20.4<23.0	>24<70	21.3-22.9	21-26	18.6-19.5	87-114	>18.8<19.5	>38<61

epihyale	47	39	21.1-21.6	68-75	>20.4<23.0	>24<70	19.6	21	16.6-18.2	58	<17.9	<38
hyomandibulare	48	34.5	21.1-21.6	73-75	>20.4<23.0	>24<70	19.6	21	16.6-18.0	44-58	<17.9	<38
quadrato-jugale	49	43.5	21.1-21.6	68-75	>20.4<23.0	>24<70	21.4	26	16.6-18.2	65	<17.9	<38
vomer	50	53	21.1-21.6	68-75	>20.4<23.0	>24<70	21.4-22.3	26-28	16.6-18.8	80	18.8	38
hypohyale	51	48	21.1-22.3	68-97	>20.4<23.0	>24<70	21.3-22.9	21-28	16.6-18.8	80	<17.9	<38
ectopterygoideum	52	60	21.1-21.6	68-75	>20.4<23.0	>24<70	21.4-22.0	26	18.6-19.5	80-114	>18.8<19.5	>38<61
dorsal fin pterygiophore	53	56.5	21.1-21.6	73-75	>20.4<23.0	>24<70	22.3	30	16.6-19.6	87	>18.8<19.5	>38<61
prooticum	54.5	48	21.1-22.3	73-97	>20.4<23.0	>24<70	22.9	28	16.6-18.8	80	<17.9	<38
metapterygoideum	54.5	48	21.1-21.6	73-75	>20.4<23.0	>24<70	22.3-25.2	30-40	16.6-18.8	80-114	<17.9	<38
supraoccipitale	56	52	21.1-23.4	73-97	>20.4<23.0	>24<70	22.3-23.9	26-30	16.6-18.8	80	17.9	38
epuralia	57	54.5	21.1-22.3	73-97	>20.4<23.0	>24<70	22.3	28-30	16.6-19.6	87-106	>18.8<19.5	>38<61
parietale	58	65.5	23.4-25.0	73-97	>20.4<23.0	>24<70	22.3-22.9	26-30	23.2	93-119	19.5-21.8	61
anal fin pterygiophores	59	58.5	21.1-22.3	73-97	>20.4<23.0	>24<70	24.5-25.2	33-40	18.6-19.6	87-114	>18.8<19.5	>38<61
vertebral centra	60	58.5	23.8-23.9	80-86	23.0	70	22.3-24.5	28-30	18.2-18.6	80-114	>18.8<19.5	>38<61
lacrymale	61	62	21.1-23.4	73-97	>20.4<23.0	>24<70	25.5-26.3	40-44	19.6	87-114	21.4	61
supraethmoideum	62	79	23.8	80-86	>20.4<23.0	>24<70	25.0-25.5	40-44	24.1	114-119	25.0-31.1	102
basibranchial plate	63	54.5	26.8-27.0	120	>20.4<23.0	>24<70	23.0	33	16.6-19.5	87-114	>18.8<19.5	>38<61
os meckeli	64	71	26.8	120	>20.4<23.0	>24<70	25.9-26.6	44-47	24.1	114-119	24.1	84
vomer teeth	65	63	27.0	90	23.8	70	25.0-27.5	40-44	18.6-24.1	87-114	19.5	61
inner gill rakers	67	56.5	25.0	80	23.0	70	26.1	47	18.6	87	19.5	61
postcleithrum-1	67	65.5	23.9	86	23.8	70	26.3-26.8	47-56	23.2	93-119	21.8	61
pelvic fin girdle	67	64	23.9	86	25.0	70	25.9-28.6	56-65	18.6-19.6	93-119	>21.4<24.1	>61<84
pteroticum	69.5	74	25.2	90	>25.0<26.6	>70<88	26.1-26.8	44-47	24.1	114-119	25.2	84
opistoticum	69.5	78	23.9-25.2	86-90	>25.0<26.6	>70<88	25.9	47	24.1	114-119	25.0	102
nasale	71	71	26.8-27.0	120	26.6-27.3	88	25.9-26.3	40-47	24.1	114-119	24.1	84
epibranchialia	72	69	23.9-25.2	86-90	>25.0<26.6	>70<88	28.4	65	23.2	93-119	25.2	84
epioticum	73	86	26.8-27.0	120	27.5-28.0	>88<104	28.6	65	23.2-24.1	93-119	26.8	102
basisphenoideum	74	71	>27.0<41.0	>120<?	>20.4<23.0	>24<70	25.0-26.6	40-56	24.1	114-119	24.1	84
basibranchialia	75	68	26.8-27.0	120	27.5-28.0	>88<104	28.6	65	24.1	114-119	>21.4<24.1	>61<84
hypobranchialia	76	76.5	26.8-27.0	120	27.5	104	32.1-34.5	72-86	24.1	114-119	25.5	84
coracoideum	77.5	74	26.8-27.0	120	27.3-28.0	88-104	33.6-34.5	72-86	24.1	114-119	23.6	86
interneuralia	77.5	88	26.8-27.0	120	28.0	88-104	32.5-34.5	72-86	28.6	135	31.1	102
supramaxillare	79	81.5	>27.0<41.0	>120<?	27.0-28.0	88-104	25.0-29.1	65	25.9	119-135	25.5	84-102
3-rd otolith(asteriscus)	80	67	26.8-27.0	120	29.8	104	29.1-31.6	65-72	18.6-19.6	87-119	23.6-24.1	84
supraorbitale-2	81	83.5	>27.0<41.0	>120<?	28.0	88-104	28.6	65	25.9	119-135	25.0	102
basibranchial teeth	82	100	-	-	27.5-28.0	>88<104	28.4	65	-	-	-	-
scapula	83	76.5	>27.0<41.0	>120<?	29.8	104	32.1-34.5	72-86	24.1	114-119	25.5	84
pect.fin pterygiophores	84	81.5	26.8-27.0	120	34.8-36.4	116	36.0-38.0	79-86	25.9	119	25.0	102
epineuralia	85	83.5	>27.0<41.0	>120<?	29.8	104	31.6-37.0	72-86	24.1-25.9	135	25.0	>84<102
sphenoticum	88.5	74	>27.0<41.0	>120<?	29.8	104	32.1-37.0	72-86	24.1	114-119	25.2	84
postcleithrum-3	86.5	90	>27.0<41.0	>120<?	29.8	104	33.6-37.0	72-86	25.9	119-135	26.8	102
postcleithrum-2	86.5	89	>27.0<41.0	>120<?	29.8	104	36.5-38.0	79-86	25.9	119-135	26.8	102
mesocoracoideum	88.5	86	>27.0<41.0	>120<?	29.8	104	34.0	86	24.1	114-135	26.8	102
infraorbitalia	90	86	26.8-27.0	120	36.6-40.0	116-130	42.0	114	24.1	119	26.8	102
alisphenoideum	91	80	>27.0<41.0	>120<?	29.8	104	32.5-39.0	72-86	28.6	135-185	24.1	84
pharyngobranchialia	92	92	>27.0<41.0	>120<?	34.8-36.4	116	38.0	100	28.6	135	28.6-29.8	102-116
tabularia	93	93	>27.0<41.0	>120<?	36.6-40.0	116-130	36.0-43.0	79-100	28.6	135	34.5	116
supraorbitale-1	94	97	>27.0<41.0	>120<?	>40.0<45.0	>130<151	43.0	100-114	-	-	45.0	144
suprapraeoperculum	95	94	>27.0<41.0	>120<?	45.0	151	42.0	114	28.6	135-185	38.4	130-144
ethmoidale laterale	96	91	>27.0<41.0	>120<?	45.0	151	50.0	114	25.9	119-135	31.1	102-144
scales	97	95.5	>27.0<41.0	>120<?	36.4-40.0	116-130	>50.0	>114	35.5	185	41.1	130-165
ossification in sclera	98.5	98	-	-	58.0	180	>50.0	>114	-	-	53.0	194
stylohyale	98.5	99	-	-	>58.0<105	>180<400	>50.0	>114	-	-	>55.5<100	>194<400
orbitosphenoideum	100	95.5	-	-	-	-	71.0-?[1]	400-?	35.5	185	38.4-40.0	130-165

[1] Data on disarticulated specimens. May not ossify throughout life.

Ossification sequence

Some data on early ossification in the two species are given in Qadri (1964) and Balon (1980 b,c). Table 5 presents data on the ossification sequence of 100 skeletal elements based on the study of cleared and stained specimens. In order to trace the very beginning of ossifications only alizarin-stained specimens were used, following the recommendations of Taylor and Van Dyke (1985) and our own experience. In spite of overall similarity in the ossification sequence between different series, certain discrepancies in the order of ossification of bones, close to the time of their appearance in ontogeny, was observed between the series for each species as well as between specimens within a series. Ossification of some elements, especially of those appearing late in the ontogeny, began at considerably different lengths in different series of the same species. For instance, the first infraorbitals appeared in *S. namaycush* at FL 26.8-27 mm in +2°-series but only at FL 42.0 mm in +7°-series. In order to estimate the ossification sequence most objectively, ranking of elements, as outlined in "Materials and Methods" was performed. In Table 5, elements are listed in the sequence corresponding to *S. namaycush* with ranks of elements for the two species given in separate columns. Intervals of FL and age, separated by a dash, indicate minimum FL (age) at which the ossification was observed and maximum at which it was lacking. These are precise intervals within which the ossification appeared in a given series. Single values correspond to the minimal length (age) at which the element was observed in cases when it was present in all specimens of larger length (age). Intervals given by > and < signs indicate maximum FL (age) at which the element was not observed and minimum at which it was. These are approximate intervals resulting from gaps in sampling. In cases of serial elements (e.g. branchiostegal rays, ceratobranchialia), FL and age of the ossification of the first element are given.

As can be seen from Table 5, the overall pattern of ossification is the same for the two species. Ossification begins with the cleithrum, two pairs of otoliths, maxillare, dentale, operculum and caudal fin rays in hatchlings and terminates with a number of elements including supraorbitale-1, suprapraeoperculum, ethmoidale laterale, scales, ossification in sclera, stylohyale, and the orbitosphenoideum. Ossification of the same elements in most cases takes place in *S. namaycush* at a larger FL than in *S. fontinalis*. This is the result of the larger size of lake char embryos at hatching and of larvae at similar developmental stages, probably related to differences in mean size of parental species (Vladykov 1954; Balon 1980a, b, c). Qadri (1964), on the basis of his study of ossification of 15 skeletal elements, postulated their earlier ossification in fry of *S. namaycush* than in those of other char species, including *S. fontinalis*. We did not find such a consistent tendency. In fact, in the +4°-series, more elements appeared at the age of 2 months and more ossified earlier in *S. fontinalis* than in *S. namaycush*.

At the same time, there are certain differences in the pattern of ossification between the two species. For instance, the hyomandibulare, asteriscus, sphenoticum, and alisphenoideum ossify earlier in relation to other elements in *S. fontinalis* than in *S. namaycush*, while the supraethmoideum, epioticum, and interneuralia ossify earlier in *S. namaycush*. The difference in the time of appearance of the supraethmoideum is of especial interest: in *S. namaycush* it ossifies before, in *S. fontinalis* after, the basibranchial plate, os meckeli, vomerine teeth, inner gill rakers, postcleithrum-1, pelvic fin girdle, pteroticum, opistoticum, nasale, epibranchialia, basisphenoideum, basibranchialia, hypobranchialia, and coracoideum. At the same temperature the supraethmoideum appears more than a month later and at the same or a larger size in *S. fontinalis* than in *S. namaycush* whereas most elements, as outlined above, appear in this species at a smaller size. Thus, the more advanced adult shape of the supraethmoideum in *S. namaycush* is due not only to a higher rate of elongation but also to an earlier appearance in the ontogeny.

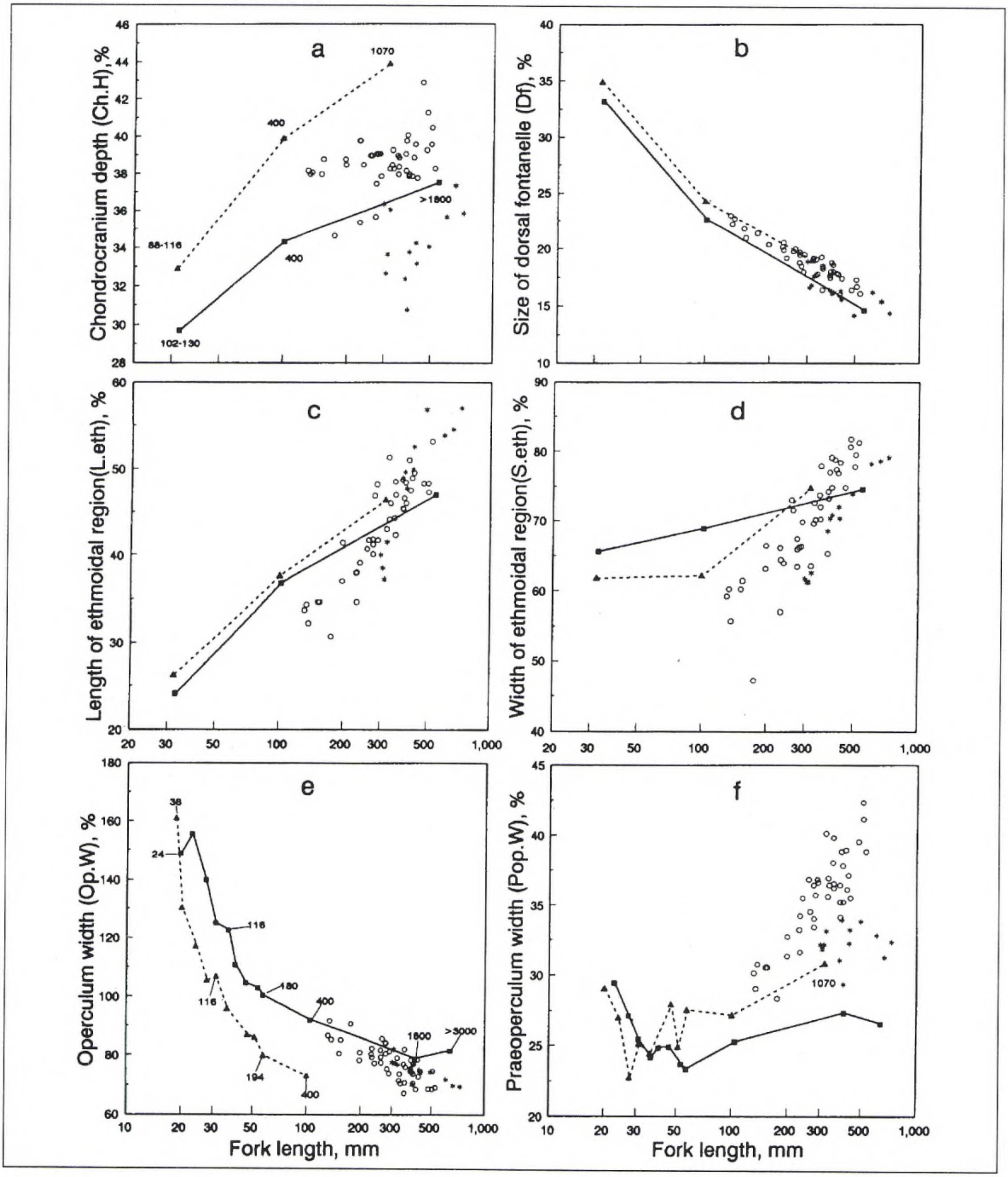

Fig. 5. Size-dependent changes of some skeletal proportions in chars. Solid squares, solid line - *S. namaycush* (0+ fish from +4°-series); solid triangles, broken line - *S. fontinalis* (0+ fish from +4°-series); asterisks - *S. alpinus* complex, different char forms from the Taimyr Peninsula lakes; open circles - other char forms of *S. alpinus* complex. Each marker represents mean sample value. Data on *S. alpinus* complex taken from Vasil'yeva (1977, 1981b) and Pichugin (1983), means for males and females shown separately. Figures indicate approximate age in days after hatching (in the + 4°-series for 0+ fish). Note, logarithmic scaling of X-axis. See text for more information.

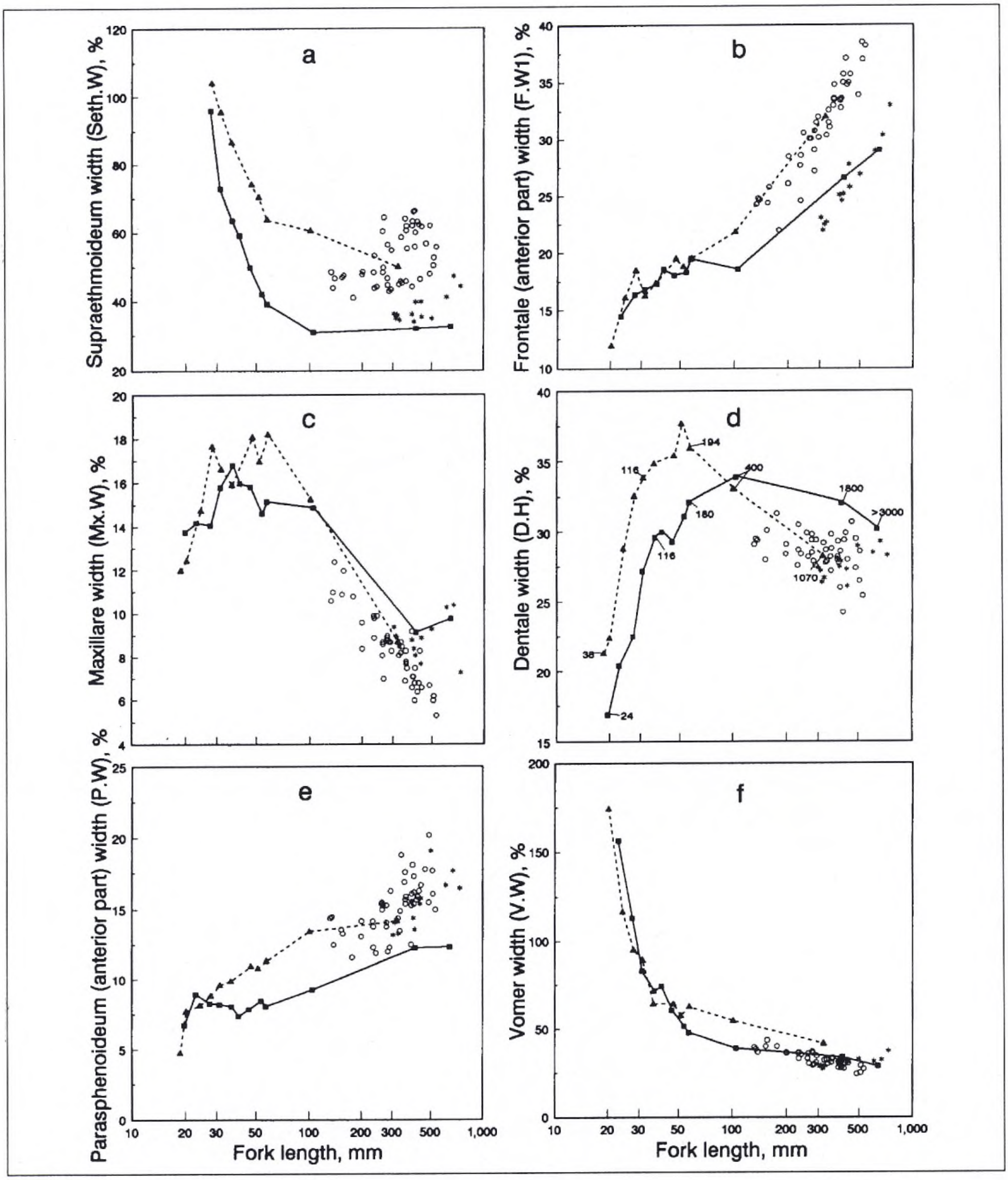

Fig. 6. Same as Fig. 5.

In *S. fontinalis* basibranchial teeth are typically lacking or there are few in contrast to *S. namaycush* (Stokell 1940; cited after Morton and Miller 1954; Morton and Miller 1954). The basibranchial plate is the last toothed bone to appear in the ontogeny of *S. namaycush* as well as in that of *S. fontinalis*, although in the latter case it can hardly be called a toothed bone. The basibranchial teeth are much closer to the end of the ossification sequence in *S. namaycush* than any other teeth except perhaps intermediate teeth on the glossohyale, as discussed above. Thus, these teeth are the first teeth to show reduced development or even to be lost when late ontogenetic stages are modified. The distribution of basibranchial teeth in other salmonids does not suggest a simple explanation of their absence-presence in different species in terms of heterochrony, as they are lacking in both juvenilized (*Brachymystax*) and ontogenetically accelerated (*Oncorhynchus*) representatives of the family. However, these teeth are characteristic of the genus *Salvelinus* and a wide range in the degree of their development is observed in the genus, *S. namaycush* and *S. fontinalis* representing the extremes (Morton and Miller 1954). Perhaps, in the case of chars, the degree of development of these teeth can be considered a paedomorphic character in *S. fontinalis* and peramorphic character in *S. namaycush.*

In *S. namaycush* approximately 30% of adults are lacking an orbitosphenoideum whereas this bone is present in all adult *S. fontinalis* (Qadri 1964). In both species, the orbitosphenoideum is the last bone to ossify in the chondrocranium and in *S. namaycush* it is the last of all skeletal elements to ossify. The orbitosphenoideum was lacking in all the young-of-the-year of *S. namaycush* we examined, both cleared and disarticulated preparations. It was also lacking in 70% and only weakly developed in 20% of the yearlings. The smallest fish with an orbitosphenoideum was 71 mm FL. In *S. fontinalis* an orbitosphenoideum was absent in all specimens less than 35 mm FL and less than four months old but present in all specimens larger than 40 mm FL. The dynamics of ossification in samples from the +4°-series was as follows: 0+ (1-5) - no ossification, 0+ (6) - orbitosphenoideum ossified in 13% of specimens, 0+ (7) - in 63%, 0+ (8) - in 78%, 0+ (10) and older fishes - in 100%. It is obvious that in *S. namaycush* ossification of the orbitosphenoideum is retarded to such a degree that in some specimens it fails to ossify at all. It should be noted that the last-but-one chondral ossification in the chondrocranium - the ethmoidale laterale - also ossifies later when the fish are considerably larger in size in *S. namaycush* compared with *S. fontinalis.*

Discussion

Taking into account differences in the life history of lake and brook chars (Morrow 1980; Martin and Olver 1980; Power 1980), coordinated heterochronic changes in development of morphotypes might be expected as the probable mechanism of morphological divergence. These species exhibit differences in size, growth, age at maturation, and longevity, which usually accompany divergences connected with heterochronies (Gould 1977). Contrary to this expectation, each species displays a mosaic of accelerated and retarded characters and the whole situation can be considered as an example of dissociated heterochrony (McNamara 1993).

Comparison with available data on the ontogeny of the skull in *S. alpinus* complex sensu Savvaitova and Volobuev (1978); taken from Vasil'yeva (1977, 1978, 1979, 1980 a, b; 1981a, b; Savvaitova et al. 1977; Medvedeva 1977a, b; Medvedeva and Savvaitova 1980; Medvedeva-Vasil'yeva 1978) shows that, in fishes >100 mm FL, which were the only sizes studied in the papers cited above, the directions, though not necessarily the rates, of ontogenetic changes of most skeletal elements in Arctic char corresponds to those in lake and brook chars outlined in Table 4. This comparison was done using the descriptions of ontogenetic changes in *S. alpinus* complex from those papers and also by plotting together mean character values in samples of *S. alpinus* complex ranging in mean FL from 133 to 735 mm taken from Vasil'yeva (1977, 1981b) and Pichugin (1983) and superimposing them on "ontogenetic trajectories" of characters of *S. namaycush* and *S. fontinalis*. Such a procedure was performed for all characters common for our study and those of Vasil'yeva (1977, 1981b) and Pichugin (1983) (the values of Pop.W from the latter paper were not used because of a probable difference in Pichugin's way of measuring the preopercle). Some examples are illustrated in Figs. 5 and 6. Samples of *S. alpinus* complex were taken from sympatric and allopatric groups of fishes of the same sex (the means for males and females are shown separately) representing different ontogenetic stages (young-adult, mature-immature), life history strategies (resident, anadromous) and forms. These forms include *S. alpinus, S. a. erythrinus, S. malma, S. taranetzi, S. neiva, S. taimyricus, S. drjagini,* and *S. boganidae* of other authors. Although representing different forms, these means when plotted together clearly illustrate size-dependent changes in the skull of *S. alpinus* complex. Except for samples from the Taimyr Peninsula, which were analysed separately, *S. alpinus* complex character values were correlated with log FL. Sample sizes ranged between 42 and 48 depending on the character. The correlations were insignificant for Ch.S, G.W and H.W and significant for the other 18 characters: r=0.38 (P<0.01) for Ch.H, r=0.49-0.93 (P<0.001) for the rest. Despite the same direction of change, *S. namaycush* and *S. fontinalis* differ from *S. alpinus* during most of their ontogeny in D.R and D.S, the coronoid process of *S. alpinus* being more anterior in position. The same applies to some extent to the dorsal process of the articulare (A.R). A different direction of change above 100 mm FL was observed for Pm.H: the depth of the premaxilla decreases in *S. alpinus* but it increases in *S. fontinalis* and *S. namaycush*. *S. namaycush* has a wider hyomandibulare than *S. alpinus* or *S. fontinalis*. *S. fontinalis* has a much deeper skull than either *S. alpinus* or *S. namaycush,* and also differs from both in vomer and operculum widths (Figs. 5, 6).

In comparison with most forms of the *S. alpinus* complex, *S. namaycush* has a juvenilized skull morphology: shallow chondrocranium, wide operculum, maxillare, dentale, narrow praeoperculum, frontale, and anterior part of the parasphenoideum. The widening of the supraethmoideum, which occurs after the accelerated "elongation phase", is not very conspicuous in *S. namaycush* but is more advanced and apparent in *S. alpinus*. No tendency towards the formation of the "wing-like" premaxilla in large specimens was seen in *S. namaycush* and Pm.H in adults begins to decrease very late. In general, the changes taking place in the skulls of adult Arctic chars are absent or less pronounced in lake char.

Within the *S. alpinus* complex, the same juvenilization tendency is shown by chars from the Taimyr Peninsula lakes (shown in Figures 5 and 6 by asterisks) described as *S. taimyricus, S. drjagini, S. boganidae* and deepwater "goggle-eyed" char ("pucheglazka"). Vasil'yeva (1980b), using a number of qualitative characters, found that among 13 forms from different parts of the range studied the "goggle-eyed" char had the most juvenilized skull, while that of *S. boganidae* was also rather juvenilized. However, Vasil'yeva's own data on skeletal proportions, when plotted together with "ontogenetic trajectories" of lake and brook char characters, shows quite clearly that all resident Taimyr chars are juvenilized. They have, in comparison with other representatives of the *S. alpinus* complex, lower values of Ch.H, S.eth, Pop.W, Seth.W, F.W1 and higher values of Mx.W (Figs. 5A,D,F, 6A,B,C), indicating that they deviate in these characters in the direction of juveniles in comparison with other Arctic chars of the same size. This juvenilization is probably one of the causes of the unexpected clustering of *S. boganidae* together with *S. namaycush* in Glubokovsky (1977). Vasil'yeva (1977, 1980b) stressed that the extent of ontogenetic changes in the skull of Arctic char is closely related to the ecology: the less migratory the chars, the less pronounced the changes. The forms of Taimyr chars discussed above and *S. namaycush* live in large lakes and never go to sea. In addition, Taimyr chars, like *S. namaycush,* have an expanded life span and late maturation (Savvaitova 1989).

A recent description of *Salvethymus svetovidovi,* a deep-water endemic form from lake Elgygytgyn in Chukotka (Chereshnev and Skopets 1990, 1993), revealed a char-like fish with such a unique morphology that the authors gave it a generic status and considered it to be very primitive, close to the common ancestor of all chars. It also deviates genetically (B.M. Mednikov pers. comm.). However, the hypothesis that it is primitive conflicts with the highly derived karyotype of this species (Glubokovsky et al. 1993). The unusual traits of *S. svetovidovi* can be explained in the context of the ontogenetic changes in chars outlined above. First, *S. svetovidovi* is characterized by a number of reductions: absence of supraorbitale-1, some tabularia, absence or weak development of supraorbital-2, orbitosphenoideum, reduction in size of basisphenoideum, and supramaximillare, and fewer interneuralia ("predorsalia" in Chereshnev and Skopets 1990). As can be seen from Table 5, these elements are among the last to be ossified in chars. The supraorbitale-1 is the last dermal bone not bearing canals to ossify. Reduction of this bone was also recorded in *S. leucomaenis* by Vasil'yeva (1977). The supraorbitale-2 and supramaxillare are the last-but-one and the last-but-two to ossify. The tabularia, together with suprapraeoperculum, are the last canal bones in the ossification sequence and the orbitosphenoideum the last ossification in the chondrocranium. The basisphenoideum also appears rather late and remains small for a long time, just as the one in *S. svetovidovi.* Interneuralia ossify late, among which the anterior ones, i.e. those which are lacking in *S. svetovidovi*, are the last to ossify. Fig. 7 shows juvenile *S. fontinalis* and *S. namaycush* with

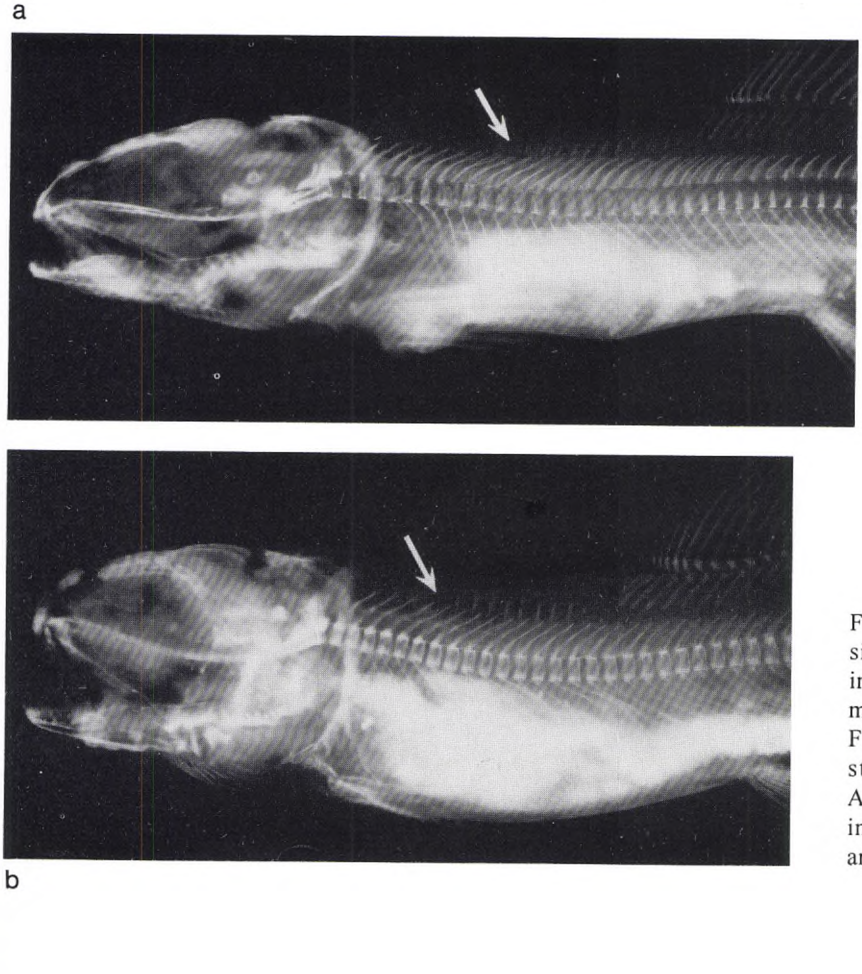

Fig. 7. Early stages of ossification of interneuralia in *S. namaycush* (a, FL 36.5 mm) and *S. fontinalis (*b, FL 30.7 mm). Cleared and stained preparations. Anteriormost ossified interneurale shown by an arrow. Scale bar: 1 mm.

anterior interneurals not ossified. The number of ossified interneuralia in brook char (10) falls within the limits for this character in *S. svetovidovi* (9-11) and in lake char (12) the number is just above the upper limit. It is well known that the last structures to appear in the ontogeny are the first to be lost or reduced when paedomorphosis occurs.

Second, a number of bones in *S. svetovidovi*, judging by Fig. 5 in Chereshnev and Skopets (1990), have a juvenile shape: narrow frontale with narrow anterior part, narrow praeoperculum, wide operculum, shallow suboperculum with weakly developed ascending process, short and wide maxillare, praemaxillare with short ascending process, deep dentale with anteriorly displaced coronoid process, narrow supraethmoideum, parasphenoideum with the posterior part wider than the anterior part, hyomandibulare with opercular and ventral posterior processes not displaced downwards, and articulare lacking the dorsal process. The vomer is long and narrow, and therefore not juvenilized. However, vomerine teeth are, as a rule, absent or there are few (1-3) and they occupy the position of the first vomerine teeth to appear in char ontogeny and are perpendicular to the vomer axis, suggesting retardation in their anlage. Another juvenile feature of *S. svetovidovi* is the gap between right and left frontale in the midline.

Thus, *S. svetovidovi* is clearly a paedomorphic form with the majority of its unique features being consequences of retardation in somatic development. Low growth rate and an extremely long life span (up to 30 years) are probably other manifestations of this retardation. Of course, *S. svetovidovi* is not just an underdeveloped char, some of its traits, like the high number of gill rakers, are not connected with paedomorphosis. The paedomorphic nature of *S. svetovidovi* suggests that it is not a primitive but a derived form, this being in accordance with the karyological data.

Alexeyev and Mina (1985) reported parallel divergence in supraethmoideum width between *S. namaycush* and *S. fontinalis* on the one hand and two forms of *B. lenok,* sharp-snouted and blunt-snouted, on the other. More detailed comparison shows a complex of parallelisms, *S. namaycush* being the analog of the sharp-snouted, *S. fontinalis* of the blunt-snouted lenok. Both sharp-snouted lenok and *S. namaycush* in comparison with, respectively, blunt-snouted lenok and *S. fontinalis*, have a more slender body, more pointed head, narrower interorbital distance, shorter jaws, more gill rakers and pyloric caeca, narrower and shallower chondrocranium with less convex ethmoidal region, narrower supraethmoideum, vomer, frontale, wider maxillare, operculum, and deeper glossohyale.

Heterochronies were found to have played a significant role in the divergence of the two lenok forms, most of the diagnostic characters being accelerated in sharp-snouted and retarded in blunt-snouted lenok (Alekseyev 1990, in press). Part of the parallelisms observed in lake and brook chars can thus be the result of similar heterochronic effects. However, these alone cannot account for all the analogies. Similar differences in adult morphology can be caused by opposite ontogenetic processes. For instance, the shorter maxilla in sharp-snouted lenok compared to blunt-snouted is the result of character acceleration and, in *S. namaycush* compared to *S. fontinalis*, the result of retardation because relative length of maxilla decreases in the ontogeny of lenoks but increases in that of chars. Thus, there seem to be other morphological constraints responsible for the observed parallelisms.

In *Salvelinus*, ontogenetic changes in the skull take place throughout the whole life cycle, some of them being even intensified in adults. In *Brachymystax,* skeletal proportions change intensively only during the first year of life (Alekseyev, in press and unpublished data). That is why the skull in *Brachymystax* has much in common with that of juvenile char: it is juvenilized in comparison with the skull of *Salvelinus*. This was noted previously by Vasil'yeva (1977). Some skull elements in representatives of the two genera differ from very early stages. The vomer differs already at the stage of paired anlage (Alekseyev 1993). The anlage of the supraethmoideum is triangular, with narrow posterior part in *Brachymystax*, more rounded with wider posterior part in *Salvelinus*. The glossohyale in juvenile char is wider than in the lenoks. The shapes of several other bones, such as maxillare are rather similar in juveniles, differences becoming more pronounced with age. This shows that, in some cases in the evolution of the Salmonidae, only modification of terminal ontogenetic stages of morphological structures took place, while in others all ontogenetic stages were modified.

If the whole family Salmonidae is considered, bearing in mind developmental data on *Salvelinus* and other genera, it becomes evident that a number of skeletal elements show non-random, developmentally determined trends throughout the family, exhibiting the most juvenilized state in *Brachymystax* and the most advanced in *Oncorhynchus*. Elongation of the vomer and infraorbitals, widening of the supraethmoid, preopercle, anterior parts of parasphenoid and frontals, disappearance of the ascending process of premaxilla and elongation of the bone, increase in size of the ethmoidal region of the chondrocranium and decrease in size of the dorsal fontanelles are most prominent in *Oncorhynchus*. The advanced states of some characters are also shared by *Salmo* and *Parasalmo*. Character states found in adult *Brachymystax,* such as the narrow supraethmoid or short premaxilla with developed ascending process, are compressed and displaced to earlier developmental stages and thus recapitulated in the ontogeny.

These few examples, described here briefly, indicate the necessity of a separate study of developmental phenomena within Salmonidae and show that the morphological evolution of the family progressed to a great extent by terminal additions to the ontogeny, although other explanations are also possible.

Conclusions

The divergence of *S. namaycush* and *S. fontinalis* is a case of "dissociated heterochrony", each species displaying both paedomorphic and peramorphic character states. *S. namaycush,* in comparison with most representatives of the *S. alpinus* complex, has a juvenilized skull morphology, changes taking place in adult Arctic chars are lacking or less pronounced in lake char. This can be partly associated with a non-anadromous way of life, prolonged life span and late maturation of *S. namaycush.* Within the *S. alpinus* complex, chars from the Taimyr Peninsula (described as *S. taimyricus, S. boganidae, S. drjagini* and deep-water "pucheglazka") are the most juvenilized. *S. svetovidovi* is a paedomorphic taxon characterized by reductions in skeletal elements appearing late in the ontogeny and by juvenilized shapes of bones. Lenoks of the genus *Brachymystax* have juvenilized skull morphology in comparison with *Salvelinus*. Shapes of some bones diagnostic to the two genera (e.g. vomer) differ from the moment of their appearance in the ontogeny. A number of morphological parallelisms are observed between *S. namaycush* and sharp-snouted lenok, *S. fontinalis* and blunt-snouted lenok. These can be partly the result of similar heterochronic effects. However, other morphogenetic mechanisms also seem to be involved. Progressive ontogenetic acceleration of skull morphology is observed in the family Salmonidae, *Brachymystax* being the most juvenilized, *Oncorhynchus* the most ontogenetically advanced genus.

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Feeding Strategy of Arctic Charr (*Salvelinus alpinus*): General Opportunist, but Individual Specialist

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Abstract

Feeding strategies and phenotypic components of the niche width were studied in a high density population of lacustrine Arctic charr, using a graphical method for analysis of stomach contents data. Niche width and feeding strategy varied markedly throughout the ice-free season. In June, the charr population had a narrow niche, feeding almost exclusively on chironomid pupae. In July, however, the niche width was large with both between- and within-phenotype components contributing to the niche width, and with a high diversity in the diet. From August and throughout autumn, the between-phenotype component predominated, increasing gradually towards October as the result of a strong increase in individual prey specialization. Strong individual specialization and a high between-phenotype component of the niche width, are both assumed to be related to strong intraspecific competition for restricted food resources in the overcrowded charr population.

Keywords: Feeding strategy, niche width, phenotype components, generalization, specialization.

Introduction

The Arctic charr is usually described as a generalistic feeder, having a wide ranging and opportunistic diet (Johnson 1980). This description is based on population studies, whereas the feeding strategy of individual fish has rarely been addressed. When an individual fish encounters a possible food item, it can respond in one of two ways; either neglect it, or pursue and try to eat it. A generalist feeder will attack most encountered prey, whereas a specialist will continue searching except when encountering prey of a specifically preferred type. A generalist individual will thus have a broad niche embracing several food categories, whereas a specialist will have a narrow niche width. It is, however, important to clearly distinguish between the niches of the different individuals and that of the whole population (Putman and Wratten 1984). A population with a narrow niche must necessarily be composed of individuals with narrow and specialized niches. A population with a broad niche may, on the other hand, consist of individuals with either narrow or wide niches, or a combination of both. In this relationship, two components have been identified as contributing to a population's total niche width. First, each individual shows variation in its own resource use (the within-phenotype component), and, second, there is variation in resource use among the individuals (the between-phenotype component) (Roughgarden 1972, 1974, Giller 1984). A population with a high between-phenotype component to the niche width would consist of specialized individuals with little or no overlap in resource use, whereas a population with a high within-phenotype component would be composed of generalists, each exploiting a wide range of overlapping resources (Fig. 1; Giller 1984, Pianka 1988). In both cases, the population would be generalistic with a broad niche width.

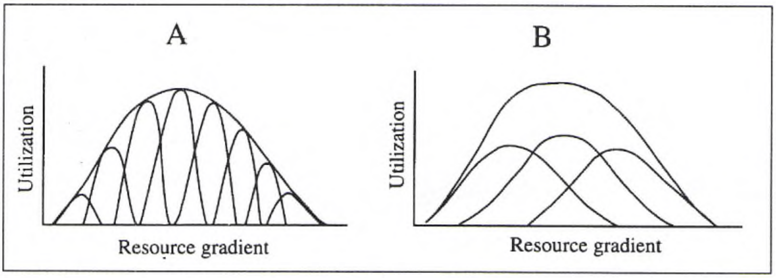

Fig. 1. Idealized representation of populations differing in the components of the niche width. A) High between-phenotype component. B) High within-phenotype component. (After Giller (1984) and Pianka (1988)).

According to optimal foraging theory, the decision whether or not to eat an encountered prey is largely related to the search and handling times. Long handling time and short search time both favour specialization, whereas short handling time compared to search time favours a generalist strategy (MacArthur and Pianka 1966, Begon et al. 1990). It has thus been predicted that both the individual and population niche width should generally increase as resource availability decreases (Emlen 1966, 1968, MacArthur and Pianka 1966, Schoener 1971, Pianka 1988). With abundant food resources, the search time is low, and the predators can afford to be selective and specialize on the superior prey type. But if the food supply is restricted and the encounter rate low, a predator can not afford to bypass many inferior prey items, and generalization is promoted (MacArthur and Pianka 1966, Pianka 1988, Begon et al. 1990). On the other hand, general niche theory predicts that although restricted resource supply and the resulting strong intraspecific competition cause expansion of the population niche, the individual niches will tend to become more restricted, as the individual organisms will specialize on different prey types (Putman and Wratten 1984, Putman 1994). There is, thus, a discrepancy between optimal foraging theory and niche theory concerning presumptions of individual feeding strategy under restricted food supply. Optimal foraging theory predicts generalization with a high within-phenotype component to the niche width, whereas general niche theory predicts individual specialization and a high between-phenotype component.

In the present study, feeding strategy has been studied both at the individual and population level in a food-restricted, stunted population of Arctic charr, using a new graphical method for analysis of stomach contents data. The influence of seasonal changes in food supply and different prey type characteristics, has been examined in relation to feeding strategy and phenotypic contributions to the niche width.

Material and methods

Fish sampling

Arctic charr were sampled in Takvatn, an oligotrophic and dimictic lake with an area of 14.2 km^2, situated in a birch-wood landscape 214 m above sea level in northern Norway (69°07'N, 19°05'E). Sampling was performed in the littoral zone using bottom gill nets once a month from July to October 1980 and in June 1981. In the presentation of the results, the sample from June 1981 is treated as representative of June 1980. The Arctic charr population in Takvatn was overcrowded and stunted, with a restricted food supply relative to the fish density (Amundsen and Klemetsen 1988). A detailed description of the lake and its biota is given by Klemetsen et al. (1989).

Each fish was weighed and measured (fork length). The stomachs were removed and frozen. In the laboratory, the stomachs were opened and the percentage degree of total fullness was determined, ranging from empty (0%) to full (100%). The food items were identified and their relative contribution to the total fullness estimated. In total, 1,046 Arctic charr were sampled and examined. The present analysis has been restricted to fish of 15-25 cm length, and with a stomach fullness of 10% or more, excluding fish with only slowly digestible remains in their stomach.

Measures for description of the diet

Three different measures for the description of the stomach contents have been used: the frequency of occurrence, the percent abundance (or mean contribution to the stomach content) and the prey specific abundance (Amundsen et al. 1995). **The frequency of occurrence** is defined as the number of fish in which a prey item occurs, expressed as a fraction of the total number of predators with prey. **The prey abundance** is defined as the percentage a prey taxon comprises of the total stomach contents in all predators, whereas **the prey specific abundance** is defined as the percentage a prey taxon comprises of the total stomach fullness of all predators in which the actual prey occurs (Amundsen et al. 1995). In mathematical terms, the occurrence (F_i), abundance (A_i) and prey specific abundance (P_i) of a prey type i can be described by the equations:

$$F_i = N_i/N \qquad (1)$$

$$A_i = (\Sigma S_i/\Sigma St) \cdot 100 \qquad (2)$$

$$P_i = (\Sigma S_i/\Sigma\ St_i) \cdot 100 \qquad (3)$$

where N_i is the number of fish with prey i in their stomach, N the total numbers of predators with stomach contents, S_i the stomach fullness of prey i, St the total stomach fullness of the fish, and St_i the total stomach fullness of fish with prey i in their stomach.

Graphical analysis of stomach contents

The graphical analysis of stomach contents data is based on a method described by Amundsen et al. (1995). For each prey type, the prey specific abundance is plotted against the frequency of occurrence on a two-dimensional graph. Prey importance, feeding strategy and phenotype contribution to the niche width can be interpreted along the diagonals and axes of the graph (Fig. 2). The product of prey specific abundance and frequency of occurrence equals the prey abundance, which increases along the diagonal from the lower left to the upper right corner as a function of prey specific abundance and frequency of occurrence (Amundsen et al. 1995). This diagonal can thus be taken to represent the □prey importance, with dominant prey in the upper end and rare and unimportant in the lower. The vertical axis represents the feeding strategy of the predator in terms of specialization and generalization. The predator has specialized on prey types positioned in the upper part of the graph, whereas prey positioned in the lower part have been eaten more randomly (generalization). Prey points in the upper left part of the diagram indicate an individual specialization, and in the upper right part a population specialization. Observations in the upper right part will necessarily be restricted to a single or a few points, reflecting a predator with a narrow niche width (Fig. 2b). If there are no prey points in the upper right part of the graph, and all points are located along or below the diagonal from the upper left to the lower right corner, the predator will have a broad niche width. The distribution of points along this diagonal is indicative of the main phenotype contribution to the niche width. Points in the upper right part of the graph represents a high between-phenotype component (Fig. 2a), whereas points in the opposite part represents a high within-phenotype component (Fig. 2b).

Measure of diet width

The diet width (B) has been quantified by Levins‘ index (Levins 1968):

$$B = 1/\ \Sigma p_i^2,\ i = 1....n \qquad (4)$$

where p_i is the fraction of prey i in the diet, and n is the total number of prey categories. p_i is equal to prey abundance (A_i) expressed in fractions rather than percentages.

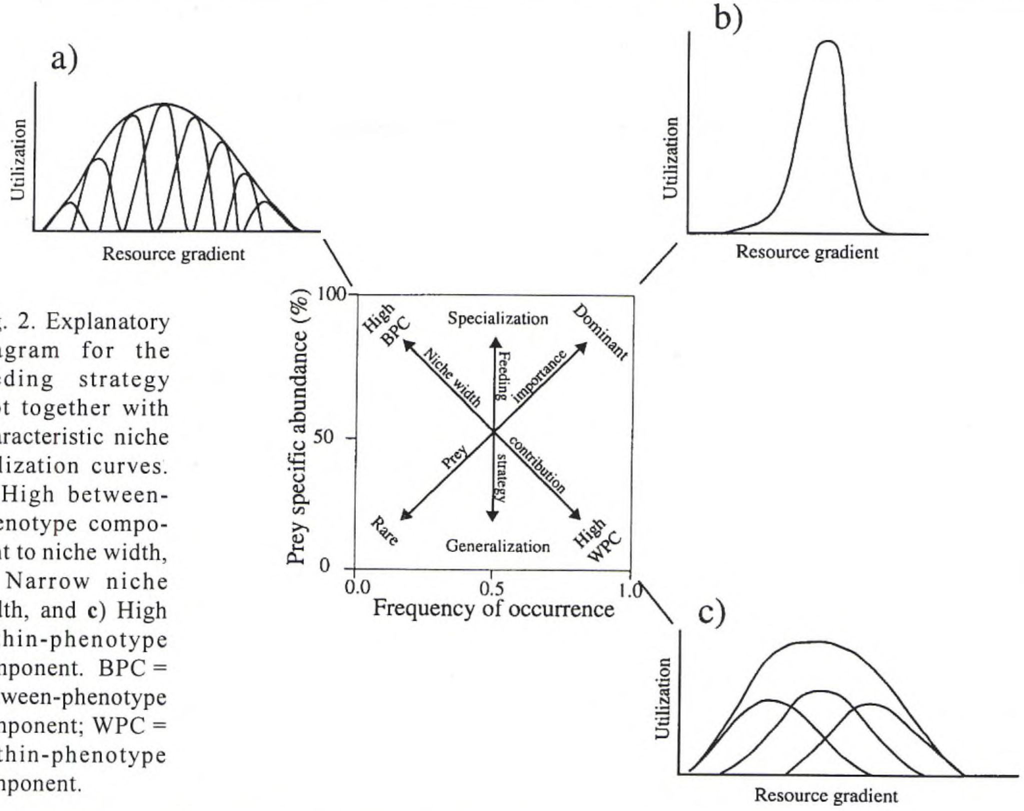

Fig. 2. Explanatory diagram for the feeding strategy plot together with characteristic niche utilization curves. **a**) High between-phenotype component to niche width, **b**) Narrow niche width, and **c**) High within-phenotype component. BPC = Between-phenotype component; WPC = Within-phenotype component.

Results

A total of 22 prey taxa grouped into 19 different categories, was found in the stomachs of the Arctic charr. The diet diversity was highest in July with 16 different prey categories recorded, and lowest in September with only 9 categories present. The maximum diet-width index was found in July, and the lowest in June (Table 1). Except for the peak value in July, the diet-width index increased towards autumn. The mean number of prey categories in the stomachs of the fish was also highest in July, and then decreased gradually towards October.

In June, the diet of the littoral Arctic charr was completely dominated by chironomid pupae, which had been the subject of a very strong population specialization (Fig. 3). Other prey categories made only minor contributions to the stomach contents, although several of these had relatively high prey specific abundances. Also in July and August, chironomid pupae were the dominant prey. The pupae had still been eaten by most of the fishes, but their prey specific abundance had decreased. Other prey types like three-spined sticklebacks, zooplankters and molluscs, had an increased importance compared to the

Table 1. Population niche width (Levins index, *B*) and mean number of prey categories in the stomachs of the Arctic charr in Takvatn during the icefree period of 1980.

	Jun	Jul	Aug	Sep	Oct
Niche width (*B*)	1.34	6.25	3.66	4.27	5.05
Mean no. of prey categories per fish	1.66	2.91	2.00	1.66	1.44

June sample. The frequencies of occurrence of these prey types were generally low, but their prey specific abundances were relatively high. Towards September, the importance of chironomid pupae was largely reduced, and they were not present at all in the stomach contents in October. Three-spined sticklebacks, planktonic cladocerans and copepods, surface insects and *Gammarus* sp. were the most important prey types in these two autumn months. All of these prey types were, however, represented only in less than half of the fish samples, but their prey specific abundances were high (>60%).

In June, there was neither a high between- nor within-phenotype contribution to the niche width (Fig. 3). The complete dominance of chironomid pupae resulted in a narrow niche width, even though several other prey categories were also represented in the diet. In July, on the other hand, there was a combination of both

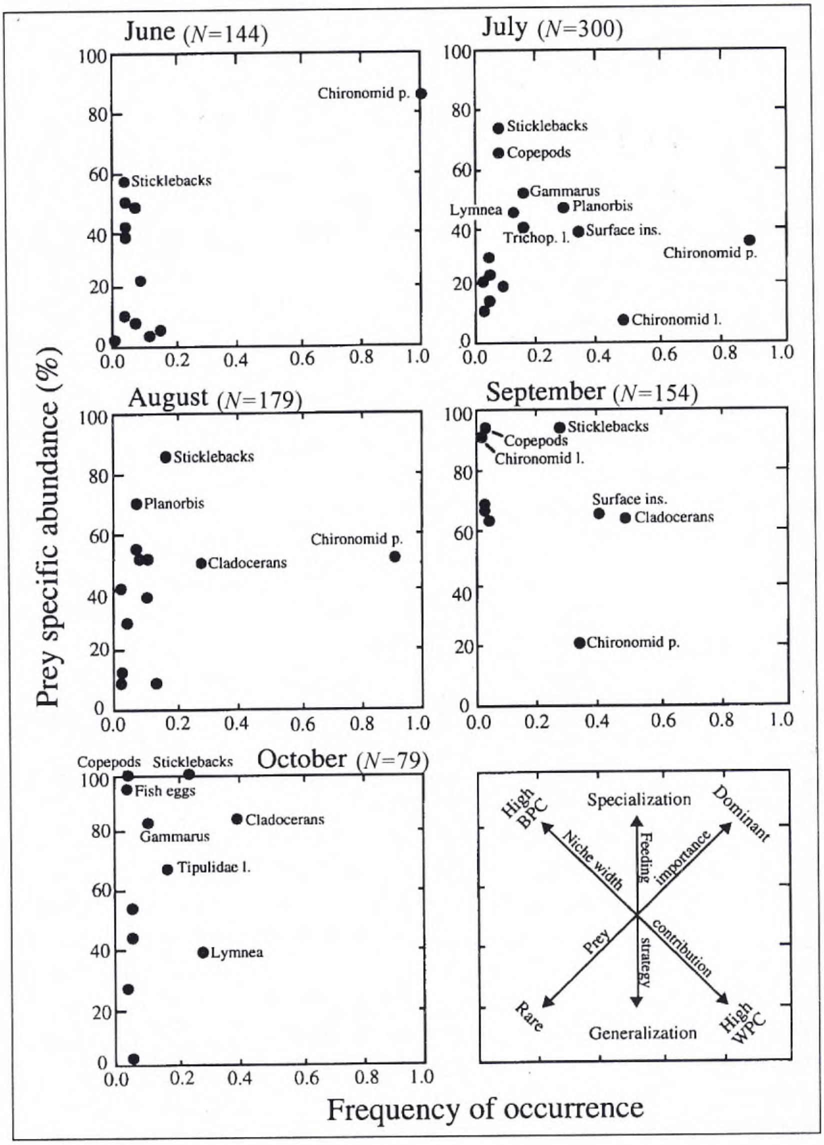

Fig. 3. Feeding strategy plot with explanatory diagram for Arctic charr from Takvatn 1980. The most important prey categories are indentified by shortened names.

relatively high between- and within-phenotype components to the niche width. Chironomid larvae and pupae were located in the lower right part of the graph, but most other prey types were found in the upper left part. Throughout the rest of the sampling season, most of the prey points were spread towards this upper left, high between-phenotype corner of the graph. This tendency was present in all sampling periods, June and July included, but became increasingly pronounced towards the autumn. Especially in September and October, several points were located in the upper left corner, illustrating a high between-phenotype component to the niche width in these sampling periods.

Some prey types, especially three-spined sticklebacks, but also copepods, had a high prey specific abundance throughout the sampling season (Fig. 3). This means that the fishes feeding upon these particular prey types, were very selective, usually excluding other prey types from their diet.

Discussion

The diet composition of the Arctic charr population in Takvatn, provides the impression of a generalist feeder. The food categories comprised both zooplankton, zoobenthos, terrestrial insects and fish. The population niche width was, however, highly variable throughout the sampling season. In June, the niche width was narrow, and the feeding of the charr population could be characterised as monophagous, with most fish predating almost exclusively on chironomid pupae. This intensive feeding on chironomids was probably related to their high availability in early summer, when they are known to be abundant and hatch in large concentrations (Grimås 1961). With a superabundance of food and a concordingly low search time, the fish could afford to specialize on this single prey type. However, chironomid pupae are probably not a highly preferred food type for Arctic charr. Their prey specific abundance decreased towards autumn as the density of pupae diminished, and the high specialization in June was most likely the result of a functional response to high abundances.

With the exception of June, the population niche width of the Arctic charr in Takvatn was broad. However, the individual niches appeared to be notably narrow. For several of the prey types, individual specialization was extensive, and this tendency increased towards autumn. Concordingly, the between-phenotype component of the niche width was high and gradually increased throughout the whole period from July to October.

Amundsen and Klemetsen (1988) estimated the food consumption of Arctic charr in Takvatn during the ice-free period of 1980. Consumption rates were generally low, and the food supply of the fish appeared to be highly restricted. Considerations of metabolic requirements indicated that feeding was surplus only in June, whereas in September and October there was a food shortage (Amundsen and Klemetsen 1988). Optimal foraging theory predicts that feeding should be specialized when food resources are abundant (Pianka 1988, Begon et al. 1990). This is in accordance with the observed feeding pattern in June. The deductions from this theory do, however, fail to predict the observed feeding strategies of the individual fish during the subsequent months of restricted food supply. The high individual specialization and the high between-phenotype components, are in fact contradictory to the optimal foraging predictions. Niche theory, on the other hand, predicts that individuals should specialize on different prey types when intraspecific competition is strong (Putman and Wratten 1984, Putman 1994). This prediction successfully fits with the observed resource use patterns of the Arctic charr in Takvatn under restricted food supply. There are, therefore, reasons to believe that the observed individual specialization and high between-phenotype component to niche widths are largely the result of a strong intraspecific competition for scanty resources. Moreover, as the food supply and consumption rates of the fish decreased towards autumn, the tendency of individual specialization and a high between-phenotype component became increasingly more pronounced, leading to a larger diversification of the diet. Apparently, as the level of intraspecific food competition increases, the individual fish enhance their feeding specialization, and thereby reduce the direct interactions with other conspecifics.

The high between-phenotype component of the diet width in most of the sampling periods, involved individual specialization on several prey categories. The individual specialization was particularly pronounced for three-spined sticklebacks, which in all sampling periods had a high prey specific abundance. Amundsen (1994) also found indications of a strong individual prey specialization in cannibalistic Arctic charr, where charr prey comprised almost 95% of the stomach contents of the cannibals. Fish prey are probably difficult to catch and handle due to their large size and ability to escape. Experience may promote capture success of prey types that are difficult to catch (Bence 1986), and individual specialization seems to be a reasonable feeding strategy for fish predation by Arctic charr. Planktonic copepods were also the subject to individual specialization by their charr predators in Takvatn. Copepods can move rapidly by using their antennae, and have been identified by several authors as prey that are difficult for fish to catch (Lazarro 1987, and references therein).

In conclusion, this study demonstrates that the feeding strategy of Arctic charr is highly flexible, depending upon factors such as prey type characteristics, seasonal changes in resource supply and intensity of intraspecific competition. At the population level, the Arctic charr in Takvatn meets the characterization of a generalistic and opportunistic feeder. However, with regard to the individual fishes, prey specialization was demonstrated to be the predominant feeding strategy. Intraspecific competition for restricted food resources in the overcrowded charr population is probably the main reason for this individual specialization and the high between-phenotype component to niche width.

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Downstream Migration of Anadromous Arctic char (*Salvelinus alpinus* (L.)) in the Vardnes River, northern Norway

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Abstract

Migrating Arctic char (*Salvelinus alpinus*) were caught in traps in the Vardnes River during 1956-63 and 1967-70. In spring, veteran migrants descended before the first time migrants. Some of them migrated downstream at a river water temperature of 0°C. The number of descenders increased with water temperatures up to 6°C, thereafter the number decreased. There was a significant negative correlation between the water temperature and the number of descending veteran migrants and a similar negative nonsignificant tendency among first time migrants. Length of the first time migrants and of the veteran migrants decreased with time during the period of descent. The number of migrants increased with water level in the river. The veteran migrants showed a significant decrease in their sea survival rate with increased water level in the river at the time of their descent. The first time migrants showed an increase in sea survival rate with water level and a decrease in survival rate with water temperature in the river. This is probably due to reduced predation risk for first time migrants when descending into the sea at elevated levels of water in the river.

Keywords: Smolt, water temperature, water level, survival, predation.

Introduction

Anadromous salmonids like the Arctic char (*Salvelinus alpinus*) live for several years in freshwater before they perform their first migration to the sea. In the Vardnes River, northern Norway, the downstream and upstream migrating Arctic char were captured in traps during 1956-63 and 1967-70. The downstream migration of the veteran migrants peaked usually between the middle of May and the beginning of June (Berg and Berg 1989, 1993).The downstream migration of anadromous salmonids appears to be triggered by environmental factors like photoperiod and meteorological conditions (e.g. Österdahl 1969, Ruggles 1980, Hartman et al. 1982, Hesthagen and Garnås 1986, Hvidsten and Hansen 1988, Jonsson 1991). Three main environmental variables seem to influence the downstream migration: dial light periodicity, increasing water temperature and increasing water flow (e.g. Hansen and Jonsson 1985, Jonsson and Ruud-Hansen 1985, Hvidsten and Hansen 1988).

The anadromous char in the Vardnes River perform their first seaward migration at a mean size of 22.2 cm, which is larger than the first time migrants of Atlantic salmon (*Salmo salar*) and the brown trout (*S. trutta*) (Berg and Jonsson 1989). The survival rate of the first time migrants of char during the summer at sea is about 30% (Berg 1991).

In this investigation the relationship between environmental parameters and the downstream migration of the char was studied. My main hypothesis was that there is no relationship between sea survival and either river water temperature or level of water.

Material and methods

Traps that separated downstream and upstream migrating anadromous salmonids were operated near the mouth of the Vardnes River (Fig. 1), located on the island of Senja in northern Norway (69°10'N, 17°30'E). When the water level rose above about 70 cm, the fence of the trap became submerged and the efficiency of the traps decreased (Berg 1977).

The catchment basin of the river is about 16.5 km^2. The mean water flow is 1 m^3s^{-1}, increasing to 16 m^3s^{-1} at periods of flood, but decreasing to 0.2 m^3s^{-1} during dry periods in the summer. The river from Vardnes Lake to the sea is about 1.2 km long and about 7 m wide. The study area is near the coast, and has a maritime climate with relatively mild winters and cold, wet summers. The midnight sun is above the horizon in the period from middle May to late July. The river and the lake generally freezes up in October. Char normally spawn in the Vardnes Lake during October. The ice-cover is usually broken up by the end of May. During the thaw, heavy flooding may occur.

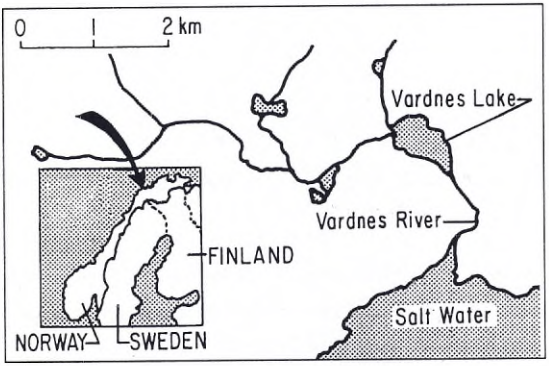

Fig. 1. The Vardnes River in Scandinavia.

All the trapped fish were examined and untagged fish were tagged with a numbered Carlin tag at the base of the dorsal fin. Total lengths (to the nearest cm) were recorded. The tagging process did not effect the growth of the fish, though tagging of descending smolts led to 30% reduction in survival rate (Berg and Berg 1990). No such negative survival effect of tagging was observed for the larger-sized char.

The descending char were divided into two groups: first time migrants (total length when descending less or equal than 26 cm, *N*=3,240) and veteran migrants (length greater than 26 cm, *N*=3,490), for details about the precision of this division see Berg and Berg (1990).

Results

Veteran migrants of Arctic char are the only fish in this river which migrated downstream at a river water temperature of 0°C (Fig. 2). The number of migrants increased with water temperature up to 6°C, where the highest number of

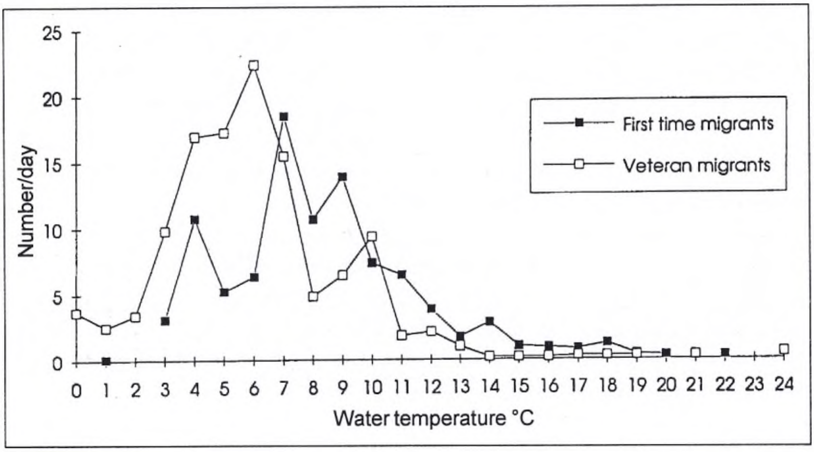

Fig. 2. Number of descending first time (filled squares) and veteran (open squares) migrants per day on the water temperature in the Vardnes River.

Table 1. The number of downstream migrants per day in relation to the level of water in the Vardnes River.

	Level of water (cm)				
	0-19	20-39	40-59	60-79	80-
First-time migrants	134	497	1,789	749	71
Veteran migrants	224	1,011	681	1,428	146
Days	157	259	219	111	52

migrants was found. The number of migrants decreased rapidly with water temperatures above 6°C. Over the entire temperature range during the period of descent, the number of descending veteran migrants decreased significantly ($P<0.01$, $r=-0.12$, $N_{days}=325$) with water temperature. Among the first time migrants there was a nonsignificant ($P<0.13$) negative correlation with water temperature. First time migrants descended about one week later than the veteran migrants. The water temperature was generally 3°C or higher and the number of first time migrants increased with water temperature up to 7°C (Fig.2).

The veteran migrants descended at lower water level than the first time migrants (Table 1), although the number of descending char increased significantly with the level of water (veteran migrants: $P<0.001$, $r=0.20$, $N_{days}=301$; first time migrants: $P<0.001$, $r=0.22$, $N_{days}=224$).

Relatively high number of veteran migrants descended during snowy and variable clouded weather (Table 2). First time migrants exhibited a significantly (Chi-square, $P<0.001$) higher tendency to migrate downstream during rainy weather.

There was a significant decrease in length of the char during the period of downstream migration. For the veteran migrants this decrease was significant ($P<0.001$). It was described by the linear equation:

Total length (cm) = -0.09 • (day number) + 39 ($r=-0.21$, $N=2{,}411$),

where day number is number of days from 1 April onwards (e.g. 2nd May = day number 32). For the first time migrants there are a similar significant ($P<0.001$) decrease in length during the period of downstream migration. This decrease was described by the equation:

Total length (cm) =-0.03 • (day number) + 24.4 ($r=-0.18$; $N=4{,}350$).

The proportion of char returning to the Vardnes River showed considerable variation. Sea survival rate (y,%) of first time migrants

Table 2. The number of downstream migrants of char per day in relation to weather conditions.

	Weather conditions									
	Clear	Lightly clouded	Variable clouded	Clouded	Drizzle	Some showers	Showers	Rain	Sleet	Snow
First time migrants	2.1	4.8	3.2	5.0	6.1	1.9	5.7	4.7	8.1	1.6
Veteran migrants	3.3	4.1	10.0	4.1	4.1	1.0	3.7	5.6	2.2	7.5
N (days)	153	138	67	171	28	67	80	69	9	17

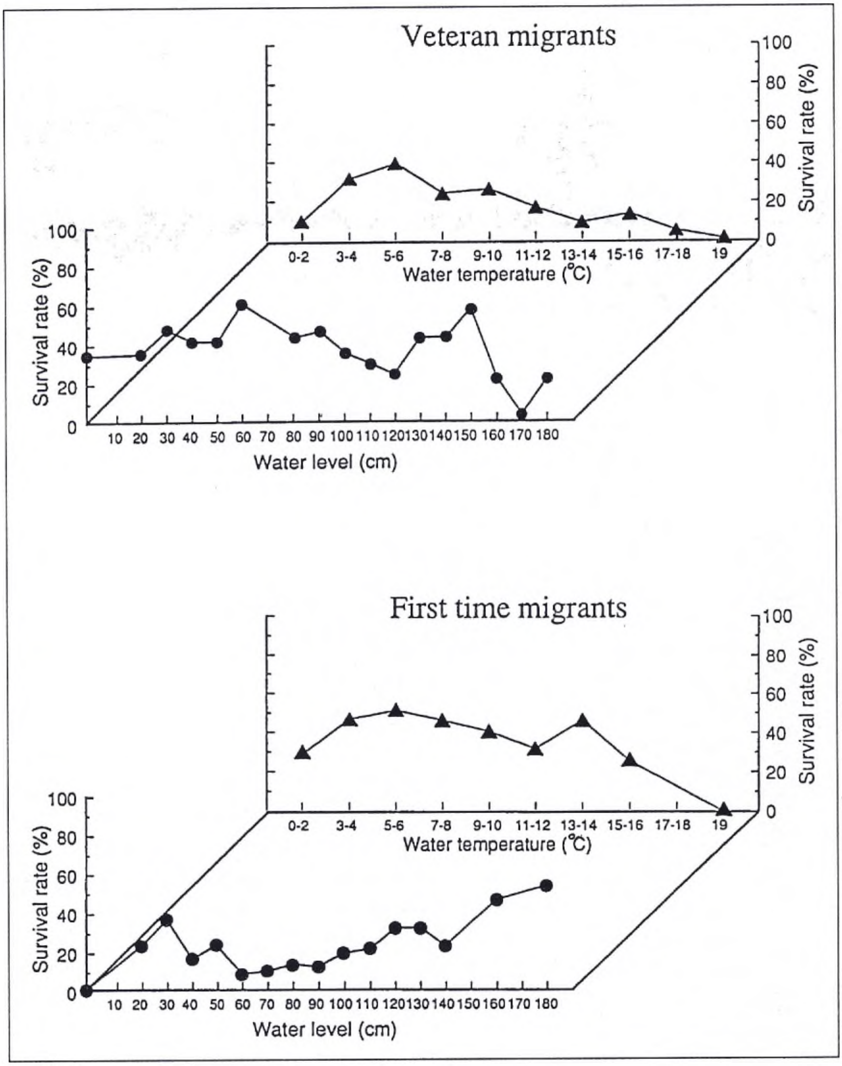

Fig. 3. Percentage of Arctic char returning from the sea relative to those decending in spring (survival rate) on water temperature (°C) and water level (cm) in the river during downstream migration.

increased significantly ($P<0.01$, $r=0.19$, $N=134$) with increases in water level (X, cm) in the river at descent (Fig. 3a) where:

$$y = 0.20 \cdot X + 13.4$$

A significant ($P<0.001$) negative correlation ($r=-0.39$, $N=134$) was found between water temperature (X,°C) and seasonal survival rate (y,%) where:

$$y = -0.20 \cdot X + 4.3$$

Sea survival rate of veteran migrants (y,%) decreased significantly ($P<0.02$, $r=-0.16$, $N=160$) with increasing water level in the river (X, cm) (Fig. 3b) where:

$$y = -0.18 \cdot X + 50$$

No significant correlation exists between water temperature and seasonal survival rate among the veteran migrants.

Discussion

The veteran migrants of char descended before the first time migrants. A period of very fast growth was recorded immediately after their sea entry. The fast sea growth ceased at sea temperatures above 10°C (Berg and Berg 1989). This may explain the early downstream migration of the char and thus the negative correlation between river water temperature and the number of migrants. The osmoregulatory tolerance of char is size dependent, and the larger veteran migrants are able to survive in sea water at lower temperatures than smaller fish (Finstad et al. 1989, Sigholt and Finstad 1990). The larger char may thus be migrating downstream earlier than the smaller char due to smaller relative osmoregulatory costs at sea.

There is little knowledge about the environmental variables which influence the river descent in anadromous Arctic char. Strand (1991) and Carlsen (1994) did not find any correlation between water temperature and the number of downstream migrating anadromous char in Halselva, Finnmark. The correlation between water temperature/level of water and downstream migration found in this investigation explained only a small part of the variance in number of descents. The statistical methods used does not control for the fact that when those fish that will migrate have done so, the descent stops even if the environmental conditions may be favourable. This will reduce the coefficients of determination (r^2) in correlation analyses between environmental factors and the number of migrants (Vøllestad et al. 1986).

Both veteran and first time migrants exhibited a significant positive correlation between the number of migrants and water level with r^2-values ranging between 4% and 6%. The results are similar to those reported by Carlsen (1994). The migration of char into the estuary probably occurs in the upper parts of the water column, in a pattern similar to that of Atlantic salmon (e.g. Fried et al. 1978, Greenstreet 1992a). As freshwater has a considerably lower density than sea water, mixing is slow and visibility is very low in the turbid mixture zone. The vision of e.g. predatory fish in this zone is probably reduced, thereby reducing the risk of being predated. Under conditions of higher discharge, the zone of turbidity is extended, probably further reducing predatory risk. If so, this may explain why sea survival increased with water level in the river during downstream descent for the first time migrants. The larger char leave the river early before the spring flood and may thus have a negative relationship between water level and survival. The larger char may also be less vulnerable to predation.

I found no specific single environmental variable controlling the seaward migration. A large number of publications have treated the connection between various environmental triggers and the seaward migration of salmonid fish species (e.g. Greenstreet 1992b), showing that there is a large number of stimuli involved. In the pattern of descent of the char from the Vardnes River the investigated environmental factors can contribute to a maximalization of both survival and growth of the char.

Acknowledgments

The author is deeply indebted to Magnus Berg who collected the original data used for this investigation and to the late Fredrik Kampevoll and his family who operated the traps and tagged the fish, to Paul Hagala, who kept the records, to Dr. William O'Connell, who improved the English and to an anonymous referee.

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Differences in Morphology and Ecology within a Stunted Arctic Char Population

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Abstract

The stunted Arctic char (*Salvelinus alpinus*) population in the lake Store Rennen (adult body lengths 150-180 mm) exhibited seasonal and ontogenetic habitat shifts. The epibenthic habitat was occupied by all age groups at all seasons. Part of the adult age groups (age-4 and older) migrated from the epibenthic to the pelagic zone in late summer and autumn (August-October). The pelagic diet was dominated by crustacean zooplankton, whereas the epibenthic diet consisted of chironomid larvae, and benthic and pelagic crustaceans. There was no difference in sex ratio between pelagic and epibenthic fish. However, significant morphological differences were found between the epibenthic and pelagic part of the population in late summer/autumn. Epibenthic fish had a higher condition factor than the pelagic fish. Discriminant analysis of 26 morphometrical variables demonstrated significant differences between sexes as well as between epibenthic and pelagic fish within sexes. Univariate analysis (ANOVA) of the variables showed that among males, the pelagic and epibenthic fish differed particularly in snout length and dorsal fin length. Among females corresponding differences were found in upper jaw length, dorsal fin length, anal fin length, eye diameter and caudal peduncle. The results are discussed in relation to phenotypic diversification and foraging strategies.

Keywords: polymorphism, morphometric analysis, seasonal habitat shifts, ontogenetic habitat shifts, diet.

Introduction

Arctic char (*Salvelinus alpinus*) is renowned for its morphological and ecological variability. The species differ in morphological and ecological characters from lake to lake and commonly occur in two to four sympatric morphs with different ecology within localities (Johnson 1980, Hindar and Jonsson 1993). Within lakes, some part of the adult population usually perform a seasonal movement from the epibenthic to the pelagic zone in response to the improved food abundance during the late summer period of high crustacean zooplankton density (L'Abée-Lund et al. 1993). In monomorphic populations, adult fish exhibiting different habitat use appear not to differ morphologically. In polymorphic populations, the groups utilizing the two main habitats of the lake, i. e. the epibenthic and pelagic zone, will often differ in characters like body coloration and trophic morphology (Hindar and Jonsson 1982, Sandlund et al. 1992). Among monomorphic populations, the most pronounced monomorphism may be found in the so-called stunted populations, which feature low juvenile growth rates, small and homogeneous size at sexual maturation, and negligible adult growth rates (Langeland and Jonsson 1990, L'Abée-Lund et al. 1993). The occurrence of this population type is generally caused by good spawning conditions yielding high recruitment relative to the food resources available.

Within stunted and morphologically homogeneous Arctic char populations, some of the subadult and adult fish also perform seasonal niche shifts from the epibenthic to the pelagic habitat (Klemetsen et al. 1989). According to the ideal free distribution model (Fretwell 1974), this may be envisaged as a movement by random individual fish among feeding patches (habitats). Alternatively, individual fish may be phenotypically adapted to different habitats. If so, the fish moving from the epibenthic to the pelagic habitat would be those individuals best adapted to a pelagic way of life. In bluegill sunfish (*Lepomis macrochirus*), cryptic morphological differences between pelagic zooplanktivores and the benthivores seem to indicate that individuals are phenotypically adapted to different habitats and foraging modes (Ehlinger and Wilson 1988, Ehlinger 1989, 1990). Based on these considerations we wanted to investigate whether the individual fish in a monomorphic Arctic char population possess different abilities with regards to living a pelagic versus an epibenthic mode of life. In other words: are there detectable morphological or ecological differences between the resident epibenthic fish and those individuals which change habitat when the food conditions in the pelagic zone become favourable?

Material and methods

Study area

The Lake Store Rennen (63°22'N, 10°59'E) is situated at an altitude of 312 m a.s.l. in the county of North Trøndelag, central Norway. The surface area is 0.35 km^2, and maximum depth is 40 m. The lake water has a high humic content (42 Pt units), resulting in a Secchi disc depth of 3 m. The littoral zone is therefore quite restricted; in this paper it has been defined to include depths from 0 to 4.9 m.

Methods

Arctic char was sampled with pelagic and epibenthic gillnets during three periods in 1990: June, early August and September. The epibenthic and pelagic nets both consisted of 11 panels with mesh sizes between 6 and 40 mm knot to knot. Each epibenthic net panel was 25 m long and 1.5 m deep, whereas the pelagic net panels were 25 m long and 6 m deep. The epibenthic survey nets were set for 24 h perpendicular to the beach in 0-40 m depth. The pelagic nets were set in the 0-6 m and 10-16 m depth zones over the deepest part of the lake. Catch per unit of effort (CPUE) was calculated as number of fish per 100 m^2 net area per 24 h. CPUE is taken as a relative measure of fish density in the various habitats within sampling periods. The survey net method is described in Sandlund et al. (1985).

A total of 653 Arctic char were caught, together with 57 brown trout. Out of the total catch of brown trout, 52 were caught in the littoral zone, 5 in the pelagic zone and none in the profundal zone. The trout were rarely larger than 250 mm in body length (Bjøru 1994). Analysis of the diet of these trout revealed no fish remnants in the stomachs. Brown trout smaller than 25 cm body length probably constitutes only a minor predation risk towards Arctic char (L'Abée-Lund et al. 1992, Næsje et al. 1992).

The char was weighed (0.1 g), measured (fork length, 1 mm), and the sex and sexual maturity stage were determined. Stomach content was dissected out for analysis. The prey types were identified, counted and measured under a strereo microscope. Dry weigths of prey types were established from dry weight-size regressions (references in Bjøru 1994). Otoliths were taken for age determination. Diet overlap between groups of fish was calculated according to Schoener (1968). Female gonads in maturity stage 5 (Dahl 1917) were dissected out, weighed and the number of eggs counted for estimation of individual fecundity. Gonadosomatic index (GSI) was calculated as ovarian wet weight (OW, g) on somatic weight (SW, g) according to Mills and Eloranta (1985). Egg weight was calculated

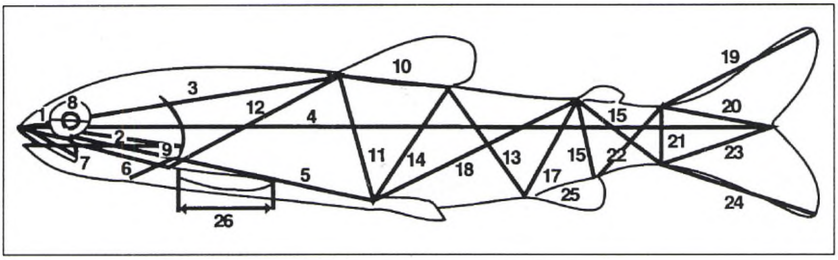


Fig. 1. Morphometric variables measured on pelagic and epibenthic Arctic char caught in Store Rennen, August, 1990.

from the number of eggs and ovarian wet weight. Asymptotic length ($L\infty$, mm) of the van Bertallanfy growth model was calculated as described by Dickie (1978).

Gillrakers were counted on the anterior left gill arch from 95 pelagic and 126 epibenthic char. The weight-length ratio was calculated the linear regression: $\log_e W = a\log_e L + b$, where W is body weight in g, and L is body length in cm. The comparison of pelagic and epibenthic fish with respect to weight-length ratio was restricted to the length groups found in both habitats. A subsample of 103 Arctic char caught in 16 mm pelagic and epibenthic nets in August were photographed laterally. A number of morphometric parameters were selected (Fig. 1) to quantify the morphology of the fish for statistical analysis (Humphries 1981). The parameters were measured on the photographs, and digitized. The morphometric variables were $\log_e$-transformed and standardized. The effect of fish size on the morphometric variables was removed by expressing the variable as the deviation from a common within-group regression between the parameter and the fork length of the fish (Kleinbaum 1978, Reist 1985, 1986).

The morphologies of males and females were treated separately, and analysed for possible differences between pelagic and epibenthic fish, resulting in four groups: pelagic males, epibenthic males, pelagic females, and epibenthic females. The first analytic step was multivariate analysis (MVA) of all morphometric variables of the four groups through discriminant analysis, to check whether the morphology of the fish coincided with the a priori grouping. The most important morphometric variables to segregate pelagic and epibenthic fish in the discriminant analysis were found through variable selection, i. e. identification of variables showing most between-group variation relative to within-group variation. Differences between groups in single variables were analysed using ANOVA. All tests were performed with SPSS-PC software.

Results

Habitat use and life history

The Arctic char were caught in the epibenthic zone during all sampling periods (Fig. 2). Highest densities were found in the littoral zone (0-4.9 m). There was a general increase in catches in the epibenthic zone from June through September. Catches in the pelagic zone were low in June and September, but high in early August. Pelagic char stayed mainly in the uppermost water layer (0-6 m).

All age and size groups of the char population were present in the epibenthic zone (Fig. 3). The age groups exhibited differential habitat use along the bottom, with age groups 1-3 mainly living deeper than 5 m, and age group 4 and older mainly living in the 0-4.9 m zone (Fig. 3; $\chi^2=152.8$, 1 df, $P<0.005$). The pelagic part of the char population was mainly restricted to age groups 4 and older (Fig. 3). The differences in age distribution between epibenthic and pelagic char ($\chi^2=23.8$, 5 df, $P<0.005$) are also reflected in the differences in length distribution ($\chi^2=20.2$, 5 df, $P<0.005$). In the catches from both habitats, size groups 150-190 mm were dominating, whereas in the epibenthic zone, a significant number of smaller fish (80-150 mm) were also

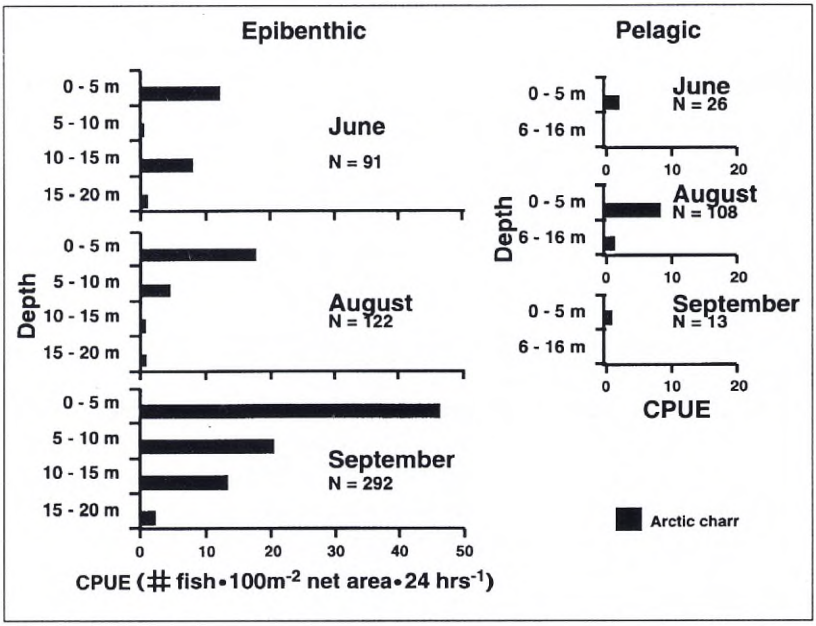
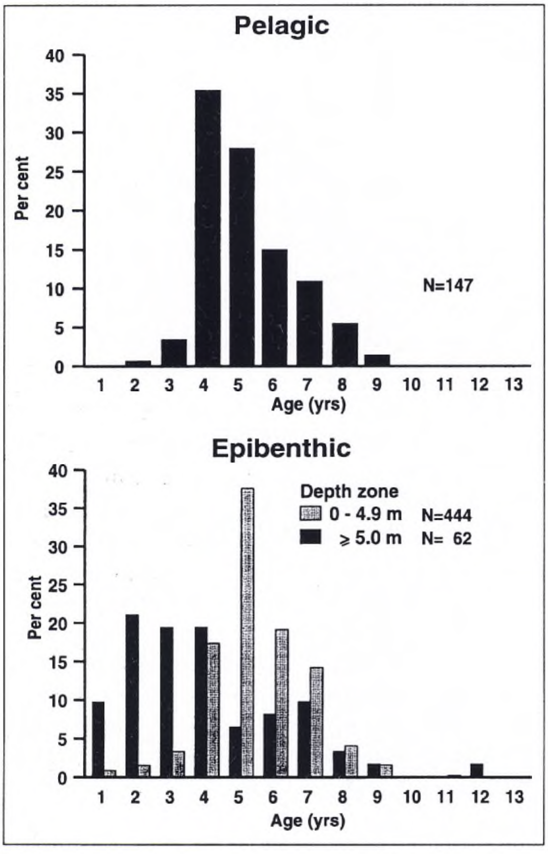


Fig. 2. Catch per unit of effort (CPUE., #fish • 100 m^2 • 24 h^{-1}) in epibenthic and pelagic gill nets in various depths, Lake Store Rennen, June, July/August and September, 1990. *N*=number of Arctic char.



caught. The sex ratios in the pelagic (M:F=1.6) and epibenthic (M:F=1.4) habitats did not differ (χ^2=1.42, 1 df, *P*>0.05). The proportion of sexually mature fish was higher in the pelagic zone (93.2%) than in the epibenthic zone (86.0%) (χ^2=5.46, 1 df, *P*<0.05).

The youngest sexually mature Arctic char in Store Rennen was 3 years old in both sexes. Among age-4 fish, a higher proportion of males (90%) than females (75%) were mature (χ^2=5.0, 1 df, *P*<0.05). The growth rates were reduced from the age of sexual maturation, when the body length of the fish was approximately 160 mm. Asymptotic body length ($L\infty$) was 180 mm. There were no significant differences in age specific body lengths between pelagic and epibenthic char except in age groups 4 and 5 in June (Mann-Whitney U-tests, Table 1). Individual fecundity was recorded in September, when most adult char

Fig. 3. Age distribution of Arctic char in the pelagic, shallow epibenthic (littoral, 0-4.9 m) and deep epibenthic (profundal, ≥5 m) habitats, Store Rennen, June, July/August and September, 1990. *N*=number of fish. Per cent distribution is based on within group *N*.

Table 1. Mean body lenghts (± SD) at age 1-9 among pelagic and epibenthic Arctic char, Store Rennen, June, early August and September 1990. *N*=number of fish. *P*-values are based on Mann-Whitney U-tests.

	Pelagic			Epibenthic	
Age	Body length (mm)	*N*	*P*-value	Body length (mm)	*N*
June					
2	-		-	91.2±10.8	6
3	-		-	133.1±17.2	9
4	163.6± 4.8	8	0.0143	152.2±11.8	17
5	172.0± 4.4	11	0.0001	159.0± 8.6	27
6	-		-	163.1±10.3	15
7	173.7±11.8	6	0.2907	168.9± 9.2	11
8	181.0	1	-	173.0±13.8	5
9	-		-	174.0	1
August					
1	-		-	79.0	1
2	-		-	111.7±17.8	6
3	153.4±18.6	5	0.6752	147.6±19.5	5
4	164.6± 7.4	41	0.4179	168.1±25.2	30
5	171.1± 7.9	30	0.3148	173.2± 6.7	43
6	176.2± 8.3	16	0.6011	177.3±13.6	21
7	174.6± 4.9	8	0.6832	176.2± 7.2	20
8	181.3± 8.4	6	0.2433	189.7± 8.5	3
9	176.5± 6.4	2	-	166	1
September					
1	-		-	89.2± 7.3	9
2	120.0	1	-	121.6±16.9	8
3	-		-	147.6±12.1	13
4	159.7±22.4	3	0.3382	158.0± 5.2	42
5	-		-	164.0± 6.6	101
6	176.5± 5.9	6	0.1033	171.3± 7.2	54
7	188.0± 2.8	2	-	173.2± 7.0	38
8	181.0	1	-	174.6± 7.7	12
9	-		-	177.5± 8.0	6

was aggregated in the epibenthic zone. Among females, the number of eggs varied greatly within length and age groups, and no significant correlation was found between female length (range 122-191 mm) and number of eggs (R^2=0.01, *P*=0.26, *N*=95). The regression did not improve by adding age as a second independent variable. Mean individual fecundity (±SD) was 146.8±32.0 eggs. The age specific gonadosomatic index (GSI) decreased from 0.187 (±0.041) in age-4 females to 0.149 (±0.019) in age-7 females. GSI in pelagic and epibenthic age-6 females did not differ significantly (*t*-test, *P*=0.25). Egg weight (We, g) increased slightly from age-4 (We=0.043) to age-8 (We=0.053). The difference was significant (*t*-test, *P*=0.009).

Diet

The main food items of Arctic char in Store Rennen were crustacean zooplankton, chironomid larvae, and the benthic crustacean *Eurycercus lamellatus* (Fig. 4). In addition, other insect lar-

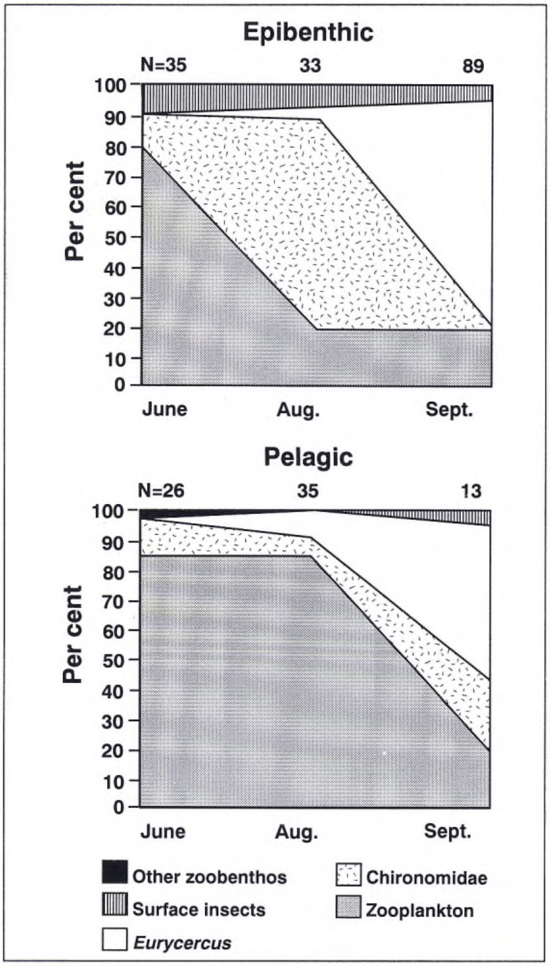


Fig. 4. Diet (per cent dry weight) of epibenthic and pelagic Arctic char, Lake Store Rennen, 1990. N=number of stomachs analysed.

vae and surface insects were taken. The composition of the diet of pelagic and epibenthic fish did not differ significantly in June and September (Mann-Whitney U-tests based on dry weights of prey, $P>0.05$). In August, however, the proportion of zooplankton was higher in pelagic char (Mann-Whitney U-test, $P<0.001$), whereas epibenthic char had taken more chironomid larvae and pupae (Mann-Whitney U-test, $P<0.001$) and other zoobenthos (Mann-Whitney U-test, $P<0.007$). The frequency of empty stomachs was low except in September when 27% of the pelagic char had empty stomachs. Diet overlap (Schoener's index) between epibenthic and pelagic char was low in July/August (D=0.44), and higher in June and September (D=0.77 and 0.71, respectively). The dry weight of the stomach content relative to fish body weight may indicate the relative energy uptake. The relative weight of the stomach content was higher in epibenthic than in pelagic fish in all sampling periods. However, the difference was significant only in June and August (Mann-Whitney U-test, $P<0.017$ and $P<0.001$, respectively).

Morphology

There was no significant difference in the number of gillrakers (*N*) in pelagic (*N*=22.5) and epibenthic char (*N*=22.7) (Mann-Whitney U-test, $P>0.05$). The length-weight ratio differed significantly between pelagic and epibenthic char in June and August (Table 2).

Table 2. Weight-length ratio of pelagic and epibenthic Arctic char in Store Rennen, June, August and September, 1990. The ratio is expressed as $\log_e W = a \log_e L + b$, where W is wet weight (g) and L is body length (cm). Body length indicates the length interval represented in both habitats, included in the comparisons. *N* is the number of fish.

	June				August				September			
Body length (cm)	15.5-18.7				12.1-20.0				12.0-19.0			
Habitat	*N*	R^2	*a*	*b*	*N*	R^2	*a*	*b*	*N*	R^2	*a*	*b*
Pelagic	26	0.80	1.98	-2.03	108	0.81	2.39	-3.14	13	0.95	2.62	-3.71
Epibenthic	53	0.39	1.42	-0.36	125	0.91	2.68	-3.97	270	0.65	2.44	-3.16
Test	$F_{(1, 76)}=22.66$, $P<0.001$				$F_{(1, 230)}=39.26$, $P<0.001$				$F_{(1, 280)}=1.01$, NS			

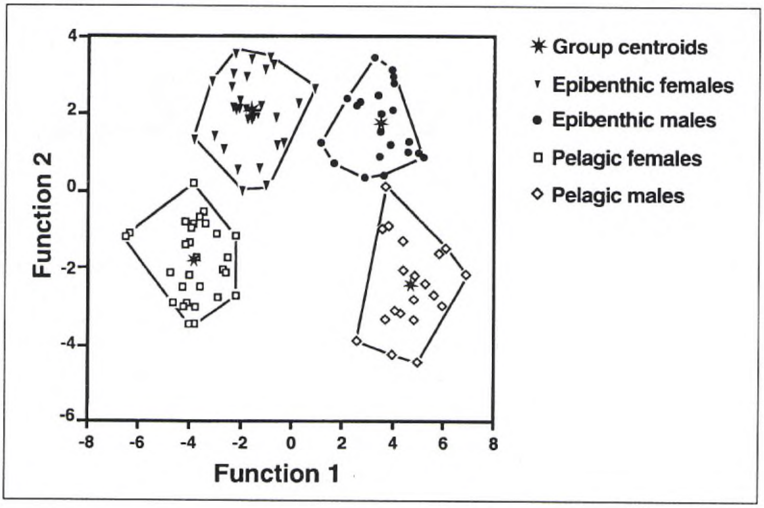


Fig. 5. Scatterplot of canonical discriminant functions based on 26 variables, among epibenthic and pelagic male and female Arctic char, Lake Store Rennen, August, 1990.

Discriminant analysis of the size-free morphometric parameters of pelagic and epibenthic male and female char demonstrated that the morphology of the fish was in accordance with the *a priori* grouping into pelagic and epibenthic males and females. The differences in morphology were significant (l=0.01, χ^2=409.3, 75 df, P<0.001). Function 1 (mainly sex differences) explained 72% of the morphological variation, whereas function 2 (mainly habitat) explained 25% (Fig. 5). Discriminant analysis of the morphometry of pelagic and epibenthic char within sexes was also able to separate all males and 90.6% of the females. Univariate (ANOVA) analysis of the variables showed that snout length and dorsal fin length were significantly different between pelagic and epibenthic males. Among females the corresponding variables were upper jaw length, dorsal fin length, anal fin length, eye diameter, and the form of the caudal fin basis.

Stepwise variable selection showed that two variables were important for the segregation of pelagic and epibenthic individuals in both sexes

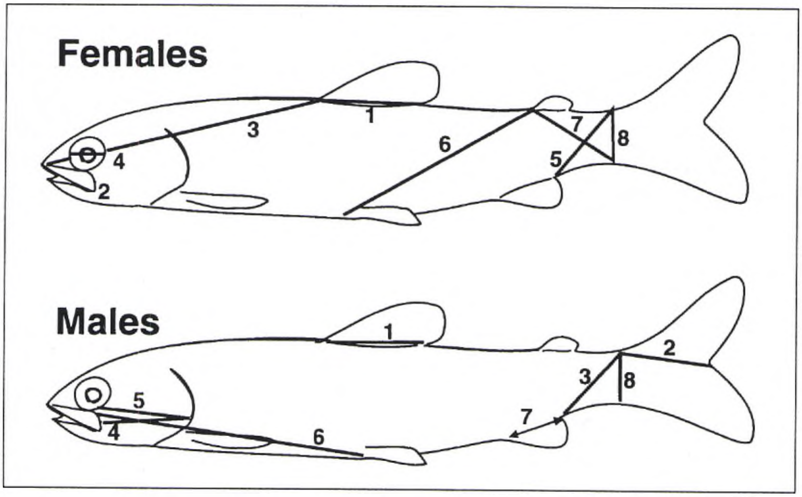


Fig. 6. Morphometric variables of major importance in classifying Arctic char from Store Rennen into one epibenthic and one pelagic group. The variables are numbered according to their importance.

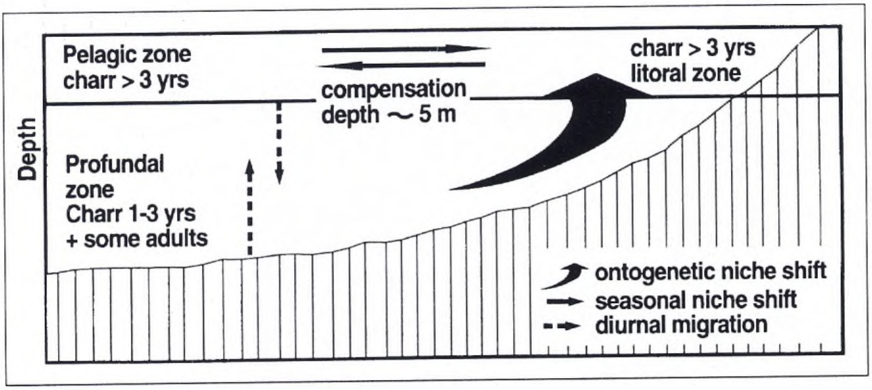


Fig. 7. Summary of the ontogenetic and seasonal habitat shifts among Arctic char in Lake Store Rennen.

(Fig. 6): the dorsal fin length and the distance from the posterior end of the anal fin base to the upper caudal fin base. Discriminant analysis based on the variables shown in Fig. 6 classified more than 90% of both sexes into the correct group (pelagic and epibenthic) (females: l=0.33, χ^2=61.8, 8 df, P<0.0001; males: l=0.31, χ^2=41.3, 6 df, P<0.0001).

Discussion

Within the stunted Arctic char population in Store Rennen, both seasonal and ontogenetic niche shifts did occur (Fig. 7). Adults performed a partial seasonal migration from the epibenthic to the pelagic zone in August, returning to the epibenthic zone in September. The ontogenetic niche shift consisted mainly of juveniles migrating from the deep epibenthic zone (>4.9 m) to the littoral zone (0-4.9 m), when reaching age-4 and a body length of approximately 150 mm. The divergence we have recorded in Store Rennen regarding body morphometrics between similarly-sized and apparently monomorphic char occupying the pelagic and epibenthic habitats in late summer has previously not been observed.

The dynamics of habitat use among the Store Rennen char is an example of the commonly observed pattern in stunted Arctic char populations (Klemetsen et al. 1989, Langeland and Jonsson 1990, Langeland et al. 1991). The proximate reason for the partial seasonal habitat shift is probably the increase in available food in the form of crustacean zooplankton, in the pelagic zone in late summer (Langeland et al. 1991, Næsje et al. 1991). Only a restricted proportion of the adult stock changes its habitat. This may be the result of one or a mixture of several alternative mechanisms. It may be an ideal free distribution (Werner and Mittelbach 1981, Ehlinger 1990), diverging preferences among age, size or sex groups within the population (Ehlinger and Wilson 1988, Ehlinger 1989, Werner et al. 1981), or a difference between competitively dominant and subdominant individuals (Hindar and Jonsson 1982, Klemetsen et al. 1989).

The ontogenetic niche shift from the deep epibenthic zone, is thought to be a result of the trade-off between available food and predation risk (Klemetsen et al. 1989). Generally, in lakes the food supply available for all size groups of fish is highest in the littoral zone. In Store Rennen, this habitat is also where both groups of potential predators (brown trout and fish-eating birds) are living. The niche shift occurs when the fish reach a body length of approximately 150 mm, i.e. when the char outgrow the body size most vulnerable to predation from brown trout (L'Abée-Lund et al. 1992, Næsje et al. 1992, Damsgård 1993).

The diet analysis of char from different habitats in Store Rennen indicates that there is some degree of continuous exchange of fish between habitats, particularly in June and September. In August, diet overlap between pelagic and epibenthic char was low, indicating good separation of fish between the habitats.

L'Abée-Lund et al. (1993) and Forseth et al. (1994) reported that the individuals which perform the seasonal habitat shift are those which have had the highest juvenile growth rate. In our data, pelagic fish in June were larger and had a higher weight/length-ratio than the epibenthic fish from this month. This may indicate that the largest fish in the best condition are the first to change habitat. The lack of size differences and the opposite weight/length-ratio in August, however, makes it difficult to draw any conclusion regarding this.

Our results show that there are significant differences in body form between pelagic and epibenthic char. This supports the notion that there are individuals specialised for the pelagic and epibenthic way of life, respectively. The morphometric differences have probably developed during juvenile ontogeny. Similar cryptic polymorphism has been reported in bluegill sunfish (*Lepomis macrochirus*) (Ehlinger and Wilson 1988). The morphological differences in that species were associated with differential feeding efficiencies towards different prey (Meyer 1989, Ehlinger 1990). It is well known that Arctic char exhibit very high phenotypic plasticity, and that living conditions during early age influences the body size, age at maturity and body morphology of adults (Nordeng 1981, Hindar and Jonsson 1992). Meyer (1987) demonstrated that different food during the larval and early juvenile stages caused divergence in the trophic morphology in a Neotropical cichlid (*Cichlasoma managuense*). A similar process may easily be envisaged during early ontogeny in Arctic char. In brook char (*Salvelinus fontinalis*), Grant and Noakes (1987) showed that a specialisation in diet and foraging techniques developed during the first year of life.

Based on the analysis of our morphometric results, we may conclude that in Store Rennen Arctic char there are morphological differences between those fish which perform the seasonal habitat shift and those which remain in the epibenthic habitat. The distribution of fish between the to major habitats may be a result of an ideal free distribution with phenotypical limitations (Parker and Sutherland 1986), with individual fish being better adapted to either of the habitats (Ehlinger 1989, 1990). However, based on the present data it is not possible to conclude whether the habitat shift influences the fitness of the fish.

Acknowledgements

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Survey, Management and Recent Rehabilitation of the Arctic Charr (*Salvelinus alpinus*) Fishery in the French-Swiss Lake Leman

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Abstract

This paper describes the survey, management and recent rehabilitation from 3-5 to 50-65 tonnes per year of the Arctic charr (*Salvelinus alpinus* L.) fishery in the mesoeutrophic French-Swiss Lake Leman (58,240 ha). Positive correlations were found between the increasing number of fingerlings stocked in summer (range 140,000 to 900,000 per year) and the catches three years later. The characteristics of the wild spawners caught on the main spawning grounds were analysed and the eggs of these wild charrs were used to produce most of the restocked fingerlings. The test fishings were mostly composed of young (2+/3+/4+) spawners and their growth indicates no tendency to stunting. The possibilities and the limits of the lake ranching practices are discussed.

Keywords: Arctic charr, lake fishery, stocking, rehabilitation, spawning.

Introduction

Lake Leman is a large (58,240 ha) and deep (mean depth = 145 m) mesoeutrophic French-Swiss lake (Fig. 1) where Arctic charr (*Salvelinus alpinus* L.) is indigenous (Dussart 1955). The charr is at the meridional limit of its distribution area (Rubin 1990). The other species of the fish community are, by rank of decreasing catches, perch, roach, whitefish, brown trout, burbot and pike. The Arctic charr spawns in the lake at great depths (30 to 120 m). The charr fishery decreased to a low level during the sixties and the seventies simultaneously with the eutrophication process. To balance the supposed poor natural recruitment of juveniles, a stocking programme started at the end of the seventies with fingerlings produced only from eggs collected from Leman's wild spawners. Changes in the Arctic charr fishery (commercial and recreational) were studied. The catches of spawners on the main French spawning grounds were accurately surveyed so that inter-year comparative data were obtained during the rehabilitation.

Material and methods

Fishery

During the open fishing season (January, 15th to October, 15th) the charr (minimal permissible total length of 27 cm) are caught by commercial fishermen using nylon monofilament bottom nets (4.2-8m x 100 m per fisherman: 10 nets with a minimum mesh size of 32 mm and 4 nets with a minimum mesh size of 40 mm) and by anglers using long-lines (a maximum of 20 plumb lines towed behind a small boat).

Survey of catches of spawners and stocking

In order to collect eggs, wild spawners were caught with nets every year on the main spawning grounds located in the upper Lake Leman (Fig. 1). The fishing effort was scattered during at least 3-4 weeks between the end of November and Christmas, covering the central part of natural spawning which occurred between the end

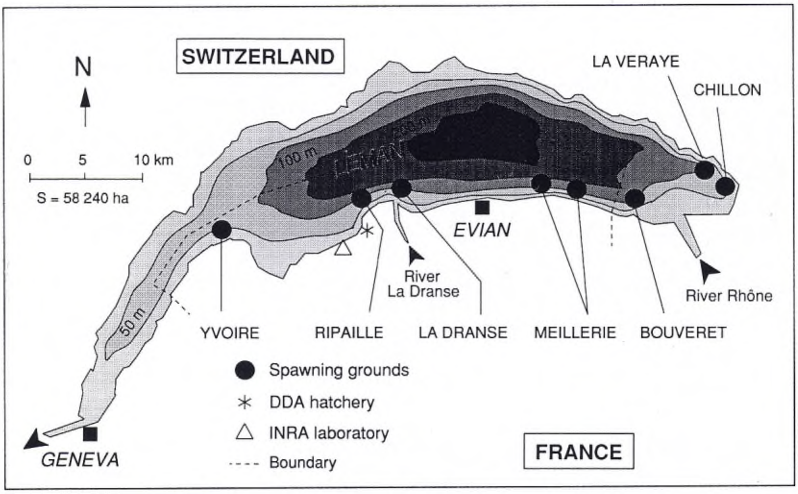

Fig. 1. Lake Leman.

of November an the beginning of January. The fry hatched from these eggs were reared in tanks with dry trout food until the fingerling stage (4 to 10 cm) and released into the lake in summer (France) or early autumn (Switzerland) with a very wide distribution in space and time for each country. The number of fingerlings released yearly increased from 144,000 (2.5 ha^{-1}) to 1,500,000 (26 ha^{-1}) per year during the period 1977-1993. During this period, the fingerlings stocked in the French part represented around 75% ± 11 of the total annual number of fingerlings and the eggs supplying them came from spawners caught on the more important spawning grounds (Meillerie, Fig.1) of the Lake (Rubin 1990). So those catches were surveyed accurately. The fishing effort was evaluated and the fish were counted and sexed. From 1981 to 1984, standard sized (80m • 6-8m) nets with meshes of 40-45 mm were fished during 2-3 nights. From 1985 to 1993 (1685 to 5749 spawners taken per year) standard-sized nets with meshes of 48-50 mm were used and controlled after only one night. Samples (314 to 662 fish/year) of the spawners caught on Meillerie spawning grounds were treated with the same methodology in the period 1985-87 and again from 1990 to 93, the period under the potential effect of the intensification of the stocking. Fish were sexed, total length was measured and age was determined by examination of the scales.

Old data on the sex ratio were available for the years 1949-50 (12,233 fish examined) and 1962-63-64 (5,305 fish examined) for two French spawning grounds (Meillerie and Dranse, Fig. 1) fished with nets of 40-45 mm mesh size during 2-3 nights in the Lake. For the period 1949-50, the size and age of a small sample (120) of spawners are given by Dussart (1952). For the period 1963-64, the size and age were determined sex by sex for 193 spawners.

Results

Lake-ranching practices

The organization in the period 1985-93 allowed the collection of around 1,400 eggs/female caught. At least two-thirds of potential ova were collected and as the survival is at least 75% from egg to fingerling stage, the result of the management practice is a minimal survival of 50% between potential ova and fingerling stage. Taking into account the poor egg survival (<10%) on Leman's natural spawning grounds (calculated by Rubin and Buttiker 1993) and the hypothesis of a maximal survival of 20% from yolksac fry to fingerling stage, survival in nature from potential ova to fingerling stage would be less than 2% at the end of the 1980's.

During the period 1983-85 when around 300,000 fingerlings were stocked annually, large marking campaigns were organized in cooperation between France and Switzerland (Champigneulle et al. 1988, Rubin 1990, Champigneulle and Gerdeaux 1993, Rubin and Buttiker 1993). The survey of adult catches indicated the strong contribution (a minimum of 51 to 75% according to the cohort) of those stockings to the corresponding year-class. The mean ponderal recapture rates for the stockings of the cohorts 1984-85 were evaluated to be in the range 40-50 kg/1,000 fingerlings (Champigneulle et al. 1992, Champigneulle and Gerdeaux 1993). As the actual production costs are low (less than 100 USD/1,000 fingerlings), the cost-benefit balance was good during the period studied.

According to Rubin (1990) who studied the age at maturity of the Arctic charr of Lake Leman at the end of the eighties, 30% of the males were mature at 1+, 79% at 2+ and 95% at 3+. The females matured at a later age: 38% at 2+ and 96% at 3+. For both sexes, all 4+ and 5+ fish examined were mature. Studies of the age composition of catches by commercial and recreational fisheries (Rubin 1990, Champigneulle et al. 1992) indicate that the fish caught are 2+, 3+ or 4+ with the 3+ representing the dominant part.

Catches by commercial fishermen

The total (French and Swiss) mean annual catches of charr by commercial fishermen were around 15 tonnes in the 1950's (Fig. 2A). They increased to 30 tonnes in 1961 and then decreased in parallel with the eutrophication process being lower than 6 tonnes per year in the sixties and seventies. From 1980 and in parallel with the restocking changes three years earlier (Fig. 2A), they have increased to a high level of 22 and 32 tonnes respectively in 1991 and 1992 with no trend to decrease the total trout catches (Fig. 2B). In the same period, the annual catches of whitefish (*Coregonus lavaretus*) have also increased, from 30-50 to 65-110 tonnes. For the period 1980-92, there were significant positive correlations between the number of charr fingerlings released during the year *n*-3 and the mean ponderal catches by Swiss ($N=13$, $r=0.928$, $P<0.001$) or French ($N=13$, $r=0.919$, $P<0.001$) fishermen during the year *n*.

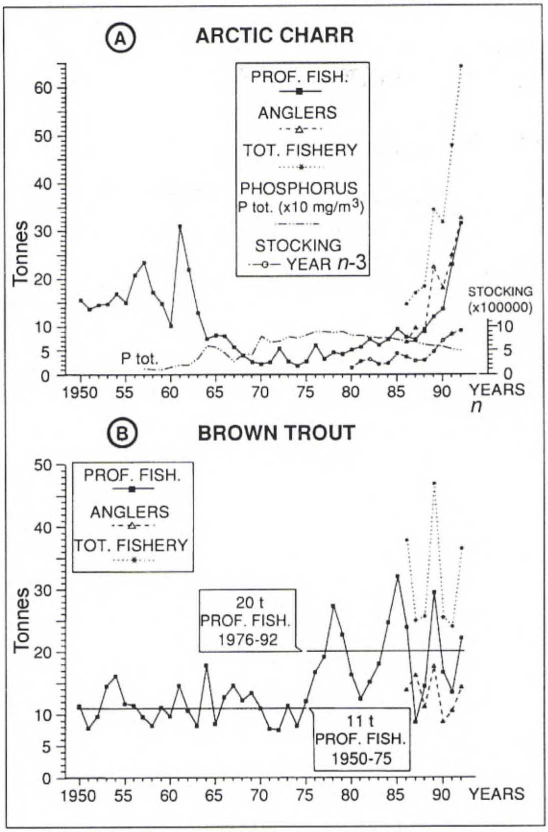

Fig. 2. Annual yield of the Arctic charr and brown trout fishery in Lake Leman during the period 1950-92. **A**: Catches of charr during the period 1950-92; mean annual total phosphorus level (P tot.•10 mg/m^3) during the year *n*; number of hundreds of thousands of fingerlings stocked during the year *n*-3. **B**: Catches of brown trout during the period 1950-92

During the recent period 1986-92, the number of professional fishermen has decreased from 185 to 130. The mean annual weight of charr caught by individual Swiss and French fishermen has increased respectively from 24.9 to 199.2 kg and from 83.6 to 486.1 kg. For each country and for the period 1986-92, there was no significant ($P>0.10$) correlation between the catches/individual fisherman for charr and trout. During this period the mean individual weight of annual catches varied between 264 and 483 g.

Catches by anglers

The total annual catches of Arctic charr for the whole recreational fishery, known from 1986, have increased from 7 to 33 tonnes during the period 1986-92 (Fig. 2A). The number of anglers has increased from 1,862 to 2,826. The mean annual number of charr caught by each French and Swiss anglers has increased respectively from 12.0 to 51.6 and from 7.8 to 27.1. For each country during the period 1986-92, there was no significant correlation ($P>0.20$) between the CPUE of charr and trout even if the CPUE of trout, in contrast to charr, was rather low in the years 1990 to 1992. The mean individual weight of annual catches fluctuated between 354 and 553 g.

Catches of spawners on spawning grounds

Characteristics of the spawners caught

Because of spawning behaviour and net selectivity, the catches do not represent the whole spawning stock and so the results are focused on inter-year comparative data and on characterization of the fish used as spawners in the restocking programme.

Age structure

The catches by nets with a 48-50 mm mesh size for years in the two periods (1985-87 and 1990-93) were composed of fish aged from 2+ to 6+ (Fig. 3A). For each sex the age class 3+ was always dominant. The 2+ were better represented among the males than among the females and the reverse was true for the 4+. The age classes 5+ and 6+ together represented only 0 to 5.4% of the males and 0 to 12.9% of the females. Some modifications appeared in the two last years 1992-93 with the percentage of males 4+ superior to the percentage of males 2+ in contrast to other years (Fig. 3A). In 1993, the percentage of female 4+ was the highest and, in contrast to other years, not significantly different (Chi-square test, $P>0.05$) from the percentage of 3+.

Size

For each given year, the size structure of females was significantly different (Kolmogorov-Smirnov test, $P<0.01$) from the size structure of males with a larger size of females being caught (Fig. 4) in relation to a larger size at age, longer longevity and later maturity. The lowest percentage of charr with a size ≥38cm was observed in 1990 and 91 for males and in 1991 for females. In contrast, the following years 1992 and especially 1993 were characterized by a marked increase in the percentage of fish ≥38cm but <50 cm (Fig. 4).

For each year (except 4+ in 1991: too small a sample of females), the mean size of females 3+ and 4+ was significantly (*t*-test, $P<0.001$) higher than the mean size of males of the same age (Fig. 5A). For a given sex and age-class, there was an increase in the mean size between 1991 to 1993. The mean rank by size of the males 2+ and 3+ and females 3+ caught in 1993 was significantly higher (Kruskall and Wallis test, $P<0.05$) than for fish of the same age for the other years.

CPUE

The CPUE of total spawners (mean number caught per night per standard net) on Meillerie spawning grounds during the period 1983-93 indicated the presence of higher fish densities in comparison with the years 1981-82 (Fig. 6). During the period 1985-93 the CPUE of total spawners on Meillerie spawning grounds did not vary in the same manner for males and females (Fig. 6). For the females there was a contrast between the high CPUE of 1989 and the low CPUE of 1990. In contrast to the males, the CPUE of females increased between 1991 and 92.

For the period 1985-91, there was a significant positive correlation between the CPUE of French commercial fishermen (kg/fisherman) during the year *n* and the catches of males on the Meillerie spawning grounds at the end of the

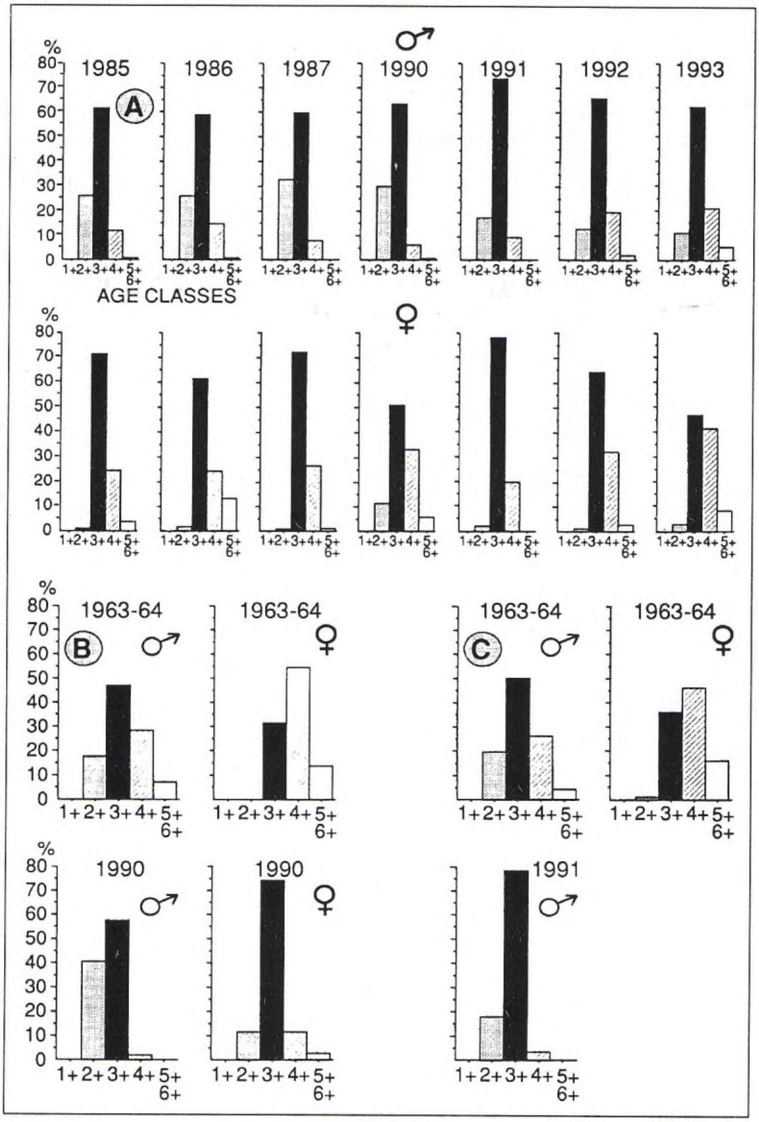

Fig. 3. Age structure of male and female Arctic charr spawners caught on French spawning grounds of Lake Leman. **A:** Meillerie spawning grounds fished with nets of 48-50 mm mesh size during the periods 1985-87 and 1990-93. **B**: Meillerie spawning grounds fished with nets of 40-45 mm mesh size during the years 1963-64 and 1990. **C**: Dranse spawning grounds fished with nets of 40-45 mm mesh size during the years 1963-64 and 1991.

same year (r=+0.959, P<0.001, N=7). The correlation between the CPUE of French anglers (n/angler) during the period 1986-91 and the CPUE of males on the spawning grounds was also significantly positive (r=+0.974, P<0.001, N=6).

However the situation changed in 1992 and 1993, the years with the highest total catches (>60t/yr) during the season, and there was a decrease in the CPUE of males on the Meillerie spawning grounds (Fig. 6.). For the two years 1992 and 93, the CPUE of males 2+ was smaller than in the two previous years. In contrast, the CPUE of older spawners (males or females aged 4+ or more) in 1992 and 93 was significantly higher than for the previous years (Fig. 6). Between 1992 and 93, in contrast to the trends on the Meillerie spawning grounds, there was an increase in the CPUE of males and females (Fig. 6) on other spawning grounds surveyed recently (Dranse, Fig. 1). Moreover, important captures of mature Arctic charr spawners with ovulated females were made in 1992 and 93 outside the

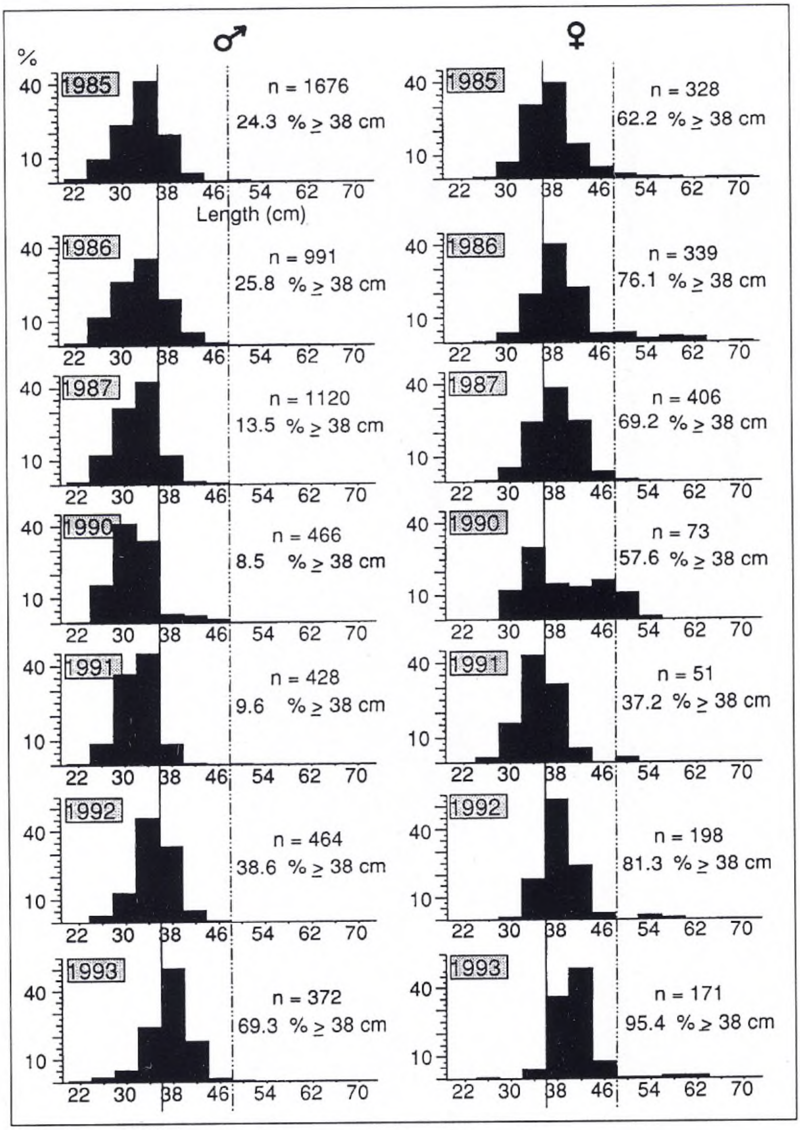

Fig. 4. Size structure of male and female Arctic charr spawners caught on French spawning grounds of Lake Leman with nets of 48-50 mm mesh size during the period 1985-87 and 1990-93.

traditional spawning grounds, a phenomenon never observed before with such an intensity. This suggests a recent redistribution of natural reproduction in Lake Leman.

For the cohorts 1982-83-84-87-88-89, there was a significant positive correlation ($P<0.05$) between the number of fingerlings stocked and the CPUE of males 3+ ($r=+0.838$) of the same cohort caught on the Meillerie spawning grounds. However the correlation was no longer significant ($r=+0.593$, $P>0.05$) when the cohort for 1990 was added.

For the cohorts 1981-82-83-86-87-88-89 and for each sex, there was a significant positive correlation between the number of fingerlings stocked and the CPUE of male 4+ ($r=+0.826$, $P<0.05$) and female 4+ ($r=+0.844$, $P<0.05$) of the same cohort caught on the Meillerie spawning grounds with nets of 48-50 mm.

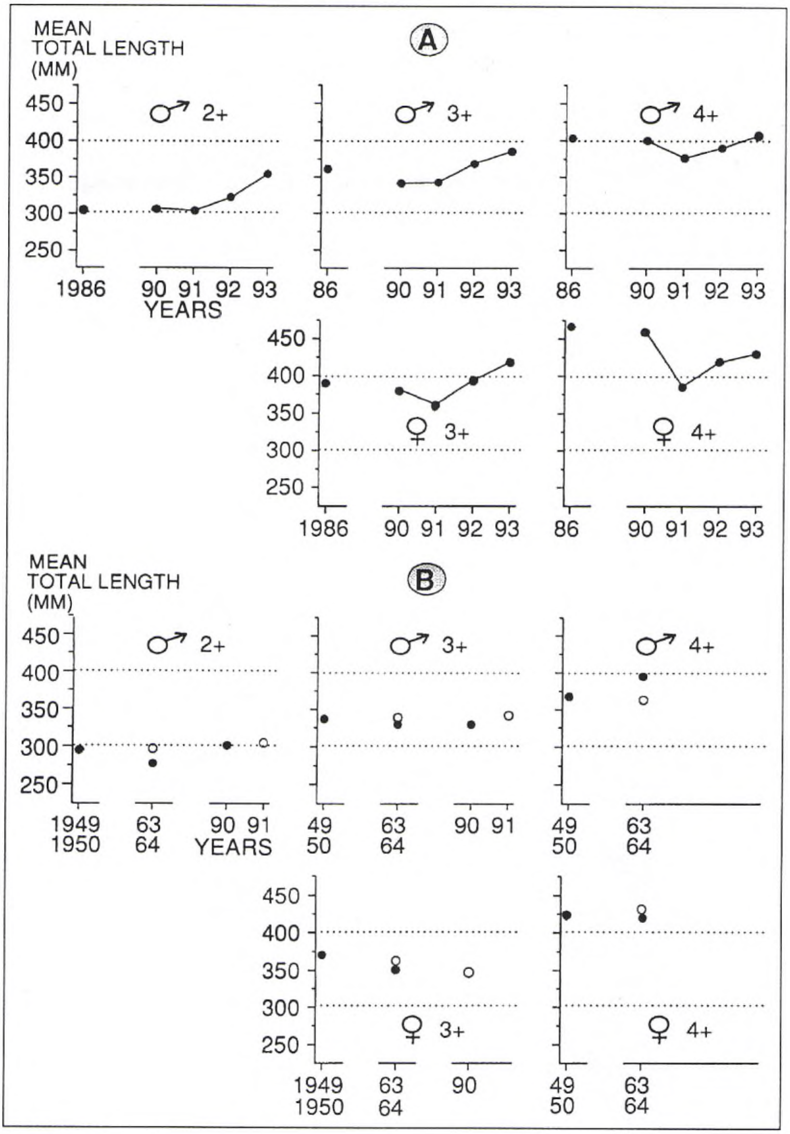

Fig. 5. Mean total length of male and female Arctic charr spawners caught on French spawning grounds of Lake Leman. Confidence limits at 95% level are not indicated as they are smaller than point size. **A**: Meillerie spawning grounds fished with nets of 48-50 mm mesh size during the years 1986 and 1990 to 93. **B**: Meillerie (•) and Dranse (○) spawning grounds fished with nets of 40-45 mm mesh size.

For the cohorts 1982-83-87-88-89, there was a significant correlation (r=+0.951 for males and r=+0.935 for females; $P<0.02$) between the CPUE of 3+ and the CPUE of 4+ of the same cohort caught the next year on the Meillerie spawning grounds with nets of 48-50 mm.

The males of cohorts 1982-83 and 1987-88-89 were present at stage 3+ at very different densities (range of CPUE: 26-118 males 3+/net/night) but, however, they had a rather similar and high (0.75 to 0.87) annual apparent loss rate between the stage of spawner 3+ and 4+.

Comparison with old data

For a given spawning ground and mesh size, the age structures were significantly different (Kolmogorov-Smirnov test; $P<0.01$) between the beginning of the sixties and the beginning of the nineties with a higher proportion of young fish in 1990-91 (Fig. 3B and C). For the same spawn-

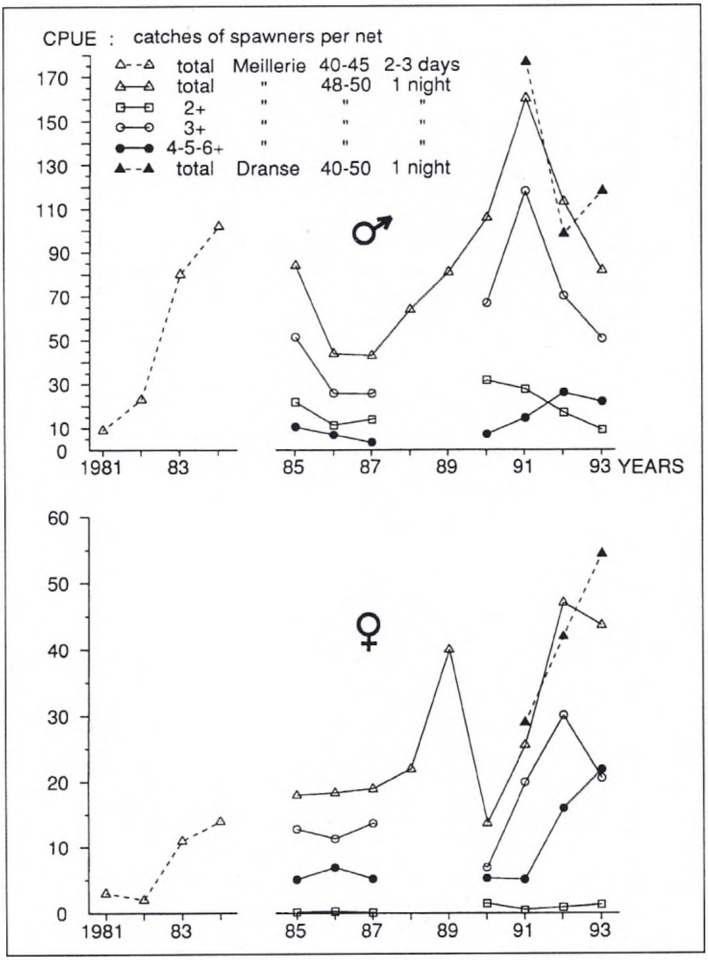

Fig. 6. CPUE of Arctic charr spawners on French spawning grounds of Lake Leman (mean of numeric catches of males or females per net laying).

ing grounds fished with the same kind of nets, there was no difference in the mean size of males 2+ and males or females 3+ and 4+ between the years 1990-91 and 1949-50 and 1963-64 (Fig. 5B). However, 1990 and 1991 were the years with the lowest growth for the recent period. The percentages of females in the catches of the years 1949-50 and 1962-63-64 varied between 49 and 63% which was, for every year, significantly higher (Chi-square, $P<0.001$) than the percentage of females observed for each year of the period 1981-84 on the same spawning grounds fished with the same technique. The increase of mesh size and the practice of a one night fishing in the period 1985-93 did not change the poor percentage of females in the catches which remained (12-35%) for each year of the period significantly smaller (Chi square, $P<0.001$) than in 1949-50 and 1962-63-64. The same observations were also true for the Dranse spawning grounds.

General discussion

The expectation of rehabilitation of the Arctic charr fishery in Lake Leman made by Champigneulle et al. (1988) is now being realized. Stocking up to a level of around 900,000 fingerlings/yr (16/ha) facilitated this increase and sustainability of the catches. The results confirm the very good potential of Arctic charr for lake ranching under the present conditions of Lake Leman. Several factors can explain this situation :

- the stocking facilitates the suppression of the major bottle-neck of charr production which, according to Rubin (1990), is the deficiency of the natural recruitment linked to high mortality during egg incubation. The large volume of the lake and the abundance of zooplancton, benthos and forage fish (juveniles of perch and roach) in relation to the mesoeutrophic state provide a high carrying capacity.
- the fingerlings used are reared only from eggs of Lake Leman's spawners.
- thanks to well developed rearing practices, young charr are now easily produced with a good survival (>75%) from green ova until the fingerling stage. Because of their negative phototaxis and avoidance of warm surface water, the fingerlings stocked in summer swim immediately to deep water, a behaviour which probably decreases the success of surface predators during or just after stocking. The rather large individual size at stocking and the good distribution of stocking in space and time are additionnal factors for predator limitation.

The carrying capacity of Lake Leman for the charr, optimal stocking densities and exploitation rate are not yet well known. Old statistics indicate however that the catches had already attained an average of 30 tonnes per year (0.5 kg ha^{-1}) during ten successive years (1921-30) when the lake was oligotrophic and the charr stock was exploited only by commercial fishermen. There are some indices suggesting that the stock is not in an extreme situation (i.e. clearly over or underexploited). Indeed, after the main exploitation phase, the CPUE of spawners remained at a high level and the recent increase of older (4+) individuals suggests no critical overexploitation. The smaller size of spawners noticed in Leman in 1990-91 was most probably due to a selective exploitation of individuals with the quickest growth (Champigneulle and Gerdeaux 1993). The present study confirms that there was no trend towards the stunting which could suggest underexploitation. Recent experiments in Scandinavian lakes indicate that higher exploitation rates of stunted charr populations (Amundsen et al. 1993) promote a better growth for the remainers.

Champigneulle et al. (1988) and Rubin (1990) found that fingerlings reared in tanks on dry diets and stocked in Leman survive until the spawner stage and are abundant on the deep Leman's spawning grounds. So a probable and important indirect effect of stocking is an increase in the number of eggs laid in Lake Leman. If there is no decrease in survival at the egg stage or later, the increased stocking could have also increased the level of recruitment issued from the spawning in the wild. However the surface of good spawning grounds is restricted in Lake Leman (Rubin and Buttiker 1993). So, on the contrary, the laying of too many eggs could induce density dependent mortality at the egg or first feeding stages, a phenomenon already demonstrated by Elliott (1994) for some trout populations. The problem is that the present situation between these two extremes is unknown and the consequences of the redistribution of the spawning between and outside traditional spawning grounds are unknown. The survey revealed a smaller percentage of females in the catches of spawners during recent years in comparison with 40-50 years ago. The examination of the sex-ratio in some samples of the catches at 3+ stage shows a dominance of females during the summer (Rubin 1990, Champigneulle et al. 1992). However, other explainations could be examined such as the sex-ratio of the stocked fingerlings.

In Lake Leman the charr are generally not present in the littoral (depth <15m) which is heavily fished with nets for the perch catch. The survey revealed some recent modifications in the vertical distribution of Arctic charr in 1992 and 1993. Indeed during the fishing season, an increasing quantity of charr was caught in the upper part of the lake, most of them having adopted piscivory (mainly young perch but also roach).

For example, most of the charr (around 90% of the fish with a filled stomach) caught by anglers during the beginning of autumn 1993 had eaten small perch of 4 to 10 cm. This phenomenon was not pronounced during the eighties. It can be linked to the very strong cohorts of perch which were born in 1992 and 93 and the habitat shift could also have been favoured by the high charr density. A risk is that life in the upper part of the thermic range and overpopulation could favour the expansion of diseases like bacterial diseases (*Aeromonas salmonicida* and *Carnobacterium piscicola*) which have recently been detected on a few of the charrs caught. Another risk is the overlap with the habitat and trophic resources for trout in the pelagic zone of Lake Leman. Indeed as found by L'Abbée-Lund et al. (1992), both species can be piscivores in this habitat but there are strong inter-year fluctuations of forage fish (young perch and roach) in Lake Leman. The resource partitioning and niche shift of the two species has been accurately studied in Norvegian lakes (Langeland et al. 1991) but is still too poorly known for Lake Leman.

It is important to continue the survey of the fishery and the evaluation of the relative contributions of natural and artificial recruitment whilst the trophic stage of the lake is changing in relation to the limitation of the phosphorus input. Recent development of mass-marking techniques (Rojas Beltran et al. 1995) will be useful to compare contribution, characteristics, spatio-temporal distribution and exploitation of charr originating from natural and artificial recruitment.

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Life History of Trout, *Salmo trutta* L., in The Varsina River Estuary, (The Barents Sea)

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Abstract

This paper describes the ecology of trout associated with the estuary of a small Barents Sea river. The trout feed in the estuary during the summer. Estuarine trout retain a hyper-osmotic type of regulation of the water-salt balance. The migratory trout move up and down within the estuary, confined to water masses with a salinity not exceeding 12‰. The movement of such water masses in the tidal cycle allows the brown trout to leave the estuary at low tide and migrate farther into the open sea and feed on marine organisms.

Keywords: Brown trout, *Salmo trutta* L., Migrations, Physiology, Estuary, Hydrology

Introduction

The brown trout, *Salmo trutta* L., lives in a variety of habitats. Some trout populations are environmentally divided during their life cycle; one part of the stock may be permanent freshwater residents, whereas the other part become sea-run migrants (Jonsson 1989, Hindar et al. 1991). The latter separate into long distance migrants which go into the open sea and remain in a hyperosmotic environment, while short distance migrants stay in estuaries. The analysis of the osmoregulatory system of the Varsina River brown trout smolts shows that they include two groups (Chernitsky 1993). The first change their type of osmoregulation to the hypoosmotic and are apt to migrate for feeding into the salt water as a sea-run trout, the second conserve hyperosmotic regulation of salt-water balance and are apt to remain in the estuary. Trout from estuaries have been studied by several authors (Calderwood 1930, Nall 1935) who pointed out that estuarine fish movement is dependent on the tidal phenomenon. Here we investigate the physiological and ethological mechanisms that allow the trout to survive in a very unstable estuarian habitat. The question addressed was: do estuarine brown trout adapt to changes in the hypo- and hyperosmotic environment, or do they maintain a stable osmotic environment by active habitat shifts.

Study area

The Varzina River is located on the Kola Peninsula (Russia) at 68°20'N, 38°10'E (Fig. 1). It comes from Lake Yenozero and flows into Varzina Bay in the Barents Sea. The length of the river is 30 km. The estuary of the Varzina River is 8 km long from the marine border with the Barents Sea to the point of maximum penetration of salt water. Morphologically the estuary can be divided into two parts. The river section is shallow (about 3 m at high tide) and extends for 5 km from the mouth of the Varzina. The Grave Brook flows into this part of the estuary. The marine part begins where the bottom drops sharply and the depth reaches 30 m.

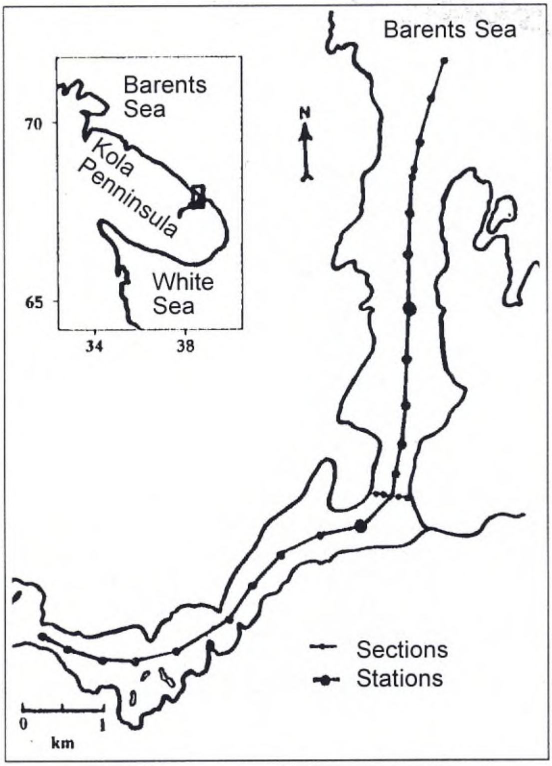

Fig. 1. The Varsina River Estuary.

The Varsina River estuary has a regular half-diurnal tidal period. The mean tidal level at neap tides is 3.8 m, in spring tides it is 5.2 m. The tidal wave is progressively standing.

Material and methods

Fish

Trout distribution in the estuary was estimated by angling. Netting was impossible due to strong tidal currents. Angling gave us an indication of trout presence during their migration. The estuary was separated into areas for regular fishing at all times of the day from July 5 until July 29 1990. Area "A" included the place where the river discharges into the estuary, area "B" included the border between the river and marine parts of the estuary. In other areas of the estuary, fishing was carried out only when fish appeared.

Fork length and weight were determined. The fish were aged by the use of scales. A total of 243 trout was caught. Most of the fish were released after scaling, 48 fish were individually tagged with numbered Carlin-type external tags, 22 were used for biochemical analyses.

Analysis

Hydrological measurements were made on stations and on sections along and across the estuary (Fig. 1). Temperature and salinity were measured from surface to bottom using a vertical interval as small as 5 cm. Temperature was measured using TEZ-3 electrothermometer. Water samples for salinity determination were taken utilizing a special portable pump, then treated on a salinometer GM-65. A total of 19,000 water samples were analyzed for salinity. Based upon an examination of the salinity, the movement of isohalina 12‰ in the tidal cycle was determined. The water with this salinity was selected because the sodium content is approximately the same as in the estuarine trout blood (Zabruskov et al. 1990).

Fish blood for analysis was taken from the caudal vein with a quartz pipette. Blood serum was used in the investigations. Concentration of Na in blood serum samples was determined using a flame photometer "Zeiss-111" in an air-propane flame.

Sucrose content was determined by its anthrone reaction on a "Ziess-11" spectrophotometer (Aleinikova and Rubtsova 1988). The activity of succinic dehydrogenase (SDH E.C. 1.3.99.1) of the chloride cells was determined cytochemically and measured on a cytophotometer using methods described earlier (Chernitsky 1980)

Groups means were compared using Student's *t*-test.

Results

Characteristics of estuarine trout

The trout catchment was desirably constant in all the study period. 6 of 48 tagged fish were recaptured in 5 (2 fish), 8, 11, 13 and 16 days after release.

Table 1. Age structure (%) of estuarine trout (N=243).

		Riverine					
		2+	3+	4+	5+	6+	Σ
Estuarine	0+	-	0.8	15.3	6.6	1.2	24.0
	1+	-	7.9	22.3	11.2	2.5	43.8
	2+	-	5.4	13.6	5.0	0.8	24.8
	3+	0.4	2.5	2.5	0.8	0.4	6.6
	4+	-	0.8	-	-	-	0.8
	Σ	0.4	17.4	53.7	23.6	5.0	

The estuarine trout scale structure makes it possible to distinguish river and estuarine age of a fish. The trout were divided in 18 age groups, formed by a combination of 5 grades of river age (2+ - 6+) and 5 grades of estuarine age (0+ - 4+). Age group 4+, 1+ was the most prevalent (Table 1). As the data of Table 2 suggest, fish size changed according to their estuarine age, whereas river age did not affect the size of the fish.

Biochemical characteristics of trout caught in high and low water are presented in Table 3. There is no difference between these two groups in SDH activity of chloride cells and sodium level in blood serum. Fish caught in high water, however, have larger amounts of food in their stomachs and an elevated concentration of sucrose in the blood.

Trout movement in estuary

Trout distribution in the estuary is mainly dependent on the phase of the tidal cycle which is divided into 4 periods for ease of analysis: low water, mid-flood water, high water and mid-ebb water. The duration of each period is approximately 3 hours. Fig. 2 gives the positions of 12‰ isohalina averaged over an observation period. An actual position changed from day to day with changes in tide height, river flow and wind conditions.

Low water

At this phase, fresh water occupies all the river section of the estuary. In the marine section, a freshwater layer of 10-25 cm thickness is established over the salt water (Fig. 2).

Trout are found everywhere in the estuary, especially in sections with rapid current. Maxi-

Table 2. Length (cm) and weight (g) of estuarine trout of different age, mean ±SE.

		Riverine age					
		2+	3+	4+	5+	6+	Σ
Estuarine age	0+	-	37.5±2.5	35.7±1.2	36.3±1.4	42.0±3.5	36.6±0.9
		-	700±100	627±56	686±71	763±73	653±41
	1+	-	36.5±1.7	39.3±0.7	39.8±1.0	38.9±2.2	38.9±0.5
		-	724±76	824±36	810±55	795±146	801±27
	2+	-	38.9±1.9	40.0±1.0	42.2±1.1	47.2	40.4±0.7
		-	848±85	855±51	1036±77	1275	892±40
	3+	40	40.0±2.3	43.7±1.9	45.8±2.3	50	42.7±1.3
		1100	980±90	1028±119	985±169	1400	1033±61
	4+	-	42.2	-	-	-	42.2±0.25
		-	1275	-	-	-	1275±25
	Σ	40	38.0±1.0	38.7±0.6	39.5±0.7	42.0±1.8	38.9±0.4
		1100	813±49	784±27	809±40	918±102	806±20

Table 3. Biochemical characteristics of trout from the Varsina River estuary. Mean ±SE. Significant: ** $P<0.01$; *** $P<0.001$

Characteristic	High water	Low water
Sodium concentration in blood, mmol l^{-1}	154±4 (7)	155±3 (9)
SDH activity of the chloride cells, arb. un.	32±3 (6)	33±2 (7)
Stomach content weight, % of weight of gastro-intestinal system	19.7±3.2 (12)	6.7±1.8** (10)
Sucrose content in blood, mmol l^{-1}	2.7±0.3 (9)	1.1±0.1*** (4)

mum trout aggregation is located from the river mouth to where a peninsula narrows the estuary (Fig. 3). Salinity here is 3-4‰ at the surface and 12-15‰ in the bottom layers. In the marine part of the estuary, fish prefer to occupy shallow water in a layer of 0.5 m thickness where fresh and salt water are mixing very intensively and the salinity does not exceed than 10‰. In the estuary sections where the salinity in all areas is high (32-34‰), we did not manage to catch trout. All trout caught during low water were well fed. The main component of the diet was the amphipod (*Gammarus oceanicus*). Sand eels (*Ammodytes marinus*) were found in the stomachs of trout from the marine part of the estuary.

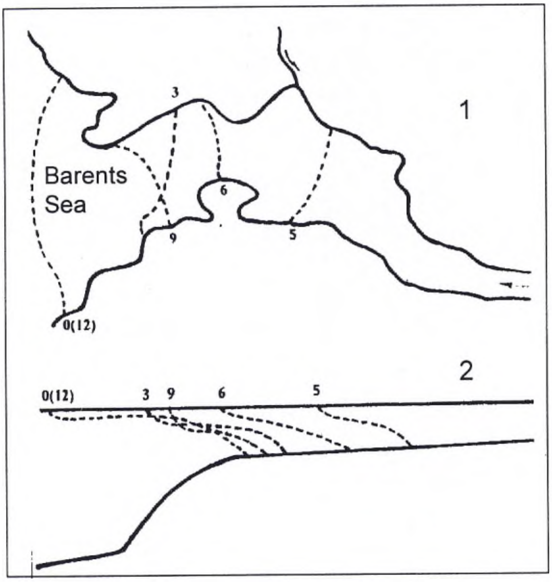

Fig. 2. The position of 12‰ isohaline at different times after the start of flood tide. 1. View in horizontal section. 2. View in vertical section. 0-12 hours after the start of flood tide.

Mid-flood water

A wedge of cold salt water moves up the estuary with the beginning of the flood stream (Fig. 2). Water with a salinity 12‰ appears at the bottom where the estuary narrows about 3 hours

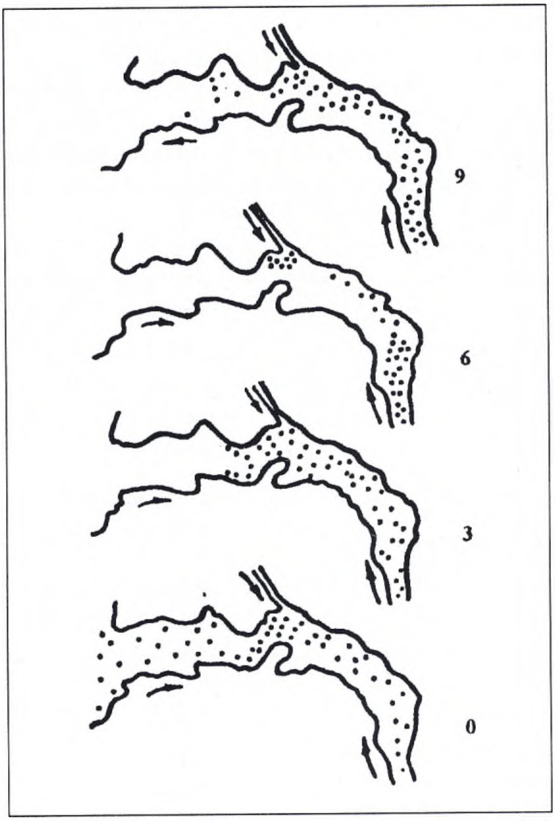

Fig. 3. Distribution of trout at different times after the start of flood tide. 0-9 hours after the start of flood tide.

after the tide starts. One hour later the 12‰ water rises to the surface here. The flood stream flows to the deep parts of the estuary, consequently the shallow inlets and creeks are still filled with fresh or brackish water. After mid-water, the rate of the flood stream decreases. The progress of the salt water wedge halts, but the increase in estuary water level continues. Salt water fills all estuary sections and reaches the surface. At this moment the river flow is stopped by the flood stream. The frontal zone of salt and fresh water interaction is clearly recognized by surface bars of foam and ripple. The temperature and salinity difference on both sides of the frontal zone is 7°C and 20‰.

Two hours after the flood tide begins, small trout (200-300 g) can be caught near the left bank of the peninsula marine site where surface salinity is 3‰. Larger trout (700 g) can be found here within 30 min, when salinity increases to 5-7‰. In the next hour the largest trout (1,500 g) appear in this section. All fish disappear from this part of the estuary after another 45 min when the subsequent surface salinity reaches 15-18‰.

Trout appear near the right bank shortly and remain there until high water (Fig. 3). Salinity during the mid-tide period is 1‰ and small to middle size trout (70-850 g) can be caught. In the next hour salinity increases to 3‰ and trout larger than 1 kg appear. Fish are well fed with large amphipods and sand eels.

High water

One hour before high water, the rate of the surface flood stream decreases and becomes less than the river run-off. River water breaks through the lateral frontal zone and flows down to the sea. The bars of foam draw along the estuary surface. At high water the flood stream is replaced by ebb stream across the whole width of the estuary. The rate of ebb increases gradually and reaches its maximum in three hours. Fresh and sea water move in the same direction, however, the freshwater current is more rapid at the beginning of ebb. That creates an intensive turbulent mixture of fresh and underlaying sea water.

At high water, trout accumulate close to the Varsina River mouth (Area "A") and along the right bank near mouths of brooks (Fig. 3). Small fish remain within a salinity level of not more than 5‰. Large ones can be found in sections with 25-30‰ salinity but here the presence of a surface layer of fresh or brackish water is necessary. Amphipods in fish stomachs are digested.

Mid-ebb water

At this moment, fresh and sea water currents have the same direction and rate. The intense mixing of fresh and sea water decreases. Estuarine water mass doubles its layers of structure with a clean horizontal border between fresh and salt water. River run-off is pressed to the right bank and refreshment occupies there earlier than near the left one. During further ebb, all water in the river part of the estuary becomes vertically homogeneous. Salinity drops from 10 to 0‰ during the period from middle to low water.

In the marine part of the estuary, fresh water spreads over the salt water. Between the fresh and salt water, a sharp boundary is formed. Fresh water is found 350-400 m seaward from the physical boundary of the estuary.

Large fish appear in the estuary narrows within 3 hours of high water, following the retreating wedge of salt water. Salinity of the run-off is 30‰ at the bottom and 5‰ in the upper 20 cm - thick layer. In the next hour, large trout as well as small ones occupy the marine part of the estuary (Fig. 3), where bottom salinity is 15-20‰ and surface is 0-5‰.

Discussion

Trout are well known from the estuaries of many rivers discharging into different seas (Calderwood 1930, Nall 1935, Jonsson 1989, Zabruskov et al. 1990). In the Varsina River, part of the brown trout population is feeding in the estuary. This is confirmed by the observations of the trout movement upward in the estuary and by the results of the tagging of the small number of the fish. Genuinely sea-run migratory trout are easily distinguished from the estuarine trout and return into the rivers of the Barents Sea coast at the end of August (Zabruskov et al. 1990).

Poulsen (1934), who investigated sea trout in the River Gudenaa, found that juveniles spent only one summer in the estuary and then migrated to the sea. Brown trout from the Varsina River reside in the estuary for several years, running with periods for overwintering in the river (Table 1).

Estuaries are the semi-enclosed bodies of water connected freely with the open sea and within which measurable dilution of sea water, by fresh water, occurs. The productivity of estuaries is considerable but abiotic conditions, for instance salinity, are very variable (Perkins 1984). Thus, there are two strategies for a homoosmotic organism that settles in the estuary permanently. The first is to adapt to systematic changes in hypo- and hyper-osmotic water, and to be able to reverse the type of osmoregulation, but maintain a steady position in the estuary. The second is to migrate within the estuary according to the tidal cycle and maintain an unchanging type of osmoregulation.

As our observations show, the estuarine trout move up and down within the estuary twice per day. Due to this migration, the fish confine themselves to fresh or brackish water masses. Even the trout found in sections with 25-30‰ salinity actually occupy the surface layer of fresh or brackish water subsequently present here. According to the results of biochemistry analysis (Table 3) the sodium concentration in fish blood serum is 154-155 mmol l^{-1}, and is equal to sea water with 12‰ salinity. If trout occupy waters with less salinity, an osmotic concentration in the interior medium is higher than in the exterior medium. Osmoregulation in such case will be the hypo-osmotic type. Low activity of chloride cells SDH (32 arb. un.) reflects this hypo-osmotic type of osmoregulation. Trout from the Varsina River estuary show a fatty acid composition of total lipids similar to freshwater salmonids (Belkovsky et al. 1991). This is also an indication of the hypo-osmotic type of osmoregulation.

The comparison of trout caught at high and low waters does not depict the difference in SDH activity and sodium level in blood serum (Table 3). Fish that were angled at high water have however a larger amount of food in the stomach and an elevated concentration of sucrose in the blood. These results support our suggestion concerning spatial and temporal distribution of estuarine trout. The estuary is filled by hypotonic water masses at low water and trout migrate further into the open sea and feed on plentiful marine amphipods (Fig. 3). With the beginning of flood tide, well fed trout move up to the river and brook mouth escaping sea salt water entering the estuary. In an ebb tide, fish that managed food digestion during high water, again return to the marine feeding grounds.

Thus the movement of hypotonic water masses in the tidal cycle permits trout to use feeding resources of offshore sea regions and to retain the hyper-osmotic type of osmoregulation. There is much evidence, however, that brown trout, even non-anadromous ones, easily adapt to full-strength sea water and change the type of osmoregulation (Aass 1982, Hogstrand and Haux 1985, Faure 1991). However, estuary trout prefer to migrate up and down within the estuary twice a day rather than change the type of osmoregulation and remain in the same zone.

The analysis of the Varsina River brown trout smolt-run shows that it includes fish pre-adapted for salt water feeding as sea-run trout and smolts without this pre-adaptation (Chernitsky 1993). The present study shows that fish retained a hyper-osmotic type of regulation of the water-salt balance and are feeding in the estuary. The estuarine trout move up and down within the estuary, confined to water masses with a salinity not exceeding 12‰. The movement of such water masses in the tidal cycle allows the brown trout to leave the estuary at low tide and migrate farther into the open sea and feed on marine organisms.

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Arctic Charr, *Salvelinus alpinus* (L.), as Prey for Piscivorous Fish - A Model to Predict Prey Vulnerabilities and Prey Size Refuges

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Abstract

To study if stocking of piscivorous fish such as brown trout, *Salmo trutta* L., can be used to regulate density and growth in slow growing populations of Arctic charr, *Salvelinus alpinus* (L.), I used simple models to predict maximum prey length and relative prey vulnerabilities based on the gape sizes of predators, and body depths of prey. Brown trout had larger relative gape size than Arctic charr (8.8 and 7.5% of total length), but neither of them selected prey sizes up to gape limitation. Assuming a random encounter between predators and prey, the probability of being eaten for prey of a particular size is the product of the relative vulnerability and the relative frequency of occurrence. In a full-scale experiment with piscivorous brown trout, the model revealed an increase in the number of Arctic charr in prey size refuges. Furthermore, this method can be used to predict the effects of piscivorous predation in multispecies lakes, and regulate fishing to protect large piscivorous fish.

Keywords: Arctic charr, brown trout, predator, piscivorous, gape.

Introduction

Arctic charr, *Salvelinus alpinus* (L.), populations often consist of slow growing, small sized individuals (Dahl 1920, Langeland 1986, Amundsen and Klemetsen 1988, Amundsen 1989, Klemetsen et al. 1989, Langeland and Jonsson 1990). This situation is found in both exploited and unexploited populations and is not necessarily human-induced (Johnson 1983, Sparholt 1985, Parker and Johnson 1991).

Many attempts have been made to reduce the number of fish in densely populated lakes, and thereby increase individual growth rate and asymptotic body length. Intensive harvest or predator releases are alternatives to remove unwanted fish. In Norway, promising results have been achieved by releasing large zander, *Stizostedion lucioperca* (L.), as predators on roach, *Rutilus rutilus* (L.) (Brabrand and Faafang 1993). Similarly, stocking of brown trout, *Salmo trutta* L., (Aass 1984) and lake trout, *Salvelinus namaycush* Walbaum (Nilsson and Svärdson 1968) have decreased the number of prey fish in populations.

In a previous experiment (Damsgård and Langeland 1994), 200 large brown trout (two years old, 671 g, total length 36.8 cm) were released in oligotrophic Lake Forramovatn, northern Norway, supporting slow growing, small sized Arctic charr. Number of charr, measured as catch per unit effort, decreased from 6.3 fish before to 1.7 fish after the trout release. In the same period, mean body length of the charr increased significantly.

The purpose of this study was to test simple models to predict piscivorous prey selection based on gape sizes of the predators and body depths of the prey. Based on this, I developed models for use in lake management to prevent slow growth in freshwater populations. For comparison reasons, gape sizes of piscivorous brown trout were compared with gape sizes of cannibalistic Arctic charr.

Methods

Maximum prey length

Salmonids open their mouth to 60° during feeding (Wankowski 1979), and for this angle internal heights between pre-maxilla and mandible were measured in brown trout and Arctic charr. Lateral body depths (maximum body heights) of the prey were measured by a calliper at the anterior end of the dorsal fin. Relative gape sizes and prey body depths were expressed as a percent of total length. A total number of 153 brown trout and 223 Arctic charr from the Hals River, northern Norway, were measured. The total length ranged from 9.1 to 49.2 cm, and from 6.4 to 47.0 cm, respectively.

The linear relationship between predator gape in mm (G_{pred}) and predator total length in cm (TL_{pred}) was calculated as:

$$G_{pred} = a_{pred} \cdot TL_{pred} + b_{pred} \qquad (1)$$

The linear relationship between prey total length in cm (TL_{prey}) and prey body depth in mm (BD_{prey}) was calculated as:

$$TL_{prey} = a_{prey} \cdot BD_{prey} + b_{prey} \qquad (2)$$

Maximum prey length according to gape limitation was based on the fact that the body depth could not exceed gape size ($BD_{prey} = G_{pred}$), and thus the maximum prey length (TL_{prey}) could be calculated according to the formula:

$$TL_{prey} = a_{prey} \left(a_{pred} \cdot TL_{pred} + b_{pred}\right) + b_{prey} \qquad (3)$$

Relative prey vulnerabilities

According to Hambright et al. (1991), gape sizes and body depths are appropriate measures in models of piscivorous predator-prey interactions. Assuming that all prey fish with body depths less than or equal to the predators gape size can be

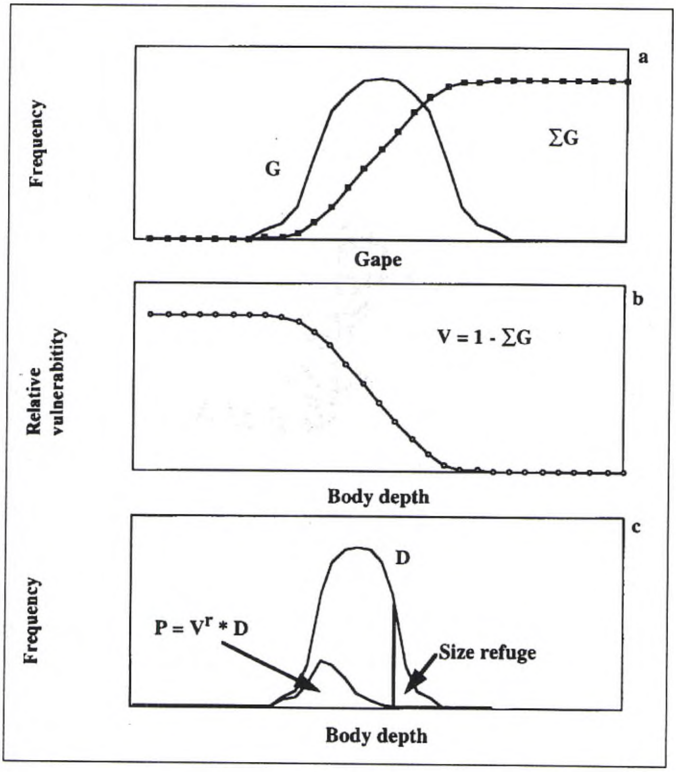

Fig. 1. A model of piscivorous prey selection based on gape sizes of the predators and body depths of the prey (after Hambright et al. 1991). **(a)** Frequency (*G*) and cumulative frequency of gape sizes (ΣG) in the predator population. **(b)** Relative vulnerabilities (*V*) of the prey population. **(c)** Frequency of body depth in the prey population (*D*). The probability of being eaten by a predator (*P*) and the prey size refuge are indicated with arrows.

eaten, the relative prey vulnerabilities (V) for a particular body depth (bd) could be calculated as:

$$V_{bd} = 1 - \Sigma G \qquad (4)$$

where G is the frequency of gape sizes in the predator population and ΣG is the cumulative frequency of gape sizes (Fig 1a). Relative vulnerability varies between 0 and 1 for each body depth. For all body depths smaller than gape sizes of all predators, $V_{bd} = 1$, while $V_{bd} = 0$ for all body depths greater than the largest gape size (Fig 1b).

Assuming a random encounter between predators and prey, the probability (P) for a certain size group of prey of being caught by a predator could be calculated as:

$$P = V_{bd}^{\ r} \cdot D \qquad (5)$$

where r is a constant (0.8) used to incorporate increasing consumption as a function of predator size, and D is the frequency of body depths in the prey population (Fig 1c). The probability is expressed as a proportion of the prey population and prey sizes beyond the range of vulnerable sizes according to equation (5) are regarded as a prey size refuge (Hambright et al. 1991).

To test this model, I compared predicted prey vulnerabilities with experimentally observed prey selection by piscivorous brown trout eating Arctic charr prey (Damsgård 1993). Furthermore, the results from Lake Forramovatn (Damsgård and Langeland 1994) were fitted to the model in order to understand the importance of prey size refuges in stocking experiments with piscivorous fish.

Results

Maximum prey length

There was a significantly difference (t-test, $P<0.001$) between gape sizes in percent of total length in brown trout (8.8±0.1% [mean ± SE], $N=153$) and Arctic charr (7.5±0.1%, $N=223$), and the relative gape sizes increased slightly with total length in both species. For further analysis, gape sizes of fish longer than 20 cm were used. Gape size (G_{trout}, mm) of brown trout (>20 cm) increased as a function of total length (TL_{trout}, cm): $G_{trout} = 1.124 \cdot TL_{trout} - 6.364$ ($r=0.90$, $P<0.001$, $N=86$). Compared with trout, charr (>20 cm) had a relatively smaller gape size (G_{charr}) as a function of total length (TL_{charr}): $G_{charr} = 0.999 \cdot TL_{charr} - 8.523$ ($r=0.92$, $P<0.001$, $N=157$) (Fig. 2).

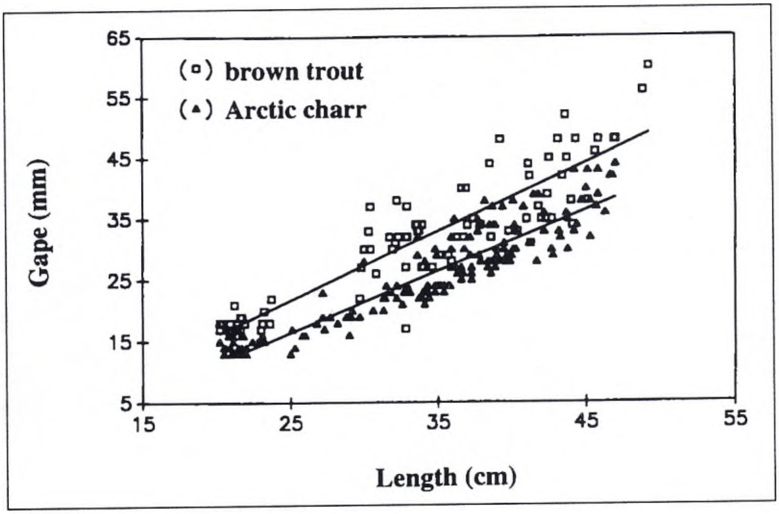

Fig. 2. Gape sizes of brown trout, *Salmo trutta*, (squares) and Arctic charr, *Salvelinus alpinus*, (triangles) as a function of total length.

Mean body depth of Arctic charr was 15.6 ±0.1% (N=91) of the total length, and relative body depth increased as a function of fish length. For prey <20 cm, total length in cm (TL_{prey}) increased as a function of body depth in mm (BD_{prey}) according to the formula: $TL_{prey} = 0.476 \cdot BD_{prey} + 2.542$ (r=0.98, P<0.001, N=91).

Calculation of maximum prey length revealed that piscivorous trout may take a relatively larger prey than cannibalistic charr. For predatory trout, maximum length of Arctic charr prey (TL_{prey}, cm) could be described as a function of trout total length (TL_{pred}, cm): $TL_{prey} = 0.535 \cdot TL_{pred} - 0.487$. For Arctic charr the corresponding function was: $TL_{prey} = 0.476 \cdot TL_{pred} - 1.515$. For example, the maximum prey length for a 30 cm piscivorous trout was 15.6 cm as compare to 12.8 cm for a 30 cm cannibalistic charr, or approximately 50 and 40% of the total length, respectively.

Relative prey vulnerabilities

The experimentally observed relative prey vulnerabilities were far less than the predicted vulnerabilities (Fig. 3), violating the assumption that predators randomly catch all prey they encounter up to a gape limitation.

The results from Lake Forramovatn indicated that prey size refuges may play a crucial role in determining the effects of stocking with piscivorous predators. Before the release of predators, many Arctic charr prey had body depths within the limit of prey vulnerabilities (Fig. 4a). Due to predation and the increase in individual growth of Arctic charr, fewer prey were vulnerable to the predators two years after the release (Fig 4b). Before and after the release of brown trout, 12 and 38% of the prey were within this prey size refuge, respectively. Corresponding with the experimentally observed prey selection of piscivorous trout, body depths of Arctic charr eaten by brown trout in Lake Forramovatn (Fig. 4c) were less than predicted prey vulnerabilities (Fig. 4d).

Discussion

The regulatory roles of predators in aquatic ecosystems are generally accepted and the present study demonstrated a method to evaluate piscivorous predator-prey interactions, and furthermore, plan management programs to prevent extinction of large, piscivorous fish.

Both brown trout and Arctic charr may be facultative piscivorous predators. In fresh water, piscivorous brown trout feed on a wide range of fish species, including Arctic charr, whitefish, *Coregonus lavaretus* (L.), and three-spined stickleback, *Gasterosteus aculeatus* L. (Hunt and

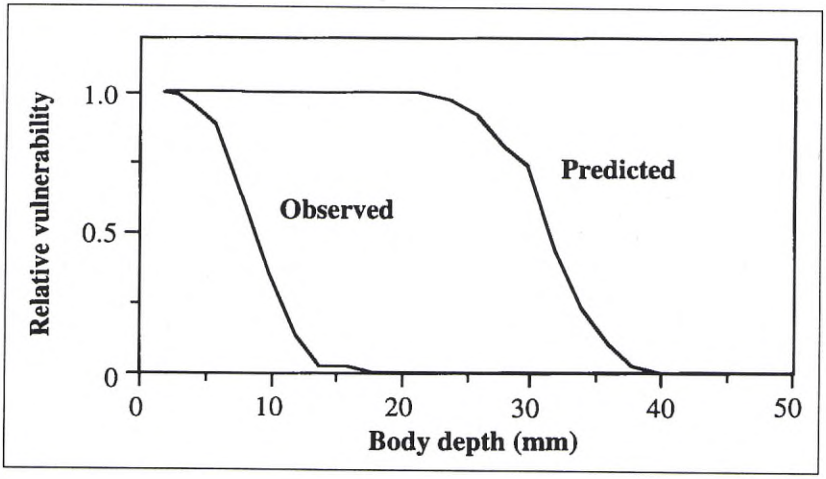

Fig. 3. Experimentally observed and predicted relative vulnerabilities of Arctic charr, *Salvelinus alpinus*, eaten by brown trout, *Salmo trutta*.

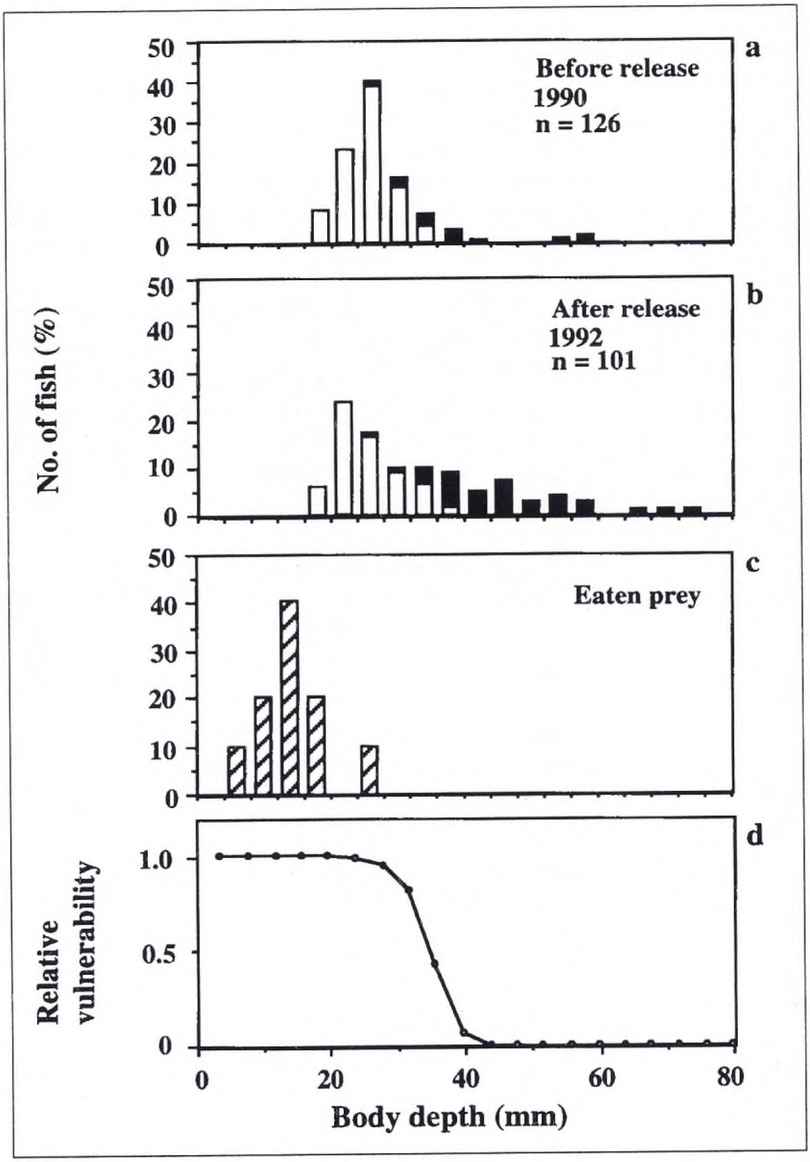

Fig. 4. Stocking experiment in Lake Forramovatn, northern Norway. **(a)** Body depths of Arctic charr, *Salvelinus alpinus*, before and **(b)** after release of piscivorous brown trout, *Salmo trutta*. Dark bars indicate prey size refuges for Arctic charr. **(c)** Body depths of eaten Arctic charr. **(d)** Predicted relative vulnerabilities.

Jones 1972, Campbell 1979, Aass 1984, L'Abée-Lund et al. 1992). Arctic charr are commonly described as an opportunistic feeder, taking many different food items, including fish (Nilsson 1955, Moore and Moore 1974, Adalsteinsson 1979, Johnson 1980, Grønvik and Klemetsen 1987, Amundsen and Klemetsen 1988, Amundsen 1989, L'Abée-Lund et al. 1992). Piscivorous fish are generally prey size selective. Prey size increases with increasing predator size, described both for brown trout (Campbell 1979, Garman and Nielsen 1982, Grønvik and Klemetsen 1987, L'Abée-Lund et al. 1992), and Arctic charr (L'Abée-Lund et al. 1992, Malmquist et al. 1992). Since neither trout nor charr tears their prey apart before swallowing, one might expect that gape size represents the maximum prey size. Accordingly, handling time for each fish eaten increases markedly for prey sizes close to gape limitation (Hoyle and Keast 1987). In the present study, brown trout had significantly larger gape than Arctic charr. The maximum prey length observed by Damsgård (1993) was less than the limitation set by gape size, being approximately 80% of maximum prey length in both 20 cm trout and charr predators, and 60% of maximum prey length in 40 cm predators. However, since both species are prey size selective, and the prey size on average is only approximately half of maximum prey length (Damsgård 1993), one may not consider trout and charr as gape-limited predators, but rather as size-dependent predators (*sensu* Zaret 1980). Despite this fact, gape-limitation is still the ultimate threshold determining the prey size refuge.

Piscivorous fish species have generally a larger gape size than non-piscivorous species (Popova 1978). There are also differences in gape size between different populations of Arctic charr, feeding on different prey sizes (Barbour 1984). In Lake Thingvallavatn, Iceland, both gape size and gape morphology varies between different morphs of Arctic charr. A subterminal mouth is typical of benthivorous fish, while planktivorous and piscivorous fish have a terminal or undershot mouth (Sandlund et al. 1991, Malmquist 1992). A similar adaptive intraspecific morphological difference is described between morphs of bluegill sunfish, *Lepomis macrochirus* Rafinesque, within single lakes, where pelagic bluegill have more fusiform bodies as compared with the more round benthic feeders (Ehlinger and Wilson 1988). It is not possible however to evaluate whether the morphs actually develop different morphologies, or if the fish simply forage on the prey to which they are best adapted. Adaptive polymorphism does, however, not necessarily imply the existence of a genetic difference. Pumpkinseed sunfish, *Lepomis gibbosus* L., develop muscles and bones of the pharyngeal jaws in connection with foraging on gastropod molluscs, indicating a plasticity in transformation of the mouth as an ontogenetic response to the diet (Wainwright et al. 1991, Mittelbach et al. 1992).

The use of the present model in Lake Forramovatn clearly showed the importance of the size distribution of both predators and prey. Piscivorous fish must reach considerable sizes to catch 16-18 cm charr, and these predator sizes are not often achieved in resident freshwater populations. It is however important to stress that the existence of prey size refuges does not necessarily mean that predation is unimportant as a regulatory factor, but rather that prey fish are able to respond to the presence of predators, both directly by changes in behaviour and life-history characters, and indirectly, by selective mortality.

The practical applications of the present study are mainly to evaluate the possibilities for piscivorous predators in lakes, in order to reduce the number of slow growing, small sized fish by retaining large piscivorous fish in the lake. It is my believe that this may be done by strong restrictions on size-selective fishing for large fish, based on principles of sustainable yield.

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Trends in Population Characteristics of an Exploited Anadromous Arctic Charr, *Salvelinus alpinus*, Stock in northern Labrador

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Abstract

Information in the literature suggests that anadromous Arctic charr, *Salvelinus alpinus*, populations are extremely vulnerable to overfishing and stocks cannot withstand periods of intense exploitation. Few studies, however, have examined in detail temporal changes in population characteristics from areas where stocks were reported to have collapsed or were subject to continuous high levels of exploitation. In northern Labrador, 936 tonnes of charr (539,000 fish) have been harvested from one stock unit over a 20 year interval (1974-93). Long term investigations have examined trends in catch, catch rates, size, and age composition in relation to conventional expectations of the effects of exploitation on a stock. Total catch and catch rates have declined and there are some indications of growth overfishing. However, there is no evidence of a stock collapse. These results are discussed in relation to confounding influences of change in distribution and timing of the fishery, and in relation to the general concept of the inability of Arctic charr stocks to tolerate exploitation.

Keywords: Arctic charr, commercial fisheries, exploitation, growth overfishing, Labrador.

Introduction

Arctic charr, *Salvelinus alpinus,* are distributed throughout the circumpolar region of the northern hemisphere. They occur as both anadromous and resident freshwater forms and are often characterized as being phenotypically plastic displaying a suite of life history tactics that have rendered the species capable of surviving in a variety of habitat types (Nordeng 1983, Barbour 1984, Svenning 1993). In addition to these generalizations, it is also commonly believed that anadromous Arctic charr stocks are extremely vulnerable to overfishing and stocks cannot withstand periods of intense exploitation (Dunbar and Hildebrand 1952, Bigelow 1963, Mattox 1973, Coady and Best 1976, Johnson, 1980, Kristofferson and Sopuck 1983, Johnson,1989).

A number of reports allude to the 'collapse' of populations as a result of overfishing (Yessipov 1935, Andrews and Lear, 1956, Mattox 1973, Hunter 1976, Power and Le Jeune 1976, Gillis et al. 1982, Kristofferson et al. 1984, Crawford 1989, Reist 1989, Boivin 1994). In reality, however, there are relatively few published studies that have provided sufficient information documenting the harvest history or other data related to the biological characteristics or dynamics of the stocks that have reportedly collapsed. This is not to suggest that Arctic charr are not vulnerable to over exploitation. Rather in the absence of specific information related to the fishery, alternate, and perhaps confounding factors, such as a reduction in directed effort, or a change in spatial or temporal distribution of the fishery, could have been responsible, or at least contributed to the ultimate conclusion that a stock has collapsed, when in fact it may not have.

Rarely is the concept of what is meant or inferred by the 'collapse' of an Arctic charr population defined, explained or qualified. Typically, a collapse has been related to a decline in landings or other index of abundance over a short period of time, coupled with a decrease in size or mean age of the catch (Gillis et al. 1982, Kristofferson et al. 1984, McGowan 1987, Crawford 1989). These events were not discussed in the context of either growth or recruitment overfishing (Gulland 1983, Sutherland 1990).

When exploited, a fish population will normally undergo changes; for example, biomass and catch rates will be reduced, mean age and size will diminish, growth rates may increase and fish may mature at an earlier age (Regier and Loftus 1972, Healey 1975, Garrod and Knights 1979, Ricker 1981, Gauldie et al. 1989, Shepherd 1992, Reznick 1993). Often these population characteristics are identifiable and the magnitude of the changes could be suggestive of excessive exploitation. In contrast, Arctic charr populations are reported to have a profound ability to maintain a rather stable size and age configuration even when perturbed or heavily exploited (Johnson 1980, 1983, 1989, 1994a, Dempson and Green 1985). This stability appears to be somewhat inconsistent with the concept that anadromous Arctic charr populations are unable to tolerate much exploitation. It has been reported that only in the final stages of stock decline do changes become apparent (Johnson 1989). This characteristic, however, is not unique to Arctic charr populations and some fish species may show no evidence of a change in stock structure or other symptoms of distress when biomass has declined significantly or the stock has collapsed (e.g. Winters and Wheeler 1987, Gauldie et al. 1989).

In addition to the long standing use of Arctic charr for domestic consumption (MacCrimmon and Gots 1980), in northern Labrador, the anadromous Arctic charr fishery has also had a long history of commercial exploitation with the first known exports of charr to Europe in 1860 (LeDrew 1984). Over the next century, the charr fishery varied in response to market conditions and abundance of cod. Beginning in 1971, the commercial fishery intensified with most of the effort now directed along a 200 km stretch of coastline and landings in excess of 200 t in some years. In this paper, aspects related to this commercial fishery are examined for one stock complex from information obtained from a commercial sampling program. Landings from this stock unit have totalled 936 tonnes over the 20 year period from 1974-93. Although the information is largely derived from the commercial fishery, with the inherent biases related to such data (e.g., Dew 1988), the information is still instructive for examining trends in catch, catch rates, size and age composition of an anadromous charr stock over a long period of commercial exploitation. These data are also considered in light of additional investigations from river-specific studies, historical sampling carried out in 1953 (Andrews and Lear 1956) and 1964 (Hunter 1964), and in relation to the general concept of the inability of charr stocks to withstand exploitation.

Materials and Methods

The Arctic charr fishing region and stock structure

The northern Labrador coast is partitioned into two commercial Arctic charr fishing regions (Fig. 1). The Nain fishing region (north of about latitude 56°) has accounted for 85% of the commercial production of charr over the past 20 years. The Nain region is divided on a geographical basis into subareas. Some of the subareas form component parts of larger stock complexes or stock units, the basis and derivation of which have been described previously by Dempson and Misra (1984) and Dempson and Kristofferson (1987). The current study concerns the Nain stock complex. This complex consists of an inshore zone made up of Anaktalik Bay, Nain Bay, Tikkoatokak Bay, and Webb Bay subareas, and an offshore island zone composed of the Dog Island and Black Island subareas (Fig. 1).

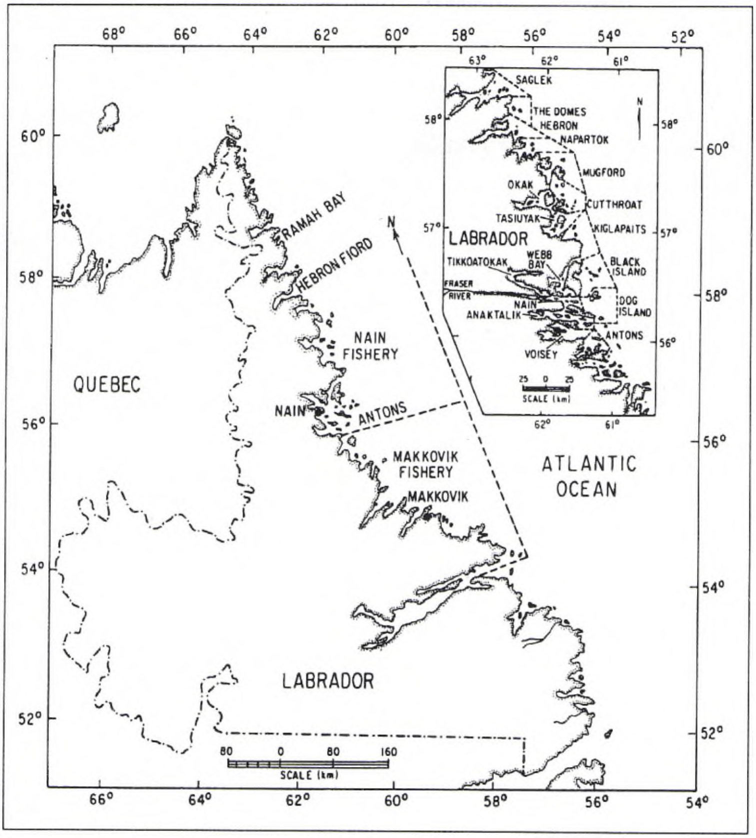

Fig. 1. Location of the Nain and Makkovik Arctic charr fishing regions in northern Labrador. The insert illustrates the location of subareas within the Nain fishing region which form component parts of stock complexes (see text).

Commercial fishery characteristics and regulations

Specific details concerning the northern Labrador commercial Arctic charr fishery are provided in Coady (1974), Coady and Best (1976), Dempson and Green (1985) and Dempson and Kristofferson (1987). Briefly, the commercial charr fishery in the area under consideration occurs entirely at sea, often in traditional fishing berths, using shore-set multifilament gill nets, with stretched mesh sizes of 114 and 127 mm. No more than 92 m of net can be used in any one fishing berth and individuals are restricted to a maximum use of 366 m of net. Nets must be at least 463 m away from river mouths. It is a licenced fishery and is restricted to residents of coastal northern Labrador. The commercial fishing season for Arctic charr extends from July 1 until September 30. In some years variation orders allow the fishery to open earlier in June. Generally few charr are caught after the end of August. Beginning in 1979, the fishery has also been under quota control. All landings are processed at the fish plant located in the community of Nain, Labrador (Fig. 1).

Commercial catch and effort information

Information on commercial landings of Arctic charr was obtained from sales slips prepared by Fisheries Statstics and Systems Branch of the Department of Fisheries and Oceans, Newfoundland Region. These sales slips are issued when fisherpersons sell their catch to the fish plant and include the following information: name of fisherperson, licence number, subarea where the fish were caught, date, weight and number of fish landed. Arctic charr are landed in the gutted head-on form and converted to round (whole) weight using the conversion factor: gutted head-on weight x 1.22 = round weight (Dempson 1984). Catch per unit effort estimates (catch rates), expressed in terms of kilograms of charr caught per person-week fished, were derived from sales slips following the method initiated by Coady and Best (1976).

A multiplicative model (Gavaris 1980) was used to standardize catch rates for the Nain stock complex and account for differences among years and weeks using the following general linear model ($\log_e$ transformed):

$$Y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij},$$

where Y_{ij} is the response variable, catch rate, α_i and β_j are class variables year and week, respectively, and ε_{ij} is the error term associated with individual observations. Inshore and offshore zones were treated separately. While landings data for the Nain stock complex are available since 1974, the analyses of commercial catch rates are for the period 1977-93.

Timing of the commercial fishery

Interpretation of catch and catch rate information for anadromous Arctic charr that are caught at sea and not directly in the river mouths, also has to be considered in light of the timing within the season when fishing occurs. This is because of the relatively short period of time charr remain at sea and the progressive change in size of fish throughout the run (Dempson and Kristofferson 1987).

Timing of the commercial fishery was determined by calculating the Day of the Year (DOY) of the 25th, median (50th), and 75th percentiles of the cumulative catch for both inshore and offshore fishing zones (Chadwick and Claytor 1989).

Biological characteristic data

Information on length, weight, and age (otoliths) of Arctic charr caught in the commercial fishery was obtained as fish were processed at the local fish plant. From 1977 to 1979, Arctic charr samples were collected from as many specimens as practical as fish were landed from specific subareas. Beginning in 1980, random samples of charr were measured for length with a stratified subsample based on length taken for ageing. In both cases sampling was conducted throughout the fishing season. These data were used to estimate the numbers and weights at age in the commercial catch from 1977-93. Additional biological sampling has been carried out to obtain information on sex ratio distribution and degree of maturity of Arctic charr at sea. Sex ratio data were also obtained from logbooks maintained by selected commercial fisherpersons. Table 1 summarizes the available data base of biological characteristic information for the Nain stock complex.

Analyses of condition were carried out following the general methods of Patterson (1992) and are fully described in Winters and Wheeler

Table 1. Summary of available biological characteristic data for the Nain stock complex Arctic charr population, 1977-93.

Year	No. of otoliths	No. of lengths	No. of fish sexed
1977	667	667	
1978	744	744	
1979	308	308	1,909
1980	638	3,978	
1981	737	4,962	
1982	888	4,652	3,720
1983	1,030	5,943	7,594
1984	1,017	7,331	3,008
1985	1,272	10,956	3,606
1986	1,160	8,317	5,864
1987	1,506	10,759	8,268
1988	1,634	11,504	2,520
1989	931	9,326	7,075
1990	852	5,862	7,323
1991	889	10,494	1,866
1992	966	5,687	3,979
1993	650	5,334	1,624
Total	15,889	106,824	58,356

(1994). The following general linear model ($\log_e$ transformed) was used to examine the response of fish weight, standardized to a common length, to various factors as:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha \bullet \beta) + b \bullet Z_{ijk} + \varepsilon_{ijk},$$

where Y_{ijk} is the response variable, charr weight (gutted, head-on), α_i and β_j are class variables month and year, respectively, $(\alpha \bullet \beta)$ is an interaction term between month and year, Z_{ijk} is the covariate fork length, and ε_{ijk} is the error term associated with individual observations. With respect to the month variable, July includes any fish also caught in June while August also includes any charr caught in September. The above model was used to calculate adjusted mean weights by year standardized to the covariate. Analyses followed the sequential procedure described by Winters et al. (1993) and Winters and Wheeler (1994). Initially, analyses were used to determine the appropriate model, i. e., common slope (b) or multiple slope (b_{ijk}). Intercept differences (μ) were tested based on class variable effects if a common slope model was appropriate. Interactions between month and year were examined to investigate the temporal distribution of condition over a period of 17 years (1977-93).

Sequential population analyses

Sequential population analyses (SPA) (Mohn and Cook 1993) were conducted to provide a general estimate of numbers at age or stock size, and past estimates of fishing mortality applied to this stock complex. The method used was the age disaggregated adaptive framework (ADAPT) as described by Gavaris (1988, 1991), Mohn (1993) and Mohn and Cook (1993). The ADAPT process is based on established methods for nonlinear parameter estimation. The minimization procedure is applied to determine a set of parameter values such that the predicted catch at age and abundance indices by age-group are closest to the observed values. Calibration of the SPA was done using both inshore and offshore commercial catch rate information disaggregated by age. Specifications of the accepted formulation are summarized in Dempson (1993a). Natural mortality was assumed to be 0.2.

Results

Trends in catch and effort data

Annual landings of anadromous Arctic charr ranged from 13 to 76 metric tonnes (mean = 47 tonnes, 1974-93), and on average have contributed 41% of the commercial catch from the Nain fishing region (Table 2). The highest catches occurred in the late 1970's and early 1980's (Fig. 2) when more than 50 tonnes y^{-1} were landed (1976-83). In total over the past 20 years (1974-93) 936 tonnes of charr were harvested from this stock complex. From 1979 to 1983, quotas applied only to the Anaktalik Bay and Tikkoatokak Bay subareas (Fig.1), but included an offshore component for 1984 and 1985. The quota area catch (QAC) in Table 2 summarizes landings for those subareas specifically under quota management only prior to the derivation of stock complex groupings in 1986. Beginning in 1986, the total allowable catch (TAC) was applied to the entire stock unit. Most of the charr were caught in the inshore zone until 1984 but since then a greater proportion were caught in the offshore island zone (Table 2).

Effort fluctuated among both fishing zones (Table 2) with the lowest level during the past three years (1991-93). This is coincident with the lowest landings recorded for the Nain stock complex.

The multiplicative analysis of catch rates for the inshore zone explained 69% (F=11.16, P=0.0001, df=29, 145) of the variation in the data. The highest catch rates occurred in the late 1970's and early 1980's, and although moderately high in 1987 and 1989, have declined over time (Fig. 2). This is suggestive of an overall decreased abundance either of the stock in general, or of that component of the stock remaining in the inshore zone. Catch rates were highest during the period July 30-August 19. The model for the offshore zone explained 73% (F=11.83, P=0.0001, df=27, 121) of the variation. In contrast with the inshore zone, catch

Table 2. Summary of catch and effort statistics for the Nain stock unit, 1974-93. Total allowable catch (TAC) and landings are in kg round weight, effort is expressed as person-weeks fished. Refer to text for information on TACs and quota area catch. CUE = standardized catch per unit effort.

	Inshore			Offshore				Total		
Year	Catch	Effort	CUE	Catch	Effort	CUE	% Catch offshore	Catch	TAC	Quota area catch
1974	30,822			6,923			18.1	37,745		
1975	31,076			2,754			8.1	33,830		
1976	50,813			2,500			4.7	53,313		
1977	70,908	115	618	5,347	81	66	7.0	76,255		
1978	70,465	109	648	3,298	63	53	4.5	73,763		
1979	54,967	88	623	11,877	92	129	17.8	66,844	61,000	52,832
1980	52,328	121	433	22,727	135	169	30.3	75,055	61,000	50,176
1981	49,956	108	462	15,676	82	190	23.9	65,632	37,160	37,223
1982	43,108	77	563	12,509	70	178	22.2	55,617	43,660	39,119
1983	33,603	99	338	17,599	91	193	34.4	51,202	51,000	19,102
1984	24,558	79	311	14,342	62	232	36.9	38,900	43,200	29,063
1985	21,527	68	316	19,631	67	295	47.7	41,158	30,500	36,019
1986	16,347	80	205	20,748	72	289	55.9	37,095	43,000	
1987	17,840	48	371	28,032	96	291	61.1	45,872	47,000	
1988	14,535	72	203	23,759	102	233	62.1	38,295	47,000	
1989	30,449	125	243	21,016	58	363	40.8	51,465	47,000	
1990	17,069	74	230	28,205	99	285	62.3	45,275	47,000	
1991	10,162	63	161	5,730	25	226	36.1	15,892	47,000	
1992	10,504	92	114	9,051	41	222	46.3	19,555	47,000	
1993	5,591	43	129	7,819	43	183	58.3	13,410	47,000	

rates offshore increased until around 1989-90 but have declined in recent years (Fig. 2). Within season, the highest catch rates also occurred during the period July 30-August 19.

Timing of the commercial fishery

On average over the 14-year period 1977-90, the median timing of the commercial catch in the offshore fishing zone was about 14 days later than the inshore zone. With respect to the inshore zone, the earliest fisheries occurred in 1979 and 1981 with a trend for progressively later timing of the fishery beginning in 1983-85, with another transition from 1986-90, followed by the latest dates in 1991-93 (Fig. 3). The median timing of the 1991-93 fisheries was 21 to 31 days later than the 1977-90 average. For the offshore zone, the earliest fisheries occurred in the late 1970's and early 1980's (Fig. 3). The latest offshore fisheries were in 1991 and 1992.

Age composition

Age composition, based on almost 16,000 fish samples since 1977, is presented in Table 3. Anadromous charr were first recruited into the fishery at age 6 but contributed little to the overall catch (<2%). In general, over 80% of the catch was made up of four age-classes represented by 7-10 year old fish (Table 3, Fig. 4), even though there were upwards of twelve different year-classes contributing to the fishery each year. Two age-classes (ages 8 and 9) contributed 51% of the catch, on average. The proportional contribution of age-groups 8 and 9 to the fishery was remarkably stable over time, even as the total numbers of charr, and undoubtedly population size, was declining. From 1977-93 it is estimated that almost 475 thousand charr were harvested from the Nain stock complex (Table 3). Recruitment was apparently sufficient to sustain the fishery on the basis of these age-groups.

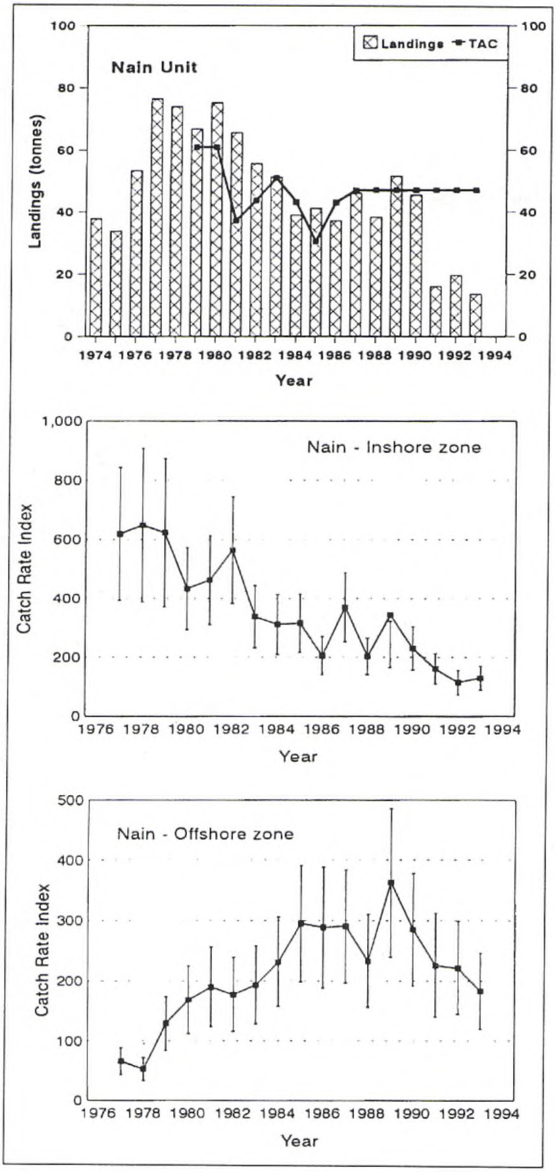

Fig. 2. Commercial landings of anadromous Arctic charr from the Nain stock complex, 1974-93, in relation to the total allowable catch (TAC) (upper panel), and estimated commercial catch rates (kg/person-week fished) for inshore and offshore fishing zones (middle and bottom panels). Vertical lines represent ± one standard error about the mean catch rate values.

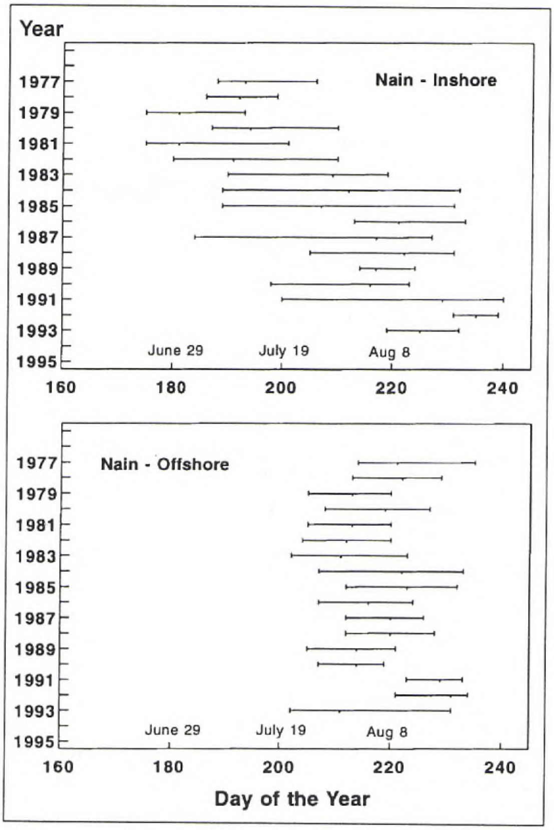

Fig. 3. Commercial catch timing of the Nain stock complex Arctic charr fishery for inshore and offshore fishing zones, 1977-93. The median date (50%), along with the 25th and 75th percentiles are illustrated.

A few charr older than age 17 were occasionally caught, but for convenience were added into their respective year-classes in the oldest age shown in Table 3 (age 17). Fish aged 12 and older contributed little to the fishery (Fig. 4) making up an average 7.9% of the catch over the 17-year period. However, from 1982-85, the percentage of these older fish in the catch rose to almost 14%. There was no apparent long term decline in the contribution of older charr to the fishery. Mean age of the catch varied little over time ($\overline{X}$=9.1 yr, CV=4.1%); however, since 1980 there has been a slight declining trend.

Table 3. Estimated catch at age from the commercial Arctic charr fishery in the Nain stock unit, 1977-93.

	Catch in numbers of fish																
Age	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
6	2,003	371	430	75	145	83	470	182	103	210	483	204	903	459	203	269	83
7	9,250	6,703	4,306	960	2,118	977	2,791	2,612	2,463	4,129	5,462	6,288	4,750	4,726	1,365	3,195	1,982
8	12,453	13,122	11,568	10,519	6,877	4,782	5,842	4,619	6,506	7,713	6,293	7,166	9,707	6,115	2,085	3,809	2,874
9	7,630	7,984	9,593	16,342	15,435	7,255	6,996	5,671	4,722	5,862	7,548	4,688	8,464	8,844	2,631	3,166	2,525
10	5,052	4,406	4,208	8,345	9,787	7,987	4,177	4,374	4,111	2,857	4,498	3,607	3,785	4,681	2,175	2,574	1,596
11	2,454	2,367	2,168	4,077	3,746	4,936	4,357	2,173	2,494	1,284	2,013	1,631	2,853	1,908	874	905	469
12	988	1,688	1,573	1,340	991	2,976	2,762	1,495	1,605	625	1,375	650	1,234	927	444	422	296
13	358	312	418	813	304	561	600	738	901	240	898	324	665	378	183	241	171
14	180	272	312	522	151	451	557	281	534	199	306	136	277	137	92	48	49
15	1	118	34	43	42	59	70	96	322	205	357	52	28	186	48	32	38
16	1	97	14	1	13	46	27	57	93	50	180	20	6	1	36	1	0
17	1	1	1	66	10	23	95	89	21	42	37	40	1	1	2	1	2
Total	40,371	37,441	34,625	43,103	39,619	30,136	28,744	22,387	23,875	23,416	29,450	24,806	32,673	28,363	10,138	14,663	10,085

	Mean age of individuals in the catch																
	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
Age	8.46	8.75	8.87	9.34	9.28	9.83	9.52	9.40	9.47	8.77	9.10	8.65	8.86	8.92	9.16	8.73	8.75

	Mean weight of individuals in the catch																
	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
Weight	1.88	2.06	1.93	1.75	1.66	1.85	1.79	1.74	1.73	1.59	1.56	1.55	1.58	1.60	1.57	1.34	1.33

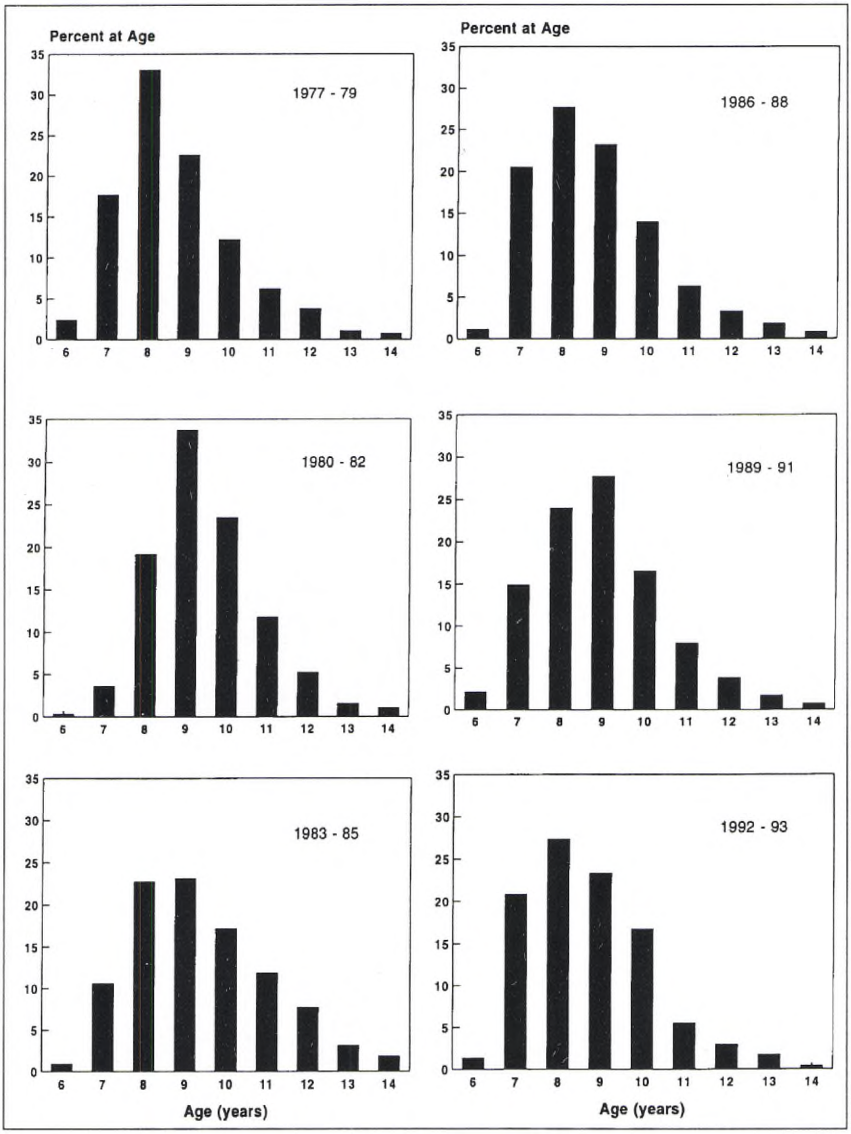

Fig. 4. Age-frequency distribution (%) of the commercial catch of anadromous Arctic charr from the Nain stock complex for various time intervals. Data are truncated to age 14.

Size composition

Length composition data were available from over 100,000 charr from the Nain stock complex. From 1980-85, modal size in the fishery was in the 50 and 52 cm length intervals (Fig. 5) but has shifted to the 48 and 50 cm length groups since 1986. Similar to the age composition of the catch where the majority of the harvest was dominated by a few age-classes, 64% of the catch from 1980-85 was contained in four length intervals (i.e. fish comprised of 48.0 to 55.9 cm overall). From 1986-93, 70% of the harvest was of fish in the range of 46 to 52 cm. Coincident with the shift in modal size of the catch, there was a corresponding decline in mean size of fish landed, beginning around 1986 (Fig. 5). While fish over 80 cm were occasionally caught, those of 60 cm and over contributed little to the catch. The overall pattern has been for a reduction in the variance of the length distribution.

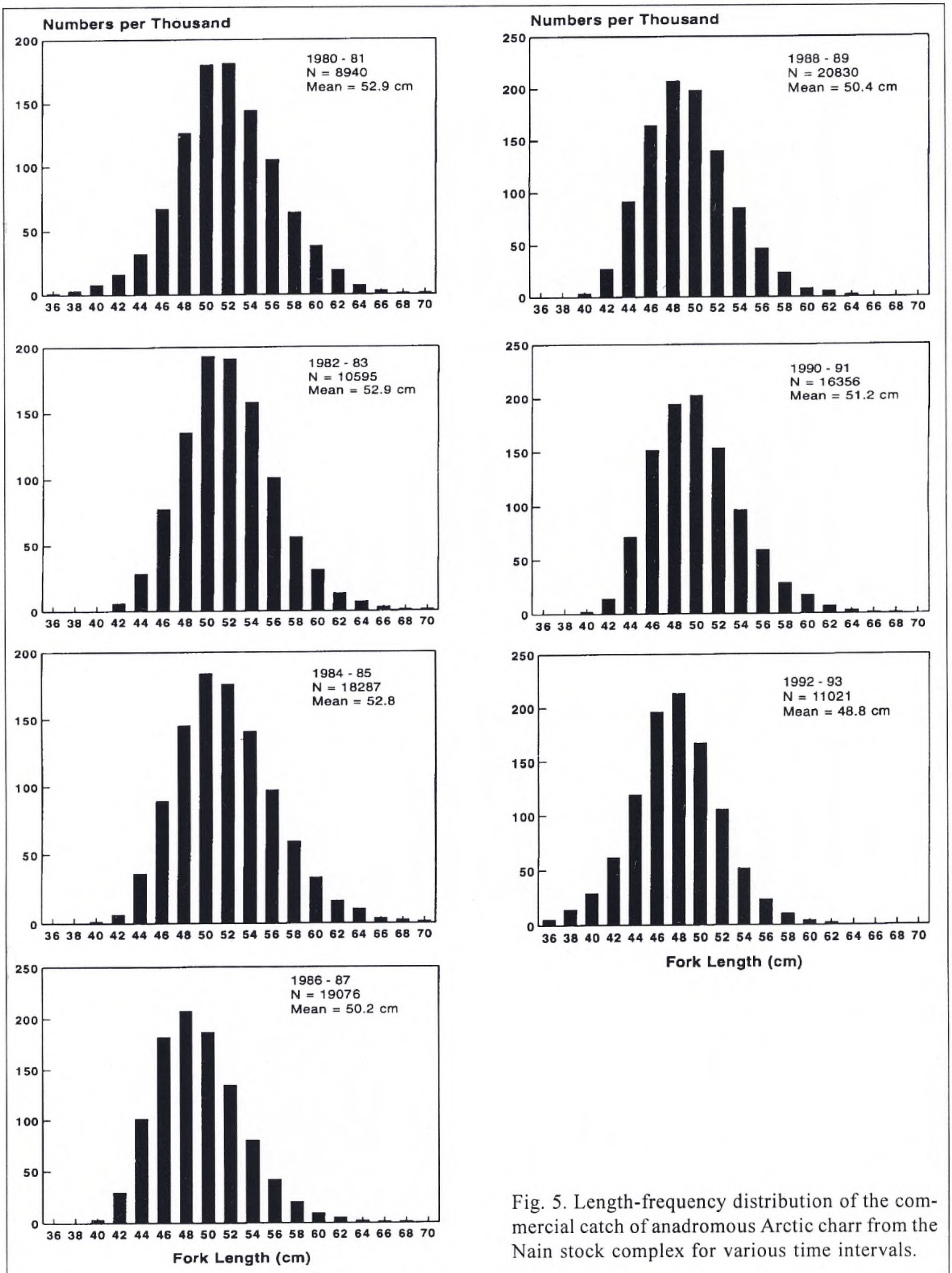

Fig. 5. Length-frequency distribution of the commercial catch of anadromous Arctic charr from the Nain stock complex for various time intervals.

Arctic charr caught in the inshore zone were 1-2 cm larger on average than those fish caught in the offshore fishing zone, until 1986. Part of this difference could be related to the timing of the fishery. There was a change in the temporal distribution of fishing particularly in the inshore fishing zone. As larger charr entered the rivers first, the inshore component of the fishery probably targeted these fish in the earlier years. By 1986, the timing of the inshore fishery could have been delayed sufficiently enough, and was now generally similar in timing with the offshore zone, to account for the similarity in sizes of charr from the two zones.

Mean weight of charr harvested in the Nain stock complex also declined over time. Regression of mean weight (Wt) of the catch on year (y) from 1980 to 1993 was highly significant ($Wt=63.61-0.031y$, $r^2 = 0.731$, $N=14$, $F=32.62$, $P<0.001$) and indicated a decrease of about 0.031 kg (31 g) per year. Comparison of the estimated values for 1980 and 1993 indicated a 22.5% drop. With respect to the four dominant age-classes in the catch, only the age 7 fish did not show a significant drop in weight-at-age over time (Fig. 6, upper panel). For the other age-classes, the rate of change increased with age of fish. The decline was also apparent when the weight-at-age of individual cohorts (year-classes) was examined (Fig. 6 lower panel).

Fig. 7 illustrates the mean length at age of charr for several different time periods in comparison with data from Andrews and Lear (1953). Lengths were estimated as unweighted arithmetic means derived from commercial sampling data in order to compare directly with the historic information. These data indicate that apart from historical data from Andrews and Lear (1956), the 1991-93 fish were generally the smallest at age. There is some uncertainty as to whether this difference in recent years reflects a later timing of the fishery, or a longer term selective removal of larger fish from the stock.

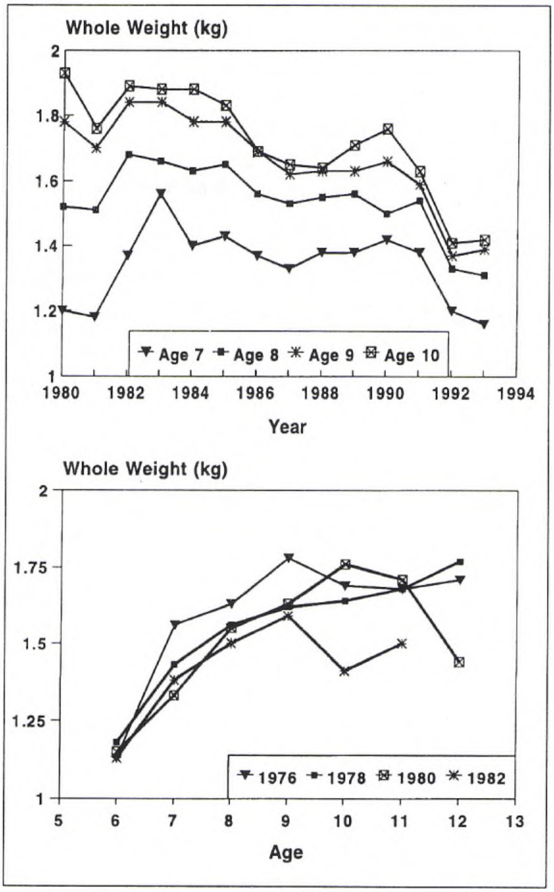

Fig. 6. Change in mean weight over time (upper panel) of various age classes of Arctic charr from the Nain stock complex. Lower graph illustrates the change in weight-at-age of various cohorts (year-classes). Reference years refer to the year of hatching (fish born in 1976 would be age 6 in 1982, age 7 in 1983 etc.).

Condition

Analysis of condition by the weight-length relationship indicated that slopes were significantly different; however, in comparison with the common slope model, the reduction in the residual (error) mean square was negligible (3%), with r^2 values virtually identical. Excluding the covariate fork length, 83% of the remaining variation in the model was accounted for by the main effects (month and year). All main effects were significant (Table 4), as was the interaction between month and year. Condition of charr caught in August was higher than those caught in July (Fig. 8). August values have fluctuated over time

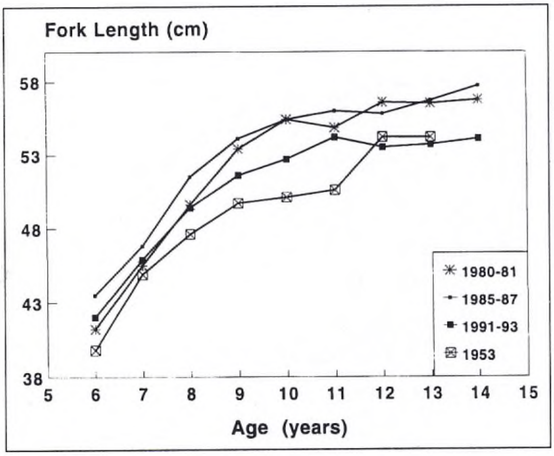

Fig. 7. Mean length-at-age of anadromous Arctic charr from the Nain stock complex at various time intervals. Data for 1953 is from Andrews and Lear (1956).

with the lowest values generally occurring during the past three years (1991-93). Condition of July caught charr, has declined more consistently over time, again with the lowest values in recent years.

Sex ratio

The percentage of female charr varied from 45.8 to 63.3%, with an average of 53.5% over all years (Table 5). Sex ratio, however, was dependent on fishing zone with a greater percentage of female charr caught inshore (54.5%) than offshore (45.6%) (G=195.5, P=0.000). Within the inshore fishing zone, the percentage of females declined over time (Table 5). Part of this may be explained by the later timing of the commercial fishery since female charr generally migrate into the

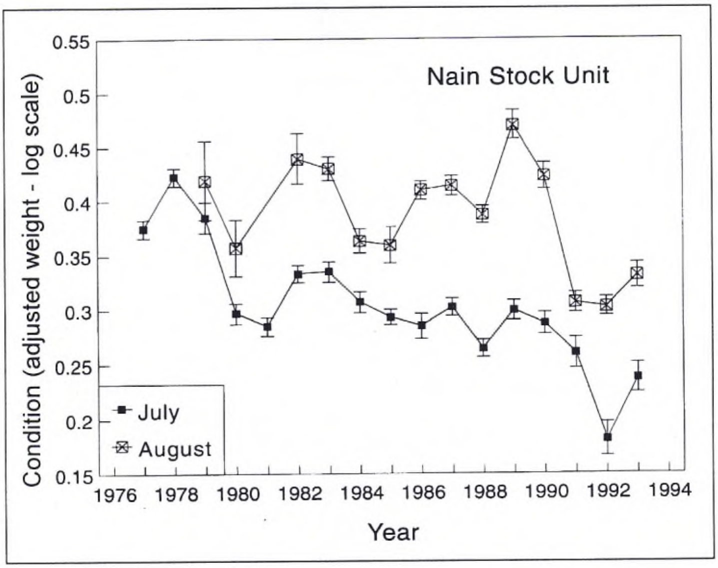

Fig. 8. Temporal variation in condition of anadromous Arctic charr from the Nain stock complex, 1977-93. The vertical lines represent ± two standard errors about the mean.

Table 4. Results of analyses of the common slope GLM weight-length regression model for the Nain stock unit. Asterisks denote significance at P<0.01.

Stock Unit	N	Slope	Intercept	r^2	Source of variation	df	Type III SS	F	P
Nain	15,896	2.83**	-10.89**	0.89	Log-length	1	1,563.94	99,999.99	0.0
					Month	1	15.96	1189.83	0.0
					Year	16	29.16	135.86	0.0
					Month•Year	13	3.41	19.53	0.0

Table 5. Summary of sex ratio data for Arctic charr from the inshore and offshore zones of the Nain stock complex, 1979, 1982-93.

	Inshore zone			Offshore zone			Nain stock unit total		
Year	No. Males	No. Females	% Female	No. Males	No. Females	% Female	No. Males	No. Females	% Female
1979	930	979	51.2				930	979	51.3
1982	1,367	2,353	63.3				1,367	2,353	63.3
1983	2,427	3,979	62.1	757	431	36.3	3,184	4,410	58.1
1984	910	1,300	58.8	397	401	50.3	1,307	1,701	56.5
1985	1,365	1,150	45.7	591	500	45.8	1,956	1,650	45.8
1986	2,061	2,533	55.1	706	564	44.4	2,767	3,097	52.8
1987	3,911	4,294	52.3	35	28	44.4	3,946	4,322	52.3
1988	1,280	1,240	49.2				1,280	1,240	49.2
1989	3,207	3,784	54.1	61	23	27.4	3,268	3,807	53.8
1990	2,884	3,342	53.7	582	515	46.9	3,466	3,857	52.7
1991	979	887	47.5				979	887	47.5
1992	1,468	1,631	52.6	368	512	58.2	1,836	2,143	53.9
1993	551	509	48.0	327	237	42.0	878	746	45.9
Total	23,340	27,981	54.5	3,824	3,211	45.6	27,164	31,192	53.5

rivers first. For the inshore zone, all years combined, the percentage of females in the catch decreased over the fishing season (e.g., 59.1% prior to August 6 and 49.7% after, *G*=450.8, *P*=0.000). With the commercial catch occurring later in recent years, fewer females would be expected to be caught.

For the offshore zone, the percentage of females was more variable on an annual basis (Table 5). Prior to August 6, female charr were less abundant (41.8%) than after that date (50.1%) (*G*=49.5, *P*=0.000). Beginning in 1985, more of the catch of charr came from the offshore fishing region, where as indicated above, there were generally fewer females caught (Table 5).

Sequential population analysis

Results of sequential population analysis indicated the estimated total population of charr declined by 44%, from about 300,000 fish in 1977-79, to about 166,000 over the period 1982-89 (Fig. 9). During the same periods, numbers of fish caught in the commercial fishery declined by 28%. Estimated population sizes have been relatively stable since 1982 (Fig. 9). For 1977-89, results indicated that, on average, 15.7% of the total population size was harvested each year in the commercial fishery (range 11.9-20.3%, CV=16.5%). Since the gill net fishery is selective for fish above a certain size (generally 38 cm and over), selectivity coefficients can be applied to the estimated numbers of fish in the population to derive the harvestable or exploitable component of the stock. In doing this, the catch as a percentage of the exploitable stock averaged 41.5% from 1977-89 (range 31.3-53.8%, CV =16.9%). Estimated fishing mortality (F) for charr aged 8-17 (weighted by population number) was 0.405 (CV=16.9%), but on fully recruited fish (age 10+ and above) F averaged 0.566 (CV=21.7%) (Fig. 9).

Discussion

Information from the present study indicates that for some characteristics, the Nain stock complex has responded to exploitation in a manner consistent with that observed in other fish species. With the commercial fishery harvesting upwards

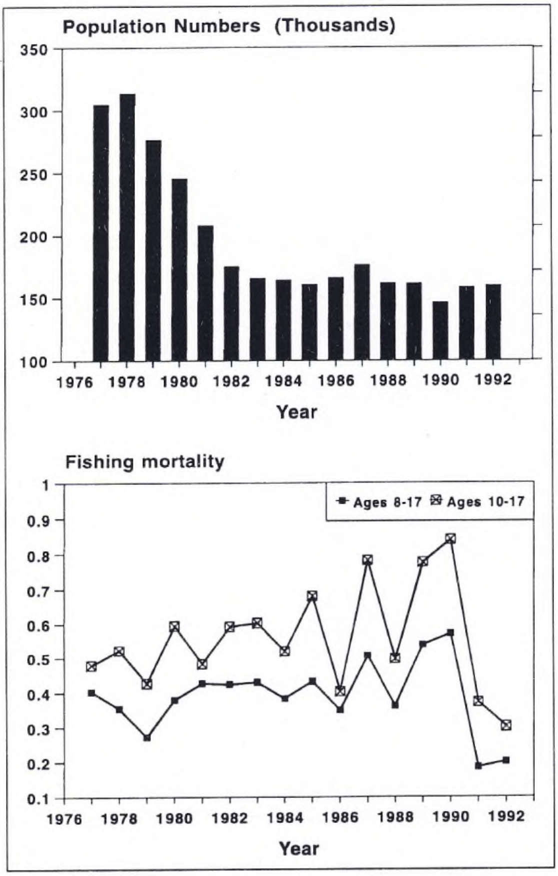

Fig. 9. Estimated population numbers of Arctic charr from the Nain stock complex in northern Labrador, 1977-92 (upper panel). Lower graph summarizes weighted fishing mortality estimates for charr aged 8-17 years, and ages 10-17 years. Population size and fishing mortality values were estimated from sequential population analyses.

of 16% of the total stock complex or 41% of the exploitable component of the stock, estimated total stock size decreased by over 40% from the late 1970's to the mid-1980's. Landings have also decreased, but this cannot be considered in isolation from the introduction of quotas and a tendency for a reduction in effort particularly during the past three years. Mean age and mean weight have also declined, but the former parameter (age) not in a consistent manner, nor has the range in ages diminished. Catch rates have continually declined in the inshore fishing zone; however, in the offshore zone catch rates increased. Only in recent years have both zones experienced a decrease.

The exploitation level in the Labrador charr fishery is in excess of those determined or recommended for anadromous Arctic charr fisheries in the Northwest Territories or in northern Quebec. Johnson (1980) indicated that an annual harvest rate of 11% was excessive at Nauyuk Lake and safe harvest levels of only 10% of the exploitable part of the stock are often recommended for stocks in the eastern Arctic (Kristofferson et al. 1991, Cosens et al. 1993). Recently, in a comprehensive evaluation of the biology and exploitation of anadromous Arctic charr in the eastern Ungava region of northern Quebec, Boivin (1994) recommended annual harvest levels of 10-15% for fish ≥50 cm in size, or a maximum of 30% of the stock if a pulse fishery once in every 5-7 years was undertaken.

In spite of the sustained high commercial exploitation rates in northern Labrador, the Nain charr complex has maintained relatively stable age and size distributions; a feature commonly associated with northern charr populations (Johnson 1980, 1989, 1994a). The fishery has been sustained on the basis of four age- classes with over 80% of the catch made up of fish 7 to 10 years of age. Continued high exploitation has not altered the age structure of the stock as has been observed in other fish species, for example, lake whitefish (*Coregonus clupeaformis*) populations (Healey 1980) or in populations of Atlantic menhaden (*Brevoortia tyrannus*) (Ahrenholz et al. 1987), to name just two. This same dependence on four age-classes was apparent forty years ago when Andrews and Lear (1956) sampled the commercial fishery at Nain in 1953 and again when Hunter (1964) conducted limited sampling in 1964. These data, in consideration of the long history of exploitation in the area, attest to the fact that recruitment overfishing has not happened. If it had, the stability in age compositions would likely not have occurred. The continuance of the fishery cannot be explained by immigration from areas to the south or north of the Nain stock complex. First, information on ocean migrations along the north

Labrador coast have indicated that extensive interchange among designated stock units does not occur (Dempson and Kristofferson 1987). Second, exploitation in other areas has also been high as more than 370 t of charr have been caught in the Voisey stock complex to the south, and over 570 t taken from the Okak stock to the north over the period 1974-92 (Dempson 1993b).

Length-frequency distributions of catch over the 12-year interval from 1980-81 to 1990-91 when 561 t or 337,000 charr were caught, also remained relatively stable. Given the concerns about the inability of charr to tolerate intense exploitation, more apparent changes might be expected. Instead, changes of a more subtle nature have occurred. Modal size has shifted to a smaller interval, and overall, there has been a reduction in the variance of the length distribution of the catch. This is in contrast with Boivin (1994) who illustrated more substantive changes in size distributions of some eastern Ungava charr (Lake Sapukkait) subject to relatively high levels of exploitation over a period of five years. The quantity of charr harvested over the five years was minimal (*N*=2,010) by comparison with harvest levels in Labrador.

The maintenance of a relatively stable size structure in anadromous Labrador charr, either as determined by commercial fish sampling or at a fish counting fence on the Fraser River (Dempson and Green 1985), is similar to that reported for resident lake populations of Arctic charr when populations are severely perturbed. This maintenance of stable modal size configurations is believed to be dependent upon coherence within the population as a whole through interaction among individuals (Johnson 1994a). These mechanisms proposed by Johnson (1994a, 1994b) may also apply to anadromous populations (Johnson 1989).

In the most recent years, there has been a more dramatic shift to a smaller modal size. This, however, has occurred when the timing of the fishery has been much later than in previous years. The later timing was due in part to heavy, and more prolonged ice conditions along the coast during the spring. Information from the Ikarut River, Labrador, clearly illustrates the pattern of return movement back into coastal rivers. Peak runs occurred in late July and early August while there was a progressive decline in the average size (Fig. 10). Thus changes in size distribution in recent years may be confounded by the affect of timing of the commercial fishery rather than direct evidence of the impacts of continued high commercial exploitation.

While overall length and age distributions have displayed rather subtle changes, mean weight of charr has declined substantially. Estimates of the decline in weight over time of about

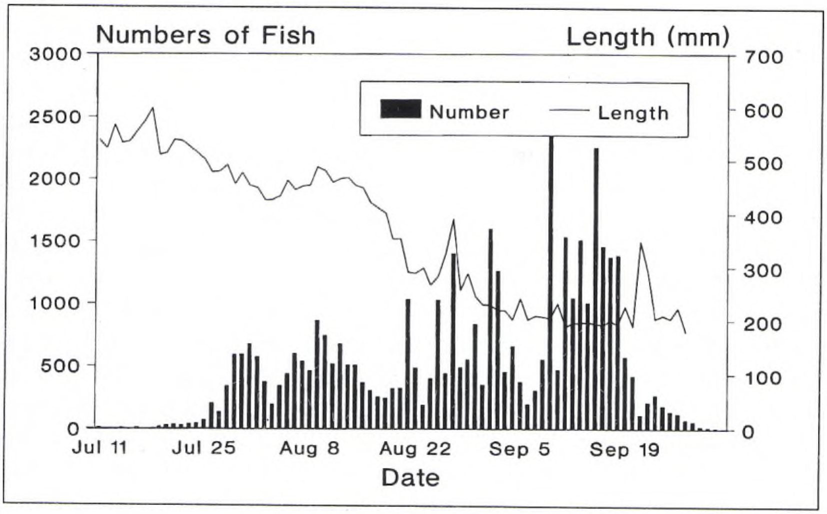

Fig. 10. Total numbers by day of upstream migrating anadromous Arctic charr at Ikarut River, Labrador, along with the change in mean length throughout the run. Data are combined for the years 1981-85.

31 grams per year since 1980 are similar to those reported by Ricker (1981) for some species of Pacific salmon (*Oncorhynchus* spp.). The rate of decline apparently increased with age in the dominant age-classes (ages 7-10) harvested in the fishery. This pattern is consistent with growth overfishing of a stock (Gulland 1983, Sutherland 1990). Growth rates often increase following high levels of exploitation (Healey 1980). In comparison with data from Andrews and Lear (1956), size at age during the early and mid 1980's increased (Fig. 7) but in recent years (1991-93) were again reduced.

Weight of fish of a standard length, or condition, is also reported to increase with exploitation. However, charr in the Nain stock complex have shown a rather consistent decline in condition of fish in July over the past 17 years, while condition of charr caught in August fluctuated with no consistent trend until declining to their lowest levels during the past three years (Fig. 8). Although speculative at the present time, there is some suggestion that, in recent years, late springs and poor environmental conditions in northern Labrador have altered the relative proportion of certain food items in the charr's diet in contrast with information from earlier years. Dempson (1993a) noted that during the mid-1980's, the contribution of capelin (*Mallotus villosus*) in the diet was 54% by weight and that this differed among inshore and offshore fishing zones (Dempson and Kristofferson 1987). In recent years, capelin have been noticeably absent in the diets of charr caught in either zone. The greater dependence on amphipods and euphausiids may be manifest in reduced condition. The scarcity of capelin in the northern Labrador area is also consistent with offshore acoustic biomass surveys conducted during the early 1990's (Carscadden 1994).

Fisheries, by their nature, are often selective, particularly for the faster growing individuals of a stock (Ricker 1981, Policansky 1993). In addition, exploitation often results in a decrease in the size and age at maturity (Ricker 1981). A comparison of the length frequency distributions of several age-classes in the commercial gill net catch from the Nain stock complex (ages 6-9) in comparison with length distributions obtained from fish counting fences in northern Labrador, illustrates the selective effect of the gill net fishery (Fig. 11). Whether or not this selection, which undoubtedly has continued for many years, has contributed to a long term genetic influence, as has been speculated for a number of other fish species (Ricker 1981, Sutherland 1990, Hutchings 1993, Law and Rowell 1993), is unknown and may be debatable. Information is lacking on age and size at maturity from earlier years. What is known is that Labrador charr mature at much smaller sizes and earlier ages, and are characterized by having return migrations to freshwater consisting of a high proportion of spawning individuals. This is inconsistent with reports of anadromous charr from other northern Canadian locations where maturing charr are uncommon in the upstream run (Johnson 1980). These features, however, are consistent with what would be predicted by life history theory, namely, with increased adult mortality, the fish should mature at earlier ages and at a smaller size (Stearns and Crandall 1984). It may be asked, then, as to whether the observed patterns are a life history adaption to the Labrador environment or a direct result of the long term exploitation and selection by the commercial fishery?

Reproductive life-history strategies of a fish species are the means by which they attempt to continue the basic premise to reproduce and ensure the continuation of the population (Wootton 1984, Thorpe 1994). In anadromous stocks of Arctic charr it is reported that few maturing individuals are found, recruitment levels are low and, as Johnson (1989) indicates, some fish may never spawn at all. In contrast, female anadromous charr as young as age 5 have been found to mature in Fraser River, Labrador, with an age at 50% maturity of 6.9 years (Dempson and Green 1985). At both Fraser River and Ikarut River, each with data from five years of study, an average of 70% of the returning adult female charr were maturing in the same year. Given ample food resources, Policansky (1983) indicated that fish will mature at their earliest opportunity. Thorpe (1994) suggests that this indicates maturation is given priority over somatic growth.

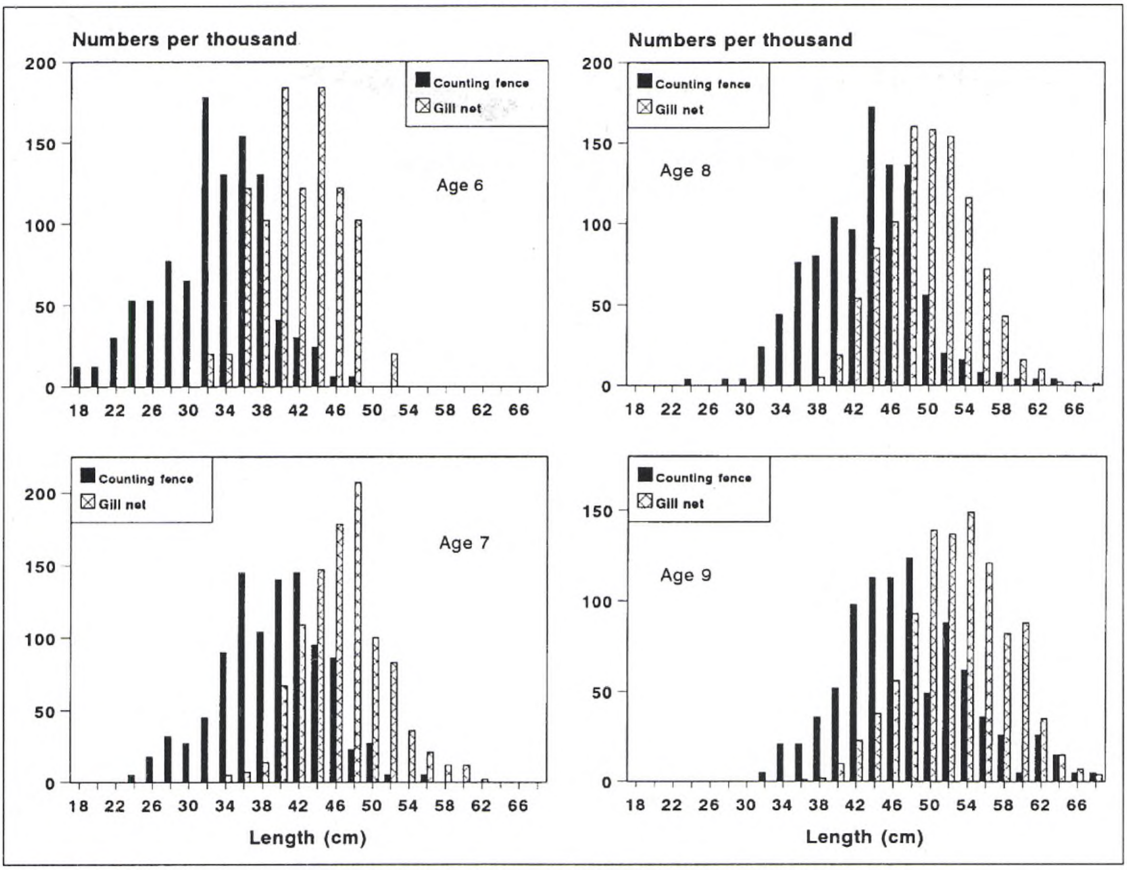

Fig. 11. Comparisons of length-frequency distributions, by specific age groups, of anadromous Arctic charr caught in the Nain stock complex commercial gill net fishery, along with similar data derived from charr captured at fish counting fences on the Fraser and Ikarut rivers, Labrador.

Labrador charr seem to follow this pattern, in contrast with other charr stocks that delay maturation until fish are 10 or more years of age and 60 cm or larger in size (Johnson 1980). This early maturity and relatively high fecundity (Fig. 12) of Labrador fish (286 eggs/100 g) has contributed to the high recruitment levels that obviously must have occurred in order to sustain an intense fishery for many years, primarily on the basis of four age-classes. The length distribution of charr from Ikarut River, Labrador (Fig. 12), had 64% of the upstream run consisting of juvenile fish less than 32 cm in size, a pattern observed in each of the five years of investigation; this is again inconsistent with most other charr populations in the Northwest Territories (Johnson 1989, McGowan 1990).

In summary, Arctic charr from the Nain stock complex of northern Labrador have been heavily exploited for many years and as such, are at odds with earlier statements indicating anadromous charr populations could not tolerate much exploitation. The stock has been overfished; stock size and catch rates have declined, and several biological indicators are consistent with a stock that has experienced growth overfishing. There is, however, no evidence that the population has collapsed. As previously discussed, some factors such as timing of the fishery, can easily confound the interpretation of specific results.

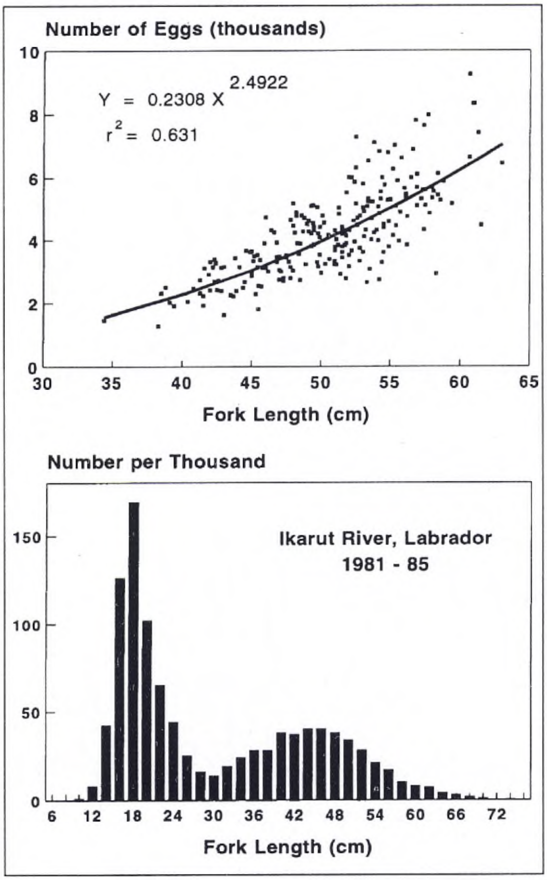

Fig. 12. Fecundity of anadromous Arctic charr (upper panel) in northern Labrador. The lower graph illustrates the size composition of upstream migrating Arctic charr at Ikarut River for data pooled over five years.

Even with a long and extensive data base, not all biological indicators have responded to exploitation in ways typically experienced by other fish species. Alternate information on actual stock sizes of fish returning to rivers is needed as an independent means from which to evaluate and determine the conservation status of the resource. However, given the high variability that has been noted in run sizes from one year to the next (Johnson 1980, McGowan 1990, McGowan and Low 1992, Boivin 1994), caution is also required when harvest level recommendations are made on the basis of a limited times series of information. At best a conservative approach should be taken.

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Many individuals have contributed to the collection of the commercial fishery data over the years. Without their assistance, long term studies such as this would not be possible. In particular I wish to acknowledge the contributions of Milton Shears, George Furey, Larry LeDrew, Steve Keats, Melvin Bulgin, Bob Whalen, Steve Dawson and Roger Johnson. Personnel at the Nain fish plant, both past and present, willingly cooperated to allow the annual sampling program to occur. Finally, appreciation is extended to Drs. Mike O'Connell and Jim Carscadden, and an anonymous referee for reviewing the manuscript critically and providing editorial advice.

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Heritability and Evolution of Meristic Variation in a Naturalized Population of Brook Charr (*Salvelinus fontinalis*)

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Abstract

We estimated heritabilities in the narrow sense and searched for evidence of selection for seven meristic characters and developmental stability as measured by fluctuating asymmetry of four bilateral characters in brook charr (*Salvelinus fontinalis*) from a naturalized population in Mykiss Lake, Algonquin Provincial Park, Ontario, Canada. Regressions of paternal values on mean progeny values were not significantly different from zero. However, regressions with maternal values of pelvic fin rays and vertebrae were significant. Thus, there is little or no additive genetic variation, but significant maternal effects for these two characters in this population. A significantly greater proportion of families showed a negative association between the number of asymmetric characters and multilocus heterozygosity at 10 protein coding loci than a positive one. This suggests that dominance genetic variation for fluctuating asymmetry exists. Individuals from different age-classes collected from Mykiss Lake varied significantly in the mean and variance of some meristic characters and asymmetry. The magnitude and direction of the difference often differed between the sexes. There was no simple relationship between the proportional change in either the mean or variance between age-classes and the estimated magnitude of additive genetic variation for a character.

Keywords: heritability, meristic characters, fishes, evolution, natural selection.

Introduction

Meristic variation is widespread in fishes. Environmental variables, notably temperature, as well as genetic factors influence the meristic phenotype (Lindsey 1988). Geographic trends in vertebral counts among subpopulations of species provided some the earliest evidence (e.g., Jordan's rule, Jordan 1892; pleomerism, Lindsey 1975) that meristic variation is of potential adaptive significance. Recent studies of meristic variation, mostly in sticklebacks (e.g., Blouw and Hagen 1984a,b; Swain and Lindsey 1984; Reimchen and Nelson 1987; Swain 1988; Swain 1992a,b), illustrate the functional and adaptive significance of such variation. Even though meristic variation is no less ubiquitous in the salmonids, there have been few tests of its selective significance.

The proportion of phenotypic variation attributable to additive genetic variation (i.e., narrow sense heritability-h^2) has been used to infer the degree of directional selection for meristic characters in salmonid fishes (Leary et al. 1985; Beacham et al. 1988; Beacham 1990, 1991). Heritabilities of characters highly correlated with fitness may be lower than for those not directly correlated with fitness (Lerner 1954; Falconer 1981). Furthermore, directional selection is expected to result in exhaustion of additive genetic variation and presence of directional dominance. Leary et al. (1985) suggested that the low heritability and the large amount of dominance genetic variation associated with fluctuating asymmetry (Van Valen 1962) of bilateral meristic characters in rainbow trout (*Oncorhynchus mykiss*) is indicative of directional selection for developmental stability. Developmental stability, as reflected by reduced fluctuating asymmetry (see Swain 1987 for an alternative view) is positively associated with fitness (Leary et al. 1984a) because it reflects the degree to which development is affected by environmental stress (Soulé and Cuzin-Roudy 1982).

The relatively large amounts of additive genetic variation detected for meristic characters in fishes (Kirpichnikov 1981; Tave 1984; Leary et al. 1985; Lindsey 1988) are perhaps incompatible with the premise that meristic characters have been the targets of directional selection. However, many of the estimates in salmonids are for cultured populations and may not be representative of natural populations. Furthermore, Swain (1992a) has argued that high levels of additive genetic variation of fitness characters can be explained by a variety of mechanisms including opposing levels of selection on positively correlated characters and changes in the direction of selection over the life cycle.

We used two approaches to search for evidence of selection for variation in seven meristic characters and fluctuating asymmetry of four bilateral meristic characters in a naturalized population of brook charr (*Salvelinus fontinalis*). First, we estimated the amount of additive genetic variation for the meristic characters as well as fluctuating asymmetry by crossing adults collected from Mykiss Lake, Algonquin Provincial Park, Ontario and rearing their offspring in the laboratory. Presence of dominance genetic variation affecting fluctuating asymmetry was inferred by performing correlations between enzyme heterozygosity at 10 protein coding loci and asymmetry. Second, we performed a comparison among three age-classes (Method VIII, Endler 1986) of brook charr collected from Mykiss Lake to provide a preliminary test of the null hypothesis that age-classes differ only by chance in their character frequency distributions. Natural selection would be reflected by significant differences in means or variances among age-classes depending upon the mode of selection (directional, stabilizing, disruptive).

The brook charr population in Mykiss Lake has many attributes which make it amenable for studies of selection. The population spawns in a single, discrete area, and experiences little gene flow with neighbouring populations. Thus, changes in character frequency distributions are unlikely to be due to complexities in population structure and gene flow. Furthermore, the founding of the population in 1962 (Fraser 1989) improves the likelihood of detecting natural selection because the founders and their descendants have been recently exposed to the natural environment.

Materials and methods

Fish collections

Brook charr were collected in 1988 from Mykiss Lake, a small (23.5 hectares), mesotrophic, soft water lake in Algonquin Provincial Park, Ontario, Canada (45°4' N, 78°14' W). Mykiss Lake has been a designated research sanctuary since 1962 when it was cleared of fish (primarily white suckers, *Catostomus commersoni*) by the Ontario Ministry of Natural Resources. Subsequently, brook charr from various sources (Dickson Lake, Algonquin Park and domestic Hill's Lake hatchery strain) were introduced to establish a self-sustaining population; the first naturally reproduced fish were surveyed in 1975. Approximately, four generations have passed since the last introductions.

To minimize the number of adult fish killed and to ensure the viability of gametes for experimental matings, we collected fish from four age-classes during two sampling trips. Forty 1 year(yr)-old and thirty-three 2 yr-old fish were collected between June 8-13, 1988 with trapnets and angling. On October 31, 1988, fifty-two 3 yr-old, ten 4 yr-old, and seven 2 yr-old sexually mature fish were sampled from trapnets set over the single spawning shoal. Limitations in the number of fish we could remove from Mykiss Lake precluded us from performing more powerful cohort analyses (Method VII, Endler 1986).

Experimental matings

Eggs and sperm were removed from 20 female and 18 male brook charr by abdominal compression, placed in dry plastic containers and transported from Mykiss Lake to the University of Guelph packed on wet ice. Thirty full- and half-sib families were produced on 31 October 1988 by combining subsamples of gametes from single males and females (Table 1). The families developed at 6°C in the common environment of a vertical incubating rack. After hatching (101 days from fertilization), each family was transferred to a 30 L tank where water temperature varied between 6-12°C depending upon the season. Until the onset of exogenous feeding, family densities ranged between 125 and 546 with a mean of 288. Each family was thinned to 125 alevins at 121 days and further thinned to 40 juveniles at 257 days. The families were reared in a single room on commercial trout food and under natural photoperiod until 378 days after fertilization. Approximately, 25 fish per family were frozen for meristic and allozyme analyses, detailed below.

Meristic counts

We determined the number of anal fin rays, dorsal fin rays, and vertebrae in laboratory progeny and naturalized fish according to the methods of Hubbs and Lagler (1958). We did not obtain vertebral counts for seventeen naturalized males and the progeny from four families. In addition, counts of the following characters on both the left and right side of each fish were determined: pelvic and pectoral fin rays, gillrakers on the upper part of the first branchial arch and gillrakers on the lower branchial arch. Development of the meristic characters is completed prior to the age of fish in our collections (Leary et al. 1984b). The bilateral meristic characters all show fluctuating asymmetry, whereby the difference between a character on the left and right sides of an individual is normally distributed about a mean of zero (Van Valen 1962). Asymmetry was quantified by summing the number of bilateral characters that possessed unequal counts on the left and right side of the body (Leary et al. 1984a). Therefore, the number of asymmetric characters ranged from 0 to 4. This measure of asymmetry provides qualitatively the same results as a second method which sums absolute values of differences in bilateral characters of an individual (Leary et al. 1984a).

Allozyme variation

The laboratory families were analyzed for polymorphism at 10 loci (*AAT-1,2*, *CK-2*, *G3PDH-1*, *GPI-1*, *IDHP-3*, *LDH-3*, *LDH-4*, *MDH-B1,2*, *MEP-1*, and *6PGD)* (Liskauskas and Ferguson 1991). Six hundred and eighty-six progeny were screened for protein variation at the subset of loci known to be segregating in their particular family based on the combination of genotypes in the parents. Multilocus heterozygosity was calculated from the number of heterozygous loci per fish and ranged from 0-4. Fish with more than one allele at each of the duplicated loci (*MDH-B1,2* and *AAT-1,2*) were considered heterozygotes at a single duplicated locus; it was difficult to assign variant alleles to one particular locus. Allozyme data for the naturalized fish collected from Mykiss Lake have been reported in Liskauskas and Ferguson (1991).

Statistics

Laboratory progeny

Heritability (h^2, narrow sense) for each meristic character (total counts) and the number of asymmetric characters was estimated by regression of maternal, paternal and midparent values (independent variables) on mean family values (dependent variable) (Falconer 1981). We used a subset of 15 full-sib families (Table 1) produced by 3 yr-old females to minimize the effects of female age. It was unavoidable to use males of different ages. The remaining 11 families produced from 3 yr-old females were excluded be-

Table 1. The association (Pearson product-moment correlation, *r*) between the number of heterozygous loci and asymmetric bilateral meristic characters per fish within families of brook charr reared in the laboratory for 1 year. The identity and age in years (in parentheses) of the male and female parents are also given.

Family	Parent		*N*	Het	Asymm	*r*
	Female	Male				
B102	11(2)	134(4)	26	1.53	1.81	-0.090
B103	30(3)	129(2)	25	0.80	1.32	0.173
B104	1(4)	133(3)	24	2.25	1.13	-0.036
B105	28(3)	136(3)	25	1.52	1.56	-0.284
B106	27(3)	126(3)	24	0.63	1.54	-0.240
B107	22(3)	130(2)	25	2.16	1.56	-0.113
B108	31(3)	128(4)	22	1.00	1.36	-0.285
B109	13(3)	127(2)	24	0.46	1.38	-0.110
B111	3(3)	116(3)	25	2.04	1.24	0.205
B112	6(3)	131(2)	26	1.19	1.58	-0.094
B114	24(4)	109(3)	23	1.70	1.91	0.025
B118[b]	16(3)	114(4)	25	2.04	1.68	-0.178
B119[a,b]	23(3)	121(4)	23	0.00	1.22	-
B120[b]	18(3)	118(3)	24	0.58	1.17	-0.114
B123[b]	30(3)	134(4)	24	1.58	1.50	0.088
B125[a,b]	28(3)	133(3)	25	0.00	1.48	-
B126[b]	27(3)	136(3)	25	2.16	1.32	0.056
B127[b]	22(3)	126(3)	16	3.31	1.44	-0.081
B128[a,b]	31(3)	130(2)	25	2.00	1.40	-
B129[b]	13(3)	128(4)	25	2.04	1.12	-0.129
B130[a,b]	14(3)	127(2)	22	0.00	1.64	-
B132[b]	6(3)	116(3)	25	1.60	1.32	0.307
B133[b]	17(3)	131(2)	25	2.20	1.52	-0.098
B134	24(4)	132(2)	23	3.26	1.04	-0.357
B135[b]	26(3)	109(3)	22	2.63	1.46	-0.161
B136[a,b]	29(3)	102(3)	25	0.00	1.04	-
B137[b]	19(3)	111(2)	15	0.60	1.27	-0.179
B138	16(3)	105(3)	13	1.31	0.77	-0.225
B140	18(3)	121(4)	24	0.33	1.29	-0.373
B141	5(3)	118(3)	11	1.73	1.82	0.096

[a] no detectable protein polymorphism segregating within family

[b] used in parent/offspring regressions for the calculation of heritability

cause they had a least one parent in common with those used above. Analysis required independence among families (different males and females in different families). In order to maximize the number of families produced by different males and females, a subset of 11 families was used (B125, B126, B127, B128, B129, B130, B132, B133, B135, B136, and B137). The remaining four families could be compiled with slightly different combinations. However, analysis of different sets of independent families produced qualitatively the same results in terms of which relationships were significant (data not shown).

Differential effects of the sexes on meristic characters (and asymmetry) will be reflected by lack of concordance among the midparent, maternal, and paternal estimates. Higher estimates from regression of maternal values on progeny values than the equivalent with paternal values suggest maternal effects. Heritability is equivalent to the slope of the regression line when midparent values are the independent variables and 2 times the slope when either maternal or paternal values are used. Variances of the eight characters did not differ between either (1) male and female parents or (2) male and female progeny. Therefore, we combined male and female progeny counts into a mean family value.

The association between the number of heterozygous loci per fish and asymmetry within families was tested with a Pearson product-moment correlation coefficient. This assumes that the effects of individual loci are equal and additive among loci. We also used multiple regression to determine if single loci (independent variables) explained a significant amount of variation in the number of asymmetric characters per fish (dependent variable). This second approach allows the effects of individual loci to be unequal and non-additive (Bush et al. 1987; Diehl 1988; Koehn et al. 1988). Here, heterozygotes at each locus were scored 1 and homozygotes 0.

Naturalized fish

We calculated two measures of selection, i and j (Falconer 1981) for each meristic character and the number of asymmetric characters per fish:

$$i = (\text{mean}_a - \text{mean}_b)/\text{SD}_b \quad \text{and}$$
$$j = (\text{var}_a - \text{var}_b)/\text{var}_b,$$

where mean_a is the mean after selection, mean_b is the mean before selection, SD_b is the standard deviation before selection, var_a is the variance after selection, and var_b is the variance before selection. The value i is the proportional change in mean between two age-classes produced by directional natural selection. We used one-way ANOVAs in conjunction with Bonferroni pairwise procedures to determine the significance of pairs of means and their corresponding i values. The Bonferroni procedure adjusts probability values according to the number of independent tests to reduce Type I error (Rice 1989). The value j measures the proportional change in variance between two age-classes produced by stabilizing (if negative) or disruptive (if positive) selection (collectively called variance selection). F_{max} tests (Endler 1986) were used to determine the statistical significance of j. These analyses were conducted separately by sex because full factorial ANOVAs (sources of variation:age, sex, age • sex) indicated either significant differences between the sexes or significant age • sex interactions. The 10 four yr-old fish (4 females and 6 males) were not included because of their small representation.

Results

Laboratory families

Regression of maternal values of pelvic fin rays and vertebrae on mean progeny values were significant as was the equivalent analysis of pelvic rays with midparent values (Table 2). No significant regression was detected for all analyses with paternal values. Moreover, regressions of maternal, paternal, and midparent numbers of asymmetric characters were not significantly different from zero.

No significant association between the number of asymmetric characters and multilocus heterozygosity per fish was detected within any of the 25 families with detectable polymorphism at any of the 10 loci (Table 1). However, 18 out of 25 families showed a negative association. This distribution of signs differs significantly from that expected from a random distribution in the predicted direction (binomial one-tailed $P = 0.022$). No single locus, expect for *MDH-B1,2* in a single family, explained a significant amount of variation in asymmetry within families; this single significant result can be explained by chance alone.

Table 2. Heritabilities in the narrow sense (SE) of meristic variation estimated from 15 full-sib families[1] of Mykiss Lake brook charr reared in the laboratory for one year. Parental values (female, male, midparent) were regressed upon mean progeny values. ** $P<0.01$; *** $P<0.001$.

Variable	Female	Male	Midparent
Anal rays	0.030 (0.128)	0.236 (0.218)	0.113 (0.129)
Dorsal rays	-0.972 (0.482)	0.312 (0.492)	-0.887 (0.630)
Lower gillrakers	-0.280 (1.120)	0.878 (0.812)	0.851 (0.892)
Pectoral rays	0.416 (0.352)	0.454 (0.334)	0.364 (0.212)
Pelvic rays	1.050 (0.170)***	-1.062 (0.574)	1.045 (0.268)**
Upper gillrakers	0.890 (0.754)	0.754 (0.904)	1.206 (0.644)
Vertebrae	1.270 (0.428)**	0.190 (0.422)	1.192 (0.594)
Asymmetry	-0.122 (0.142)	0.014 (0.102)	-0.022 (0.071)

[1] fourteen families were sampled for vertebral counts

Table 3. Means (standard deviations) of meristic counts and number of asymmetric characters in three age-classes of brook charr from Mykiss Lake, Algonquin Provincial Park, Ontario. F=female, M=male.

		Age		
Traits	Sex	1	2	3
Anal rays	F	10.00 (0.69)	9.93 (0.73)	10.61 (0.92)
	M	10.00 (0.97)	9.96 (0.96)	9.08 (0.72)
Dorsal rays	F	10.61 (0.70)	10.64 (0.50)	11.50 (0.51)
	M	10.68 (0.48)	10.46 (0.76)	9.79 (0.59)
Lower gillrakers	F	22.17 (1.43)	22.79 (2.05)	22.68 (1.42)
	M	22.32 (1.46)	22.81 (1.83)	20.58 (1.47)
Pectoral rays	F	26.83 (2.04)	26.79 (1.05)	26.36 (1.39)
	M	26.32 (1.13)	26.58 (1.30)	25.58 (1.18)
Pelvic rays	F	16.33 (0.69)	16.21 (0.70)	16.39 (0.83)
	M	16.00 (0.76)	16.42 (0.95)	16.00 (0.59)
Upper gillrakers	F	11.11 (1.61)	12.14 (1.83)	13.29 (2.09)
	M	11.14 (1.13)	12.96 (2.22)	12.67 (1.74)
Vertebrae	F	59.50 (0.92)	59.36 (1.08)	59.75 (1.18)
	M	59.73 (1.24)	59.73 (1.22)	59.67 (1.12)
Asymmetry	F	1.44 (0.92)	1.36 (0.50)	1.07 (0.72)
	M	0.91 (1.02)	1.19 (0.90)	1.38 (0.88)
N	F	18	14	28
	M	22	26	24[1]

[1] N=9 for vertebral counts in males

Naturalized fish

Fish from different age-classes varied in the mean counts of some characters (Table 3). In both sexes, dorsal rays (female: $F[2,57] = 17.63$, $P<0.001$; male: $F[2,69] = 12.80$, $P<0.001$) and upper gillrakers (female: $F[2,57] = 7.32$, $P=0.001$; male: $F[2,69] = 7.00$, $P<0.001$) differed significantly even when the number of independent tests was taken into account. Males also showed significant differences for lower gillrakers ($F[2,69]=12.91$; $P<0.001$); 3 yr-old males had the lowest counts. Vertebral, anal fin ray, pelvic fin ray, and pectoral fin ray counts as well as asymmetry did not differ among age-classes of either sex. Seven out of 28 selection differentials (*i*) were significant (Fig. 1). However, the *i* values for a given pair of age-classes

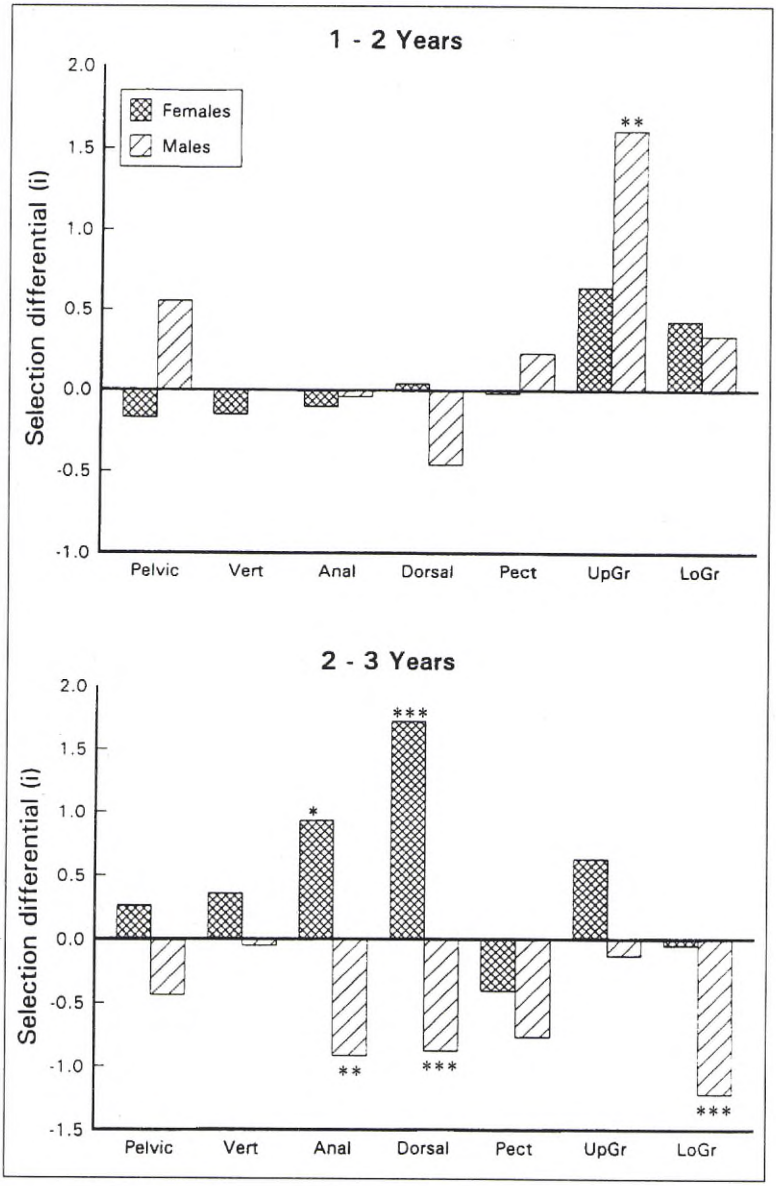

Fig. 1. Proportional changes in the means (*i*) of seven meristic characters calculated for two pairs of age-classes (1 vs 2; 2 vs 3) of brook charr from Mykiss Lake, Algonquin Provincial Park. Statistical significance was determined with ANOVA and Bonferroni adjusted probabilities (* $P<0.05$, ** $P<0.01$, *** $P<0.001$). The meristic characters have been ordered according to estimated h^2 values (sire component). The h^2 estimates are: pelvic rays (Pelvic)=-1.062; vertebrae (Vert)=0.19; anal rays (Anal)=0.236; dorsal rays (Dorsal)=0.312; pectoral rays (Pect)=0.454; upper gillrakers (UpGr)=0.754; lower gillrakers (LoGr)=0.878. See Table 3 for sample sizes.

were not necessarily the same in both sexes. Three yr-old females had significantly higher dorsal and anal ray counts than two yr-old females (positive *i* values) while the opposite relationship was observed in males (negative *i* values).

There was some evidence of variance selection for meristic counts and asymmetry based on the significance of *j* values (Fig. 2). The variance in lower gillrakers, and pectoral rays differed among some pairs of age-classes in females. Two yr-old females showed significantly lower variance in asymmetry than 1 yr-old females. In males, dorsal rays, pelvic rays, and upper gillrakers showed significant differences in variance among age-classes.

The observed proportional change in either the mean or variance of a character was not associated with the magnitude of h^2 (Figs. 1 and 2). Characters with higher estimated h^2 did not show greater proportional differences between age-classes than those with lower h^2.

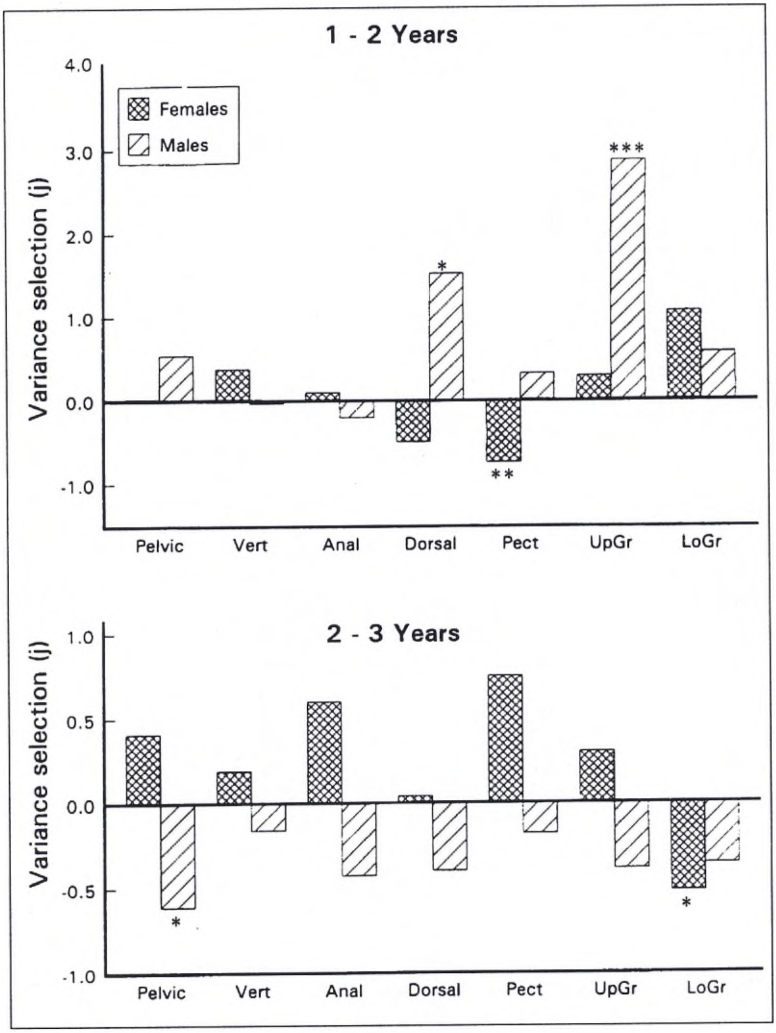

Fig. 2. Proportional changes in the variances (*j*) of seven meristic characters calculated for two pairs of age-classes (1 vs 2; 2 vs 3) of brook charr from Mykiss Lake, Algonquin Provincial Park. Statistical significance was determined with F_{max} tests (*P<0.05, **P<0.01, ***P<0.001). The meristic characters have been ordered according to estimated h^2 values (sire component). The h^2 estimates are: pelvic rays (Pelvic)=-1.062; vertebrae (Vert)= 0.19; anal rays (Anal)=0.236; dorsal rays (Dorsal)=0.312; pectoral rays (Pect)=0.454; upper gillrakers (UpGr)= 0.754; lower gillrakers (LoGr)= 0.878. See Table 3 for sample sizes.

Discussion

Heritability

Mykiss Lake brook charr showed no detectable additive genetic variation for seven meristic characters. Although the magnitude of our estimates (sire component) for five characters were moderate, they had high standard errors and were not significantly different from zero. These data stand in contrast to the general conclusion that a high proportion of the meristic variation in fishes is controlled by additive genetic variation (Kirpichnikov 1981). For example, this same set of meristic characters shows highly significant midparent heritability estimates ranging between 0.37 (±0.21) and 0.93 (±0.50) in a cultured population of rainbow trout (Leary et al. 1985). The design and power of our experiment was similar to that of Leary et al. (1985) which suggests that methodological differences cannot account for the apparent disparity. Lack of detectable additive variation in Mykiss Lake brook charr might be attributed to their genetic history. As Swain (1992a) has pointed out, most previous estimates have been conducted on domesticated stocks. Cultured stocks such as that examined by Leary et al. (1985) may be less likely to experience the same intensity of directional selection as that occurring in a naturalized population such as Mykiss Lake and thus might be expected to harbour greater amounts of additive genetic variation.

Variation in environmental history among the brook charr parents captured from Mykiss Lake and their laboratory-reared offspring might also have contributed to the large standard errors observed in the present experiment. Environmental effects on meristic variation are well documented (Lindsey 1988). The male parents captured from Mykiss Lake were from three age-classes and variation in environmental conditions among years (e.g., temperature) during the time of meristic differentiation might have led to non-genetic variation. This potential effect is unlikely to be as great in females, as only 3 yr-olds were considered in the heritability analysis. The female parents would have shared much of the same environment in Mykiss lake during the embryological, alevin, and juvenile periods given the restricted nature of the spawning and nursery area. The suggestion that genetic and environmental history are important determinants of the magnitude of heritability estimates is supported by studies with Pacific salmonids (Beacham et al. 1988; Beacham 1990, 1991). These studies, also captured parents from the wild, reared their progeny in the laboratory and observed relatively high standard errors for the heritability estimates for meristic counts. In contrast, both the parental and progeny generations of rainbow trout examined by Leary et al. (1985) were reared in the same hatchery environment. Parallel collections of quantitative genetic data from natural and laboratory populations within a single species are required to test these possibilities.

We detected significant maternal effects for pelvic ray and vertebral counts. The existence of such effects has important implications for the calculation of heritabilities in this population of brook charr because the most commonly used independent variable, the midparent value, is invalid in this circumstance. Even though maternal effects on meristic counts have been reported in other fish species (Kirpichnikov 1981; Beacham 1990, 1991), the mechanism of how they operate is unknown. Prefertilization influences such as parental thermal environment and parental reproductive history have varying influences on meristic counts (Lindsey 1988) and we cannot eliminate these as being responsible for the maternal effects. We can, however, eliminate variation in a third potential prefertilization influence, egg size (Lindsey 1988), as a primary determinant of progeny meristic counts by using data reported elsewhere (Liskauskas and Ferguson 1990). There were no significant associations between the mean egg diameter (average of 20 water hardened ova) of a female and the mean meristic counts of her progeny.

Environmental variation in progeny rearing environments is unlikely to have occluded the detection of parental effects. As mentioned previously, rearing densities did vary among families before the onset of exogenous feeding; they were controlled thereafter. Rearing density can affect meristic counts (Ali and Lindsey 1974; Leary et al. 1991). We did not, however, find any association between family rearing density either just after hatching or at the onset of exogenous feeding and the mean meristic counts of a family.

Lack of significant regression between the numbers of asymmetric characters in the male parent and the mean of his offspring suggests that there is little additive genetic variation affecting fluctuating asymmetry in Mykiss Lake brook charr. Similar low heritabilities have been observed for asymmetry of morphological characters in a variety of organisms (Mather 1953; Reeve 1960; Bailit et al. 1970; Leary et al. 1985) but not in others (Hagen 1973). In contrast, the observation that a significantly greater number of families showed a negative correlation between the number of heterozygous loci per fish and asymmetry may reflect the existence of dominance genetic variation. The presence of dominance genetic variation coupled with the lack of additive genetic variation support the suggestion of Leary et al. (1985) that there has been directional selection for increased developmental stability. Directional selection is expected to increase developmental stability (decreased asymmetry) if developmental instability is negatively associated with fitness (Leary et al. 1984a). This argument is based on the premise that fluctuating asymmetry is a reasonable measure of developmental instability, a view that has been criticized (Swain 1987). The concordance between our study and that of Leary et al. (1985) does suggest that fluctuating asymmetry as a measure of developmental instability is of evolutionary significance.

Selection

Fish from different age-classes of Mykiss Lake brook charr had significantly different means and variances of some meristic counts. This was especially apparent in the comparison of mean counts between 2 and 3 yr-old fish. Differences in meristic counts between age-classes may have resulted from natural selection on these or other correlated characters. This explanation is valid only if there is significant additive genetic variation for the characters and a consistent relationship between the values of the character and fitness is present (Endler 1986). The lack of detectable additive genetic variation for the characters which showed significant differences among age-classes casts some doubt on this explanation. Furthermore, there was no simple relationship between the proportional change in either the mean or variance and the magnitude of h^2 for a character. However, it should be noted that some characters (e.g. asymmetry), despite being associated with low heritability estimates, do respond to directional selection (Mather 1953; Reeve 1960).

Variation in environmental conditions or genetic background among year-classes could also result in meristic count differences. As stated previously, variation in the thermal regime of the early rearing environment can affect meristic counts (Lindsey 1988) and it is likely that such year-to-year variability exists in Mykiss Lake. One prediction from the temperature hypothesis is that the sexes should show the same directional change in counts between age-classes because there is no reason to believe that the sexes occupy different thermal environment during the time of meristic determination (but see Holtby and Healey 1990; Ehlinger 1991). Differences in direction of the significant selection differentials for anal and dorsal rays between 2 and 3 yr-old fish makes this explanation less tenable. We cannot eliminate variation in the genetic background of age-classes as an explanation for variation in meristic counts. Even though there was no evidence of departures from Hardy-Weinberg proportions to suggest differential strain contributions to different age-classes, heterogeneity in allele counts at protein coding loci do exist (Liskauskas and Ferguson 1991). Following the success of a cohort through time and performing replicate comparisons of meristic counts in different age-classes would provide a stronger test of selection.

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Seawater Tolerance, Migration, Growth and Recapture Rates of Wild and Hatchery-reared Arctic Charr (*Salvelinus alpinus* (L.))

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Abstract

Seawater tolerance, migration, growth and recapture rates of wild first-time migrants of Arctic charr (*Salvelinus alpinus* (L.)) were compared to those of hatchery-reared one- and two-year old fish. Seawater challenge tests showed that wild charr displayed good hypo-osmoregulatory capacity before entering the sea, while hatchery-reared charr had a slightly lower capacity. Despite having only a short stay in the sea, wild charr showed good growth, and recapture rates were high. Hatchery-reared one-year old charr had a longer sea sojourn, a low weight gain and rates of recapture were low. Growth of the two-year old hatchery-reared charr were also low but recapture rates were high. If Arctic charr ranching is to become viable, there is a need for development of production strategies that ensure good growth and high rates of recapture of hatchery-reared fish following their first year in the sea.

Keywords: Arctic charr; *Salvelinus alpinus;* sea ranching; seawater tolerance; migration; growth; survival.

Introduction

The seaward migration of Arctic charr (*Salvelinus alpinus* (L.)) is normally an annual event, and residence in seawater is limited to 40 to 50 days. The sea sojourn has been reported to be localized in coastal areas, and many of the fish return to home waters during the late summer. The charr exhibit high growth rates during their period of sea residence (Mathisen and Berg 1968; Berg and Jonsson 1989; Finstad and Heggberget 1993). The annual cycle of anadromous charr may, therefore, be divided into two distinct periods, one of rapid growth in summer and one of stagnation or weight loss in winter (Finstad and Heggberget 1993).

High rates of return (20-50%) and rapid growth during seawater residence have led to an increase in interest of the possibility of sea ranching this species (Heggberget 1991). Subsequently, charr have been reared for initial sea-ranching experiments, with the main goal being to develop production strategies that give rise to hatchery-reared charr with the same hypo-osmoregulatory capacity, growth rate, migratory pattern and recapture rate as wild charr.

The aim of the present study was to compare the physiological capacity for osmoregulation of descending wild first time migrants of Arctic charr with that of hatchery-reared one- and two-year old charr, prior to their release into seawater. Migration, growth, the duration of stay in the sea and recapture rates of these three groups were also studied.

Material and methods

The study area in the Halsvassdraget, located at 70°N, 23°E, (Fig.1) has been described previously (Finstad and Heggberget 1993). A fish trap (inclination 1:15, apertures 10.2 mm), located

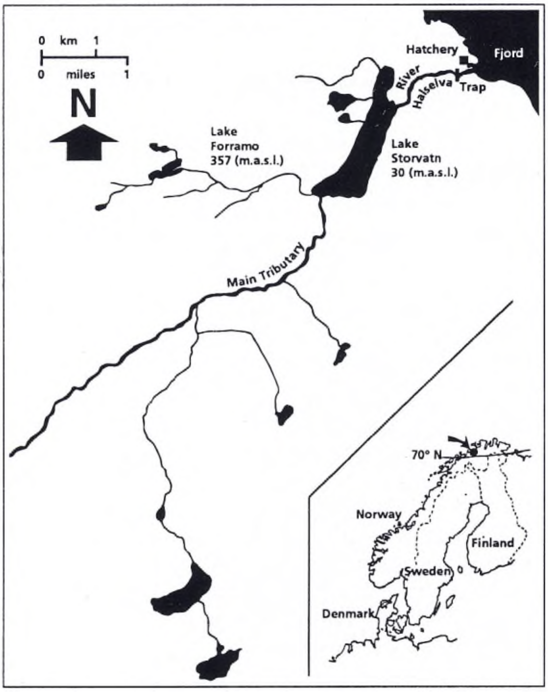

Fig. 1. Map of the Halsvassdraget, at 70°N 23°E in Finnmark, northern Norway.

about 200 m upstream from the river mouth, was used to catch all descending and ascending fish with fork length longer than 10 cm. The trap was operated during the ice-free period, from the beginning of April until November. One- and two-year old Arctic charr were reared in a hatchery located close to the river mouth.

Wild charr, caught in the trap as ascending mature fish, were used as the broodstock for the production of the hatchery-reared fish. The regimes (temperature and photoperiod) used for producing the one- and two-year old charr for release are shown in Fig. 2. Fish released at one year of age were held in warmed water for most of the production cycle, with a short winter period (2 months) at low temperatures, whereas the charr released as two-year old fish were exposed to natural water temperatures from 13 June, 1990 until the time of their release. The fish were given a simulated natural photoperiod. Commercial dry feed (Felleskjøpet), dispensed from automatic feeders, was provided in excess.

In April, about two months prior to release, the fish were anaesthetized with benzocaine (50

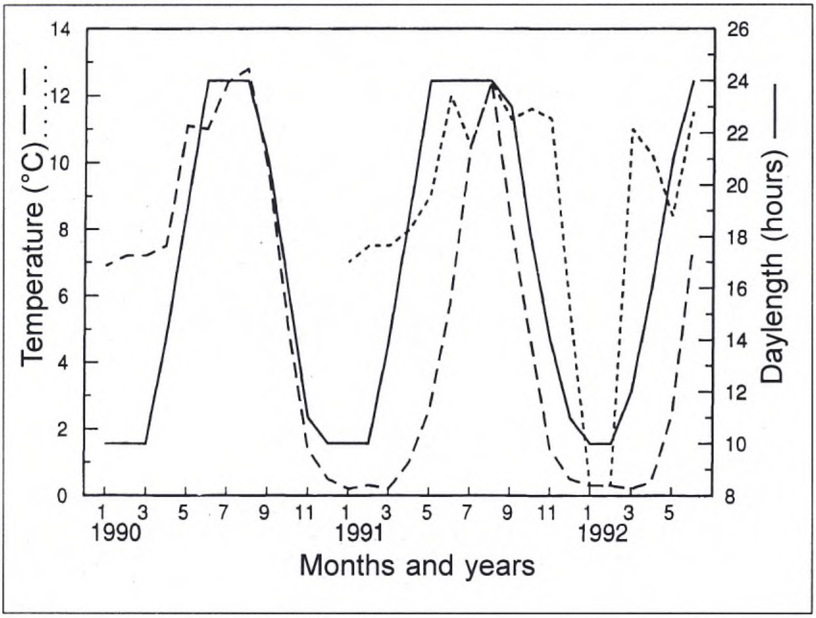

Fig. 2. Production regimes for the hatchery-reared one- and two-year old charr. The temperature regimes (left-hand axis) for the two-year old charr (long dashes) are shown from January 1990 onwards and the temperature regimes for the one-year old charr (short dashes) are shown from January 1991 onwards. Daylength values (hours of light) are shown by the solid line (right-hand axis).

mg l^{-1}) and tagged individually with numbered Carlin tags (Carlin 1955). On 10 June, two days prior to release, 200 one-year old and 200 two-year old hatchery-reared charr were weighed and their fork lengths measured. These fish were released in the River Halselva about 1 km upstream of the fish trap. The rest of the fish (988 and 1,882 for one- and two-year old charr, respectively) were not weighed in order to avoid handling stress before release.

On 12 June 1992 the hatchery-reared charr were released below the fish trap. Wild Arctic charr (*N*=907), were tagged, weighed to the nearest gram and their fork-lengths measured as they descended through the fish trap. The hatchery-reared one- year old smolts (*N*=86) and two year-old smolts (*N*=112) passing the fish trap on descent were registrated in the same period.

Prior to release, a total of 60 fish were killed by a blow to the head and the sex and maturity status of 20 fish from each group was examined according to Dahl's (1917) criteria.

On 12 June, fifty fish from each group were taken at random from the trap (wild fish) and production tanks (hatchery-reared fish), and these fish were transferred to tanks (salinity of 34 ‰ and water temperature 8 °C) for a seawater challenge test. Control samples were taken at the start (freshwater, 10 fish from each group) and sampling was repeated on day three (seawater, 10 fish from each group). The fish were anaesthetized with benzocaine (50 mg l^{-1}), whereafter blood samples were taken from all fish within four minutes. The blood samples were stored on ice and the plasma separated by centrifugation (5000 rpm for 5 minutes). The blood plasma was then frozen (-30 °C) until the analyses were made. Plasma chloride was analysed using a Radiometer CMT 10 chloride titrator. For measurements of gill Na-K-ATPase activity, the first gill arch from the right side of the fish (ventral) was dissected, carefully washed with water, blotted with filter paper, cut into small pieces and put into a plastic tube containing 1 ml isotonic SEI-solution (0.3 M sucrose, 0.02 M Na_2-EDTA and 0.1 M imidazole). The tubes were immediately frozen and stored in liquid nitrogen (-196 °C). Gill Na-K-ATPase activity was assayed as described by Finstad et al. (1989).

Fish ascending the watercourse were collected from the trap twice a day at 08:00 and 20:00. The fish were anaesthetized with benzocaine, weighed, fork lengths measured, tag numbers recorded and then released into the river upstream from the trap. Growth comparisons for the three groups were calculated on ascending fish (211, 8 and 41 for wild and hatchery-reared one- and two-year old smolts, respectively) where the weight on descent were known (907, 86 and 112 for wild and hatchery-reared one- and two-year old smolts, respectively). A size-frequency histogram of the fish used in these calculations are given in Figs. 3,4 and 5.

For the statistical calculations a Mann-Whitney U-test (gill Na-K-ATPase, plasma chloride), a Student's *t*-test (growth and duration of

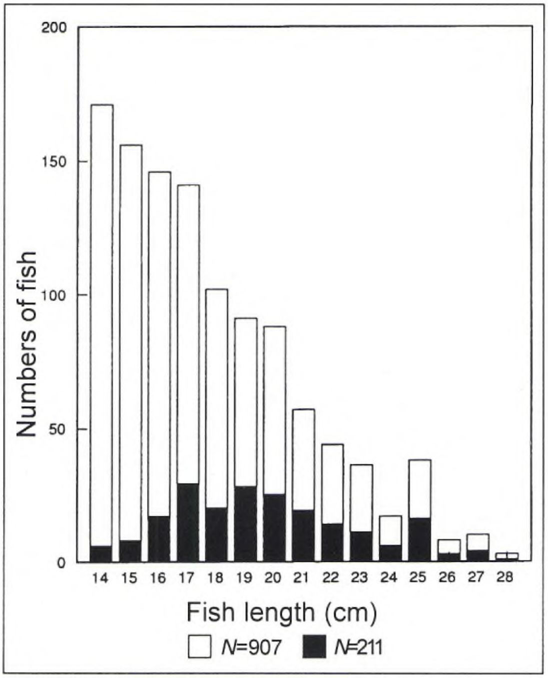

Fig. 3. A size-frequency histogram of the wild first-time migrants of Arctic charr descending (*N*=907) and ascending (*N*=211). For further explanations see material and methods.

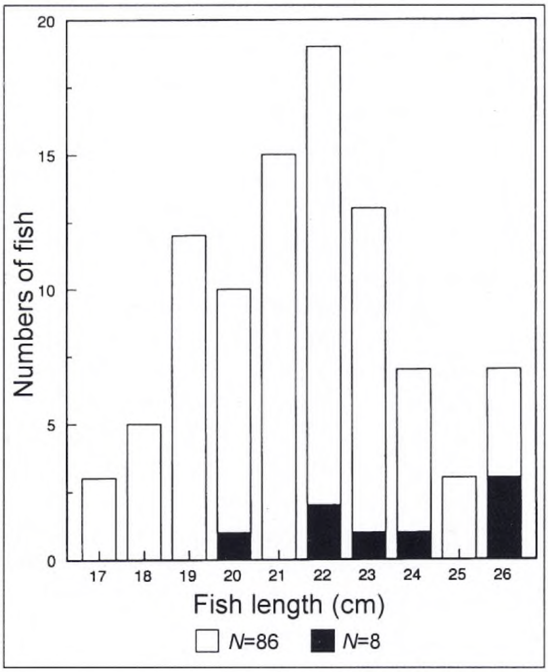

Fig. 4. A size-frequency histogram of hatchery-reared one-year old charr descending (*N*=86) and ascending (*N*=8). For further explanations see material and methods.

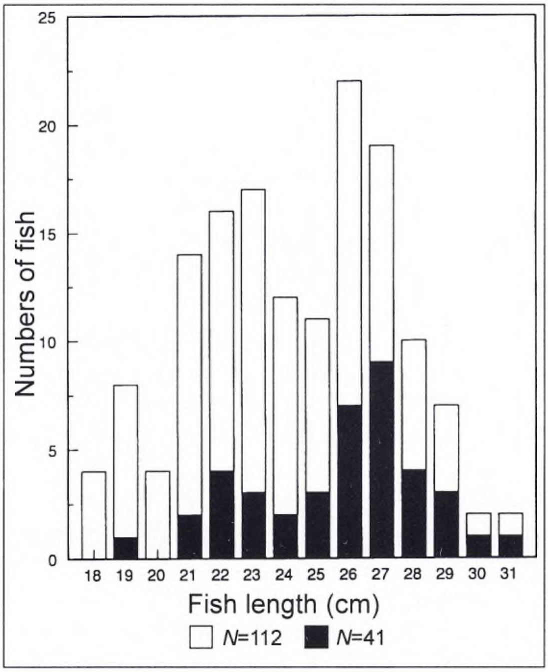

Fig. 5. A size-frequency histogram of hatchery-reared two-year old charr descending (*N*=112) and ascending (*N*=41). For further explanations see material and methods.

stay in sea) and a chi-square test (χ^2) (recapture rate) were used. Results are presented as means ± standard deviation (SD).

Results

Fig. 6 shows the cumulative captures of wild charr and hatchery-reared charr. Most of the fish descended the river between 1 June and 22 June (weeks 23 to 26). The time of ascent for most of the wild charr was between 29 June to 3 August (weeks 27 to 32), while the hatchery-reared charr tended to ascend later, and over a wider timespan. This is also shown by the fact that the wild charr stayed at sea for a significantly shorter time ($P<0.001$, *t*-test) than the hatchery-reared charr: 32±17, (N=211), 57±14 (N=149) and 46±16 days (N=574), for wild charr, hatchery-reared one- and two-year old charr, respectively. These data are based on fish which we know both date of descent and date of ascent, that is for all fish in each of the three groups. Hatchery-reared one-year old charr also spent a significantly longer time at sea than either the wild or the hatchery-reared two-year old charr ($P<0.001$, *t*-test).

One of the one-year old charr died during the seawater challenge test. The mean plasma chloride levels for wild charr after 72 hours exposure to seawater were approximately 150 mM, while for the hatchery-reared one- and two-year old charr the averages were approximately 160 mM (Table 1). For all three groups, the plasma chloride levels were significantly higher ($P<0.05$, two tailed Mann-Whitney U-test) after the 72 hour challenge test than at the start (0 hours). After 72 hours exposure to seawater, the mean plasma chloride levels for both groups of hatchery-reared charr were significantly higher ($P<0.01$, two tailed Mann-Whitney U-test) than

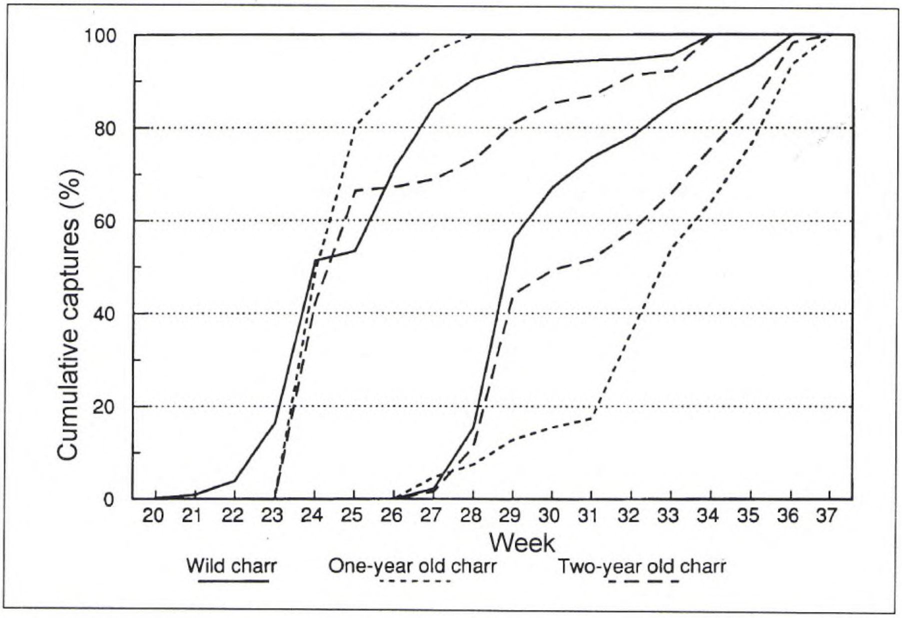

Fig. 6. Cumulative captures (%) of wild and hatchery-reared one- and two-year old Arctic charr descending (left hand) or ascending (right hand) in 1992. For descending fish the cumulative captures are based on 907, 86 and 112 individuals from wild charr and hatchery-reared one- and two-year old charr, respectively. For ascending fish the cumulative captures are based on 211, 149 and 574 individuals from wild charr and hatchery-reared one- and two-year old charr, respectively.

Table 1. Activity of gill Na-K-ATPase and blood plasma concentrations of Cl^- in wild first-time migrants of Arctic charr and hatchery-reared one- and two-year old charr during a seawater challenge test carried over 72 hours on 12-15 June 1992. The salinity was 34 ‰ and water temperature 8 °C. Values are means ±SD, *N*=10.

	Exposure time (hours)	Weight (gram)	Gill Na-K-ATPase activity (μmoles P_i•mg protein^{-1}•h^{-1})	Plasma chloride (mM)
Wild charr	0	37.1±11.0	1.88±1.52	139.3±4.3^{a}
	72	40.3±17.2		148.4±8.9^{c}
One-year old charr	0	89.3±21.6	1.16±0.40^{b}	127.9±1.7^{ab}
	72	97.1±19.4		161.2±11.1
Two-year old charr	0	155.6±37.5	2.0 ±1.66	138.4±7.1^{a}
	72	146.3±37.6		163.3±5.3

Differences were significant between: a, start (0 hours) and after 72 hours within groups; b, one-year old charr and wild- and two-year old charr at start (0 hours); c, wild charr and one- and two-year old charr, after 72 hours.

Table 2. Mean growth of wild first time migrants of Arctic charr compared to hatchery-reared one- and two year old charr. Growth data in this table are calculated on ascending fish (211, 8 and 41 for wild and hatchery-reared one-and two-year old charr, respectively) on which weight and length on descent were known (907, 86 and 112 for wild and hatchery-reared one- and two-year old charr, respectively). See material and methods for further explanations. Weight/length=mean weight/length of fish on descent; C.F.=condition factor on descent and ascent; U-weight/U-length= mean weight/length of the different groups of fish on ascent. The numbers of fish are shown in parentheses. Values are means ± SD.

	Weight (gram)	Length (cm)	C.F.	U-weight (gram)	U-length (cm)	C.F.
Wild charr	63.7±42.4^{abc} (211)	20.4±3.7^{abc} (211)	0.68±0.1^{abc} (211)	106.2±65.0^{b} (211)	22.9±4.1^{b} (211)	0.78±0.1^{ab} (211)
One-year old charr	126.8±45.9 (8)	24.0±2.2 (8)	0.88±0.1^{c} (8)	140.5±63.1 (8)	25.1±2.9 (8)	0.83±0.1 (8)
Two-year old charr	166.4±63.2 (41)	26.2±3.0 (41)	0.88±0.1 (41)	171.6±66.5 (41)	26.5±3.0 (41)	0.86±0.1 (41)

Differences significant between; a, wild charr and one-year old charr; b, wild charr and two-year old charr; c, before and after the sea stay for the respective groups.

those of the wild fish. Gill Na-K-ATPase activities of the wild and two-year old hatchery-reared charr were significantly higher than those of the one-year old charr.

As mentioned in materials and methods, growth calculations were only performed on ascending fish where the weight at descent were known (Table 2). The size-frequency histograms (Figs. 3, 4 and 5) showed that fish used in these calculations had a distribution towards a greater size at ascent when compared to weight and length for all fish measured on descent. As seen from Table 2, wild charr achieved the best growth during their sea sojourn, with a mean increase in body weight of 67 percent. One-year old charr had a mean growth of 11 percent, while that for the two-year old charr was 3 percent. The condition factor (C.F.) was significant lower ($P<0.001$, t-test) for wild fish compared to hatchery-reared fish at release. On recapture the C.F. for the wild fish had significantly increased ($P<0.001$, t-test).

The recapture rate of the one-year old charr was significantly lower (13.9 percent, $N=149$) than those recorded for both the wild (23.3 percent, $N=211$) and the two-year old charr (28.8 percent, $N=574$) ($\chi^2=25.1$ and 55.5, respectively, 2 df, $P<0.001$), but there was no significant difference in the recapture rates of the wild and the two-year old charr ($\chi^2=5.6$, 2 df, $P>0.05$).

Out of the total of 60 fish (20 from each group), 2 of the fish from the two-year old charr were sexually mature (stages III) and the sex distributions were 14 males and 6 females, 16 males and 4 females, 11 males and 9 females for wild charr, one-year old charr and two-year old charr, respectively. The degree of sexual maturity of the rest of the fish varied between stages I and II (Dahl 1917).

Discussion

Wild Arctic charr caught in freshwater whilst descending the Halsvassdraget were able to hypo-osmoregulate prior to entry into seawater. This indicates that the development of seawater tolerance was not dependent upon a period of estuarine residence. Similar results have been recorded for wild migratory Arctic charr from the River Å (69°N, 17°E) (Halvorsen et al. 1993) and from the Sila watercourse (66°N, 13°E) (Nilssen et al. submitted) in northern Norway. Only one fish of the hatchery-reared charr died during the seawater exposure and the results showed that they were able to hypo-osmoregulate. The hatchery-reared fish should therefore be fully able to osmoregulate satisfactorily in the fjord system when released.

Both wild charr and two-year old hatchery-reared charr had significantly higher gill Na-K-ATPase activities than did one-year old fish (Table 1). The increase in hypo-osmoregulatory ability of smolting salmonids has been found to be associated with a pronounced increase in gill Na-K-ATPase activity. Na-K-ATPase is the key enzyme in the NaCl extrusion mechanism of the teleost gill in seawater (Payan et al. 1984), and the increase in gill Na-K-ATPase activity during parr-smolt transformation may be a preadaptive mechanism to cope with the increased salt load when the fish enter seawater (Zaugg and McLain 1970; McCormick et al. 1987; Staurnes et al. 1993).

As seen from Table 2 wild charr achieved the greatest increase in body weight during their sea sojourn, while the hatchery-reared charr showed very poor growth. There were no differences in condition factor (C.F.) between one- and two-year old charr at release. Wild charr had a significant lower C.F. than the hatchery-reared fish at descent. The reason for the good growth response for the wild fish is almost certainly a compensatory growth response, while this not seems to be true for the hatchery-reared fish.

The change from artificial to natural food may have affected the growth at sea of the hatchery-reared fish. However, hatchery-reared brown trout (*Salmo trutta* (L.)), appeared to feed on natural prey equally as well as wild brown trout within a week after their release (Johnsen and Ugedal 1986, 1989) and hatchery-reared Atlantic salmon (*Salmo salar* (L.)) showed a preference for wild prey over pellets within 1.5 h (Stradmeyer and Thorpe 1987). If these results can be extrapolated to Arctic charr, the poor growth of the hatchery-reared charr during seawater residence is likely, to be due to other causes.

The recapture of wild fish was 23.3 percent. The size of the hatchery-reared fish at the time of their release was well above that of the wild fish. In spite of this, the hatchery-reared one-year old fish had a lower recapture rate (13.9 percent) than that of the wild fish. The hatchery-reared two-year old fish which was greater than that of the one year old fish when released (Table 2, Figs. 3, 4 and 5), had a recapture rate of 28.8 percent. Previous results have shown that the survival rate in seawater of several salmonid species increases with the size of the fish (Parry 1958; Jackson 1981; McCormick and Naiman 1984; Arnesen et al. 1992). The size of the hatchery-reared one- and two-year old charr in the present experiment was well above that mentioned in these investigations. It was also shown from the size-frequency histograms that the largest fish tended to have a better survival in sea.

Previous results obtained for Atlantic salmon indicate that a connection exists between the age/size of artificially reared smolts and the percent recapture (Peterson 1973; Hansen and Jonsson 1989), with the older and larger smolts showing the best return rates. As shown from the River Imsa, in southern Norway, wild salmon survived more than twice as well as hatchery-reared fish. Thus, the survival of hatchery-reared Atlantic salmon smolts would seem to be lower than that for wild smolts (Jonsson et al. 1991).

The results suggest that despite possessing a hypo-osmoregulatory capacity prior to migration into seawater, only the wild charr had both a satisfactorily growth and survival. Both one- and two-year old charr showed poor growth, but the latter had a recapture rate which was as good as for wild charr. If Arctic charr ranching is to become viable, there is a need for development of production strategies that ensure good growth and high rates of recapture of hatchery-reared fish following their first year in the sea.

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Inter and Intra Cohort Variation in the Life History of Arctic Charr (*Salvelinus alpinus*)

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Abstract

We tested if Arctic charr matured sexually at a specific size or age, or if maturity was correlated to growth rate as a reaction norm. This was studied in a population where fishing was markedly reduced during a four-years period because of radioactive fallout from the Chernobyl accident. Within cohorts, age at maturity was correlated with growth rate. Fast growing males matured at a younger age and smaller size than slow growing individuals throughout the study period. Fast growing females also matured at a younger age than slow growing individuals but size at maturity was similar for early and late maturing females when growth conditions were good. When growth was poor, early maturing individuals were smaller than late maturing ones. Between cohorts, male age at maturity was more variable than female age at maturity. The proportion of early maturing males decreased with decreasing size at maturity, whereas this proportion varied little among females. Sexual maturity thus appears to be more closely related to age among females than males, indicating a genetic component for maturing at a specific age.

Keywords: age at maturity, size at maturity, growth, reaction norm, phenotypic plasticity.

Introduction

Salmonids exhibit plastic life histories (Alm 1959, Jonsson et al. 1984). This plasticity is expressed in most life history traits, but age and size at maturity is of particular interest, because fitness is more sensitive to changes in this trait than to any others (Stearns 1992).

Age and size at maturity of a species may vary due to both environmental and genetic variation. Individuals may be genetically programmed to mature at a given size or age. According to Roff (1982) age appears to be more important than size in species which mature early and size is the most important of the two in late maturing ones. Sexual maturation at a certain size may often be risky because at low growth the animal needs a long time to attain that size and the risk of dying before reaching maturity increases (Stearns 1983, 1992). On the other hand, maturing at a certain age is costly, because natality will be low at low growth rates and a small adult body size. Many species may therefore neither mature at a fixed size nor age (Jonsson et al. 1984, Stearns and Koella 1986, Thorpe 1986, Forseth et al. 1994).

Based on experimental studies with brown trout, Alm (1959) argued that age at maturity is flexible and can be adjusted by variation in growth rate. He found that increased growth rate resulted in reduced age at maturity. In other cases, however, increased growth rate has delayed maturity (Jonsson et al. 1984; Jonsson et al. 1988), indicating that the connection between growth rate and age at maturation is more complex than described by Alm (1959). Stearns and Koella (1986) and Stearns (1992), by describing possible reaction norms (i.e. the description of phenotypic expression of the same genotype in different environments) between age and size at maturity and growth rate, may have solved this dilemma. However, there are few studies on the shape of these reaction norms from the field.

Most studies on optimal age and size at maturity have focused on females because female is the sex constraining natality within populations of most species (Stearns 1992). Within populations, adult females are often relatively large. This is supposed to be because female fitness is strongly size dependent; large females have higher fecundity and often larger eggs than smaller ones (Wootton 1990). Moreover, larger females may be superior in breeding competition because they are able to defend larger and better breeding territories and have more effective nest and egg defence than smaller fish (Fleming and Gross 1992, 1993). Furthermore, in salmonid species burying their eggs in the gravel substratum, one would usually expect selection for a homogeneous female phenotype. In general, large females dig deeper than smaller ones (van den Berghe and Gross 1989). Eggs of very large females may suffer high winter mortality because of lack of oxygen deep in the substratum. Eggs of small females, on the other hand, may be dug up and destroyed by larger females spawning later in the season (van den Berghe and Gross 1989). All in all, there should be strong selection for homogenous, but relatively large body size in females as is often observed (Jonsson 1989, Forseth et al. 1994). Variable female size may indicate spawning at different places (Jonsson and Hindar 1982, Nordeng 1983). Adult males, on the other hand, may be more variable in size due to alternative breeding strategies (Gross 1984).

Here, we examined intra and inter cohort variation in age and size of maturity in an eight year study of Arctic charr in the Norwegian Lake Høysjøen. This lake was contaminated by radiocesium from the Chernobyl fallout in April 1986. Fishing was dramatically reduced during the first four years after the fallout. During that period, the public were recommended not to consume fish from the lake. From 1989, however, fishing has gradually increased to the pre-Chernobyl level. Thus the mortality and growth rate of the fish have varied during the latter 8 years, and variation in life histories was expected. We predicted that within cohorts, age and size at first maturity should decrease with increasing growth rate (Alm 1959). Between cohorts, however, we expected that female size at maturity should vary little due to breeding competition between highly size-overlapping cohorts.

Material and methods

Arctic charr were sampled in Lake Høysjøen, a dys-oligotrophic (Secchi disk transparency: 2.2-3.3 m), dimictic lake (area: 1.0 km^2, maximum depth: 26.5 m) situated 222 m above sea level in central Norway (63°52' N, 11°56' E). The lake is ice-free from mid-May to early November. The lake and its watershed received about 50 kBq m^{-2} of radiocesium (^{134}Cs and ^{137}Cs) from the Chernobyl fall-out, on 28 April 1986. The radiocesium concentration in fish from Høysjøen was high in 1986 (Forseth et al. 1991), but has since decreased. Sports and subsistence fisheries ceased in 1986, and until 1989 the present sampling was the only fishing activity in the lake. Thereafter fisheries increased gradually to the pre-Chernobyl level. The lake supports a dense population of Arctic charr (*Salvelinus alpinus* (L.)) and a smaller population of brown trout (*Salmo trutta* L.) (Forseth et al. 1994).

Fish were sampled with gillnets (panel sizes: 1.5 • 25 m [epibenthic nets] and 6 • 25 m [pelagic nets]; mesh size: 12.5-16-19.5-24-29-35 mm bar mesh) on three to four occasions a year from 1986 to 1993. Each fish was weighed (g), total length (mm) measured, age determined by use of sacculus otoliths (Jonsson 1976), and sex and maturation stage was determined. Due to the uncertainty of maturation stage-determination early in the season, only fishes from sampling periods later than mid July were used. Fish samples from the 1986 and 1987 cohorts could not be included as sample size was too low.

To compare growth-rates between and within cohorts, length at earlier ages for different cohorts was back-calculated by use of otoliths (Jonsson and Stenseth 1977). Back-calculation was done by direct proportion, i. e. Dahl - Lea - method (Francis 1990). This procedure overestimated the lengths at age -1, but the relationship between the groups should not have been altered. Instantaneous yearly growth rates in length were calculated for individual fish according to Ricker (1979). Length at age -0 (first external feeding) was set at 20 mm (Johnson 1980).

Results

Arctic charr growth rates of different age groups varied during the study period (Tables 1 and 2, Fig. 1). Growth were relatively high among individuals of the 1983 to 1985 cohorts. Subsequent cohorts experienced lower growth. Body size at first maturity decreased during the study

Table 1. Back-calculated lengths (mm, ±SE) to the beginning of the second (age -1) and third (age -2) growth season and instantaneous yearly growth rates (G_L) for different cohorts of sexually immature (I) and mature (M) male Arctic charr from Lake Høysjøen. The mean lengths of immature and mature individuals were tested for significant differences with ANOVA: NS = not significant; * *P*<0.05; **:*P*<0.01; *** *P*<0.001.

Cohort	Stage	*N*	Age -1	G_L age 0-1	Age -2	G_L age 1-2
1984	I	21	78.6 (2.64) NS	1.37	134.5 (3.78) NS	0.54
	M	12	80.5 (2.37)	1.39	144.6 (3.00)	0.59
1985	I	78	74.1 (0.97) NS	1.31	130.7 (1.38) ***	0.57
	M	83	76.3 (0.95)	1.34	137.0 (1.22)	0.58
1988	I	16	70.0 (2.09) NS	1.25	121.7 (2.48) NS	0.55
	M	5	65.0 (1.70)	1.17	124.4 (4.87)	0.65
1989	I	61	68.7 (1.01) NS	1.23	113.4 (1.34) NS	0.50
	M	5	72.6 (3.68)	1.29	120.6 (4.37)	0.51
1990	I	64	68.3 (1.01) NS	1.23	116.1 (1.50) *	0.53
	M	7	71.2 (2.25)	1.27	128.2 (4.49)	0.59

Table 2. Back-calculated lengths (mm, ±SE) to the beginning of the second (age -1), third (age -2) and fourth (age -3) growth season and instantaneous yearly growth rates (G_L) for different cohorts of immature (I) and mature (M) age-3 female Arctic charr from Lake Høysjøen. The mean lengths of immature and mature individuals were tested for significant differences with ANOVA: NS = not significant; * = *P*<0.05; ** =*P*<0.01; *** = *P*<0.001.

Cohort	Stage	*N*	Age -1	G_L age 0-1	Age -2	G_L age 1-2	Age -3	G_L age 2-3
1983	I	9	84.0 (4.30) NS	1.43	142.9 (5.31) NS	0.53	183.6 (5.59) NS	0.25
	M	9	86.3 (4.99)	1.46	147.6 (5.41)	0.54	186.7 (5.85)	0.23
1984	I	91	73.1 (1.07) ***	1.30	130.0 (1.51) ***	0.58	168.3 (1.59) ***	0.26
	M	67	80.1 (1.20)	1.39	141.1 (1.48)	0.57	178.4 (1.61)	0.23
1985	I	30	73.6 (1.34) NS	1.30	130.3 (1.68) NS	0.57	166.5 (1.91) NS	0.25
	M	9	77.1 (3.72)	1.35	131.2 (4.54)	0.53	165.1 (4.00)	0.23
1988	I	21	69.4 (1.47) NS	1.24	117.0 (2.29) NS	0.52	147.8 (3.00) NS	0.23
	M	7	63.5 (2.71)	1.16	115.1 (4.34)	0.59	150.7 (2.50)	0.27
1989	I	59	66.9 (1.25) NS	1.21	110.1 (1.46) ***	0.50	145.5 (1.71) **	0.28
	M	21	71.5 (1.77)	1.27	122.2 (2.14)	0.54	157.2 (2.62)	0.25
1990	I	46	65.3 (1.32) NS	1.18	110.6 (1.74) **	0.53	138.7 (1.81) ***	0.23
	M	20	69.2 (2.14)	1.24	120.0 (2.73)	0.55	151.3 (3.19)	0.23

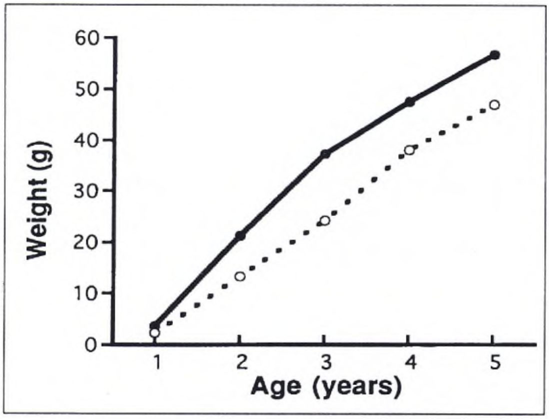

Fig. 1. Growth of Arctic charr from Lake Høysjøen: Body wet weight (g) at different ages in the 1984 (—●—) and 1988 (• ○• •) cohort as examples of growth under good and poor growth conditions.

period (Table 3). Males were sexually mature at age -2 or -3 whilst females matured chiefly at age -3 or -4. In three out of the six cohorts examined, a small fraction (1.3 to 6.7 %) of the females matured at age -2. The proportion of early maturing individuals changed during the study period. A significant positive relationship was found between the proportion (arcsin square root transformed) of mature age -2 males from different cohorts and their body size (mm) at the start of the growth season ($F_{1,4}$=22.4, r^2_{adj}=0.81, P<0.01) (Fig. 2), whereas no such relationship was found among age -3 females ($F_{1,4}$=5.9, r^2_{adj}=0.50, P>0.05).

Early maturing females were generally larger than late maturing ones from age -1 until maturity, and the differences were significant at age -1 to -3 of the 1984 cohort and at age -2 and -3 of the 1989 and 1990 cohorts (Table 2, Fig. 3b). These size differences were established by early maturing individuals experiencing higher growth than later maturing ones. The growth difference was most pronounced during their first year of life. Between females of the 1983 and 1984 cohorts, there was no significant difference in size at maturity between those maturing at age -3 and age -4, whereas early maturing females of the 1985, 1988 and 1989 cohorts were significantly smaller than those maturing one year later (Table 3).

Mature and immature males at age -2 did not differ significantly in mean size during their first year of life (Table 1, Fig. 3a), but during the second year, those maturing at age -2 grew larger. The size differences at age -2 were significant in the 1985 and 1990 cohorts only. The individuals of all cohorts that matured at age -2 were significantly smaller than those that matured at age -3 one year later (Table 3, Fig. 3a).

Table 3. Back-calculated lengths (mm, ±SE) to the beginning of the third (age -2), fourth (age -3) and fifth (age -4) growth season for male and female mature Arctic charr from Lake Høysjøen. The mean lengths at maturity for early and late maturing individuals were tested for significant differences with ANOVA: NS = not significant; * = P<0.05; ** = P<0.01; *** = P<0.001. The mean lengths of early maturing individuals from different cohorts were tested for significant differences (ANOVA, Scheffe's multiple-range tests): Mean in each column followed by different superscript letters are significantly different (P<0.05)

Cohort	Sex	*N*	Age -2	*N*	Age -3	*N*	Age -4
1983	female			9	186.7 (5.85)^{a}	41	193.6 (2.42) NS
1984	female			67	178.4 (1.61)^{ab}	25	184.0 (2.81) NS
1985	female			9	165.1 (4.00)^{bc}	32	177.8 (1.50) ***
1988	female			7	150.7 (2.50)^{c}	19	174.4 (2.97) ***
1989	female			21	157.2 (2.62)^{c}	29	170.0 (1.98) ***
1984	male	13	144.6 (3.00)^{a}	118	166.0 (1.22) ***		
1985	male	83	137.0 (1.21)^{ab}	26	162.4 (2.05) ***		
1988	male	5	124.4 (4.86)^{bc}	9	149.8 (4.06) **		
1989	male	5	120.6 (4.37)^{c}	46	146.9 (2.08) ***		
1990	male	7	128.2 (4.49)^{bc}	48	140.8 (1.55) **		

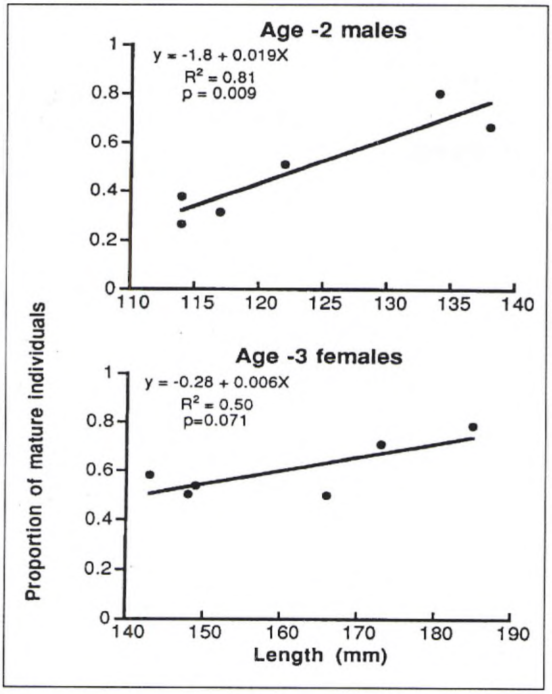

Fig. 2. The proportion (arcsin square root transformed) of early maturing (age -2 males and age -3 females) at different lengths of Arctic charr from different cohorts in Lake Høysjøen and their body size (mm). Lines represent linear regressions.

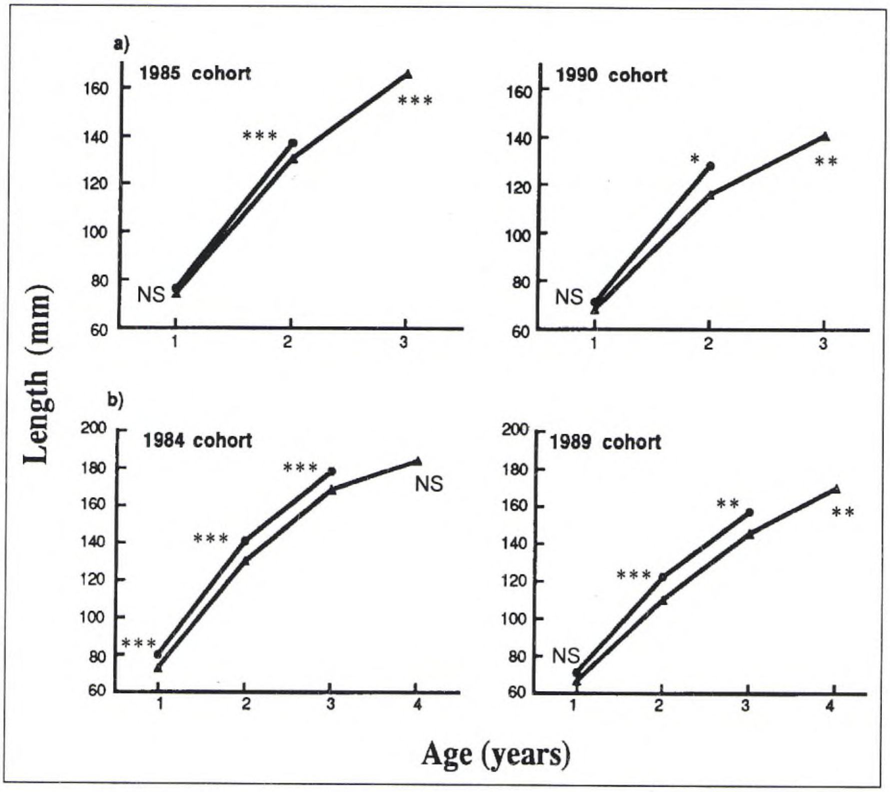

Fig. 3. Back-calculated length (mm) for early [●] (males age -2, females age -3) and late [▲] (males age -3, females age -4) maturing Arctic charr under good and poor growth conditions in Lake Høysjøen, exemplified by **a)** males of the 1985 and 1990 cohorts and **b)** females of the 1984 and 1989 cohorts. Asterisks denotes significant size differences between early and late maturing individuals (above lines) and significant differences in size at maturity (below lines) NS: $P>0.05$, $*=P<0.05$, $**=P<0.01$, $***=P<0.001$.

Discussion

Age and size at maturity in Arctic charr is flexible and closely related to growth rates. In Høysjøen, the youngest females attained maturity at age -3. These females were among the largest in their age-group, and they had higher growth rates than those maturing at an older age during the first growing season.

During the early years of this study (when growth conditions were relatively good), early and late maturing females did not differ in size at maturity. One might therefore assume that the females matured at a certain body size, and that individuals reached that body size at different ages depending on their growth rates. In a previous study of the Lake Høysjøen charr, Forseth et al. (1994) estimated optimal (i. e. the size where energy surplus is largest and relative fecundity is maximised) and maximal size at maturity for the 1984 and 1985 cohorts based on energy intake at different ages. Females matured at a body size twice the optimal size but close to the maximal size under the given conditions. By doing so, females maximise fecundity and increase competitive ability (Magurran 1986, Wootton 1990, Fleming and Gross 1992, 1993).

When growth was poor due to reduced fishing mortality, however, early maturing females became smaller at maturity than late maturing ones (Fig. 4), and the assumption of maturity at a certain body size is therefore not correct. On the other hand, the proportion of each cohort that matured early changed little when growth rates decreased, indicating that maturity in females is influenced by the age of the fish. This finding is contrary to experimental evidence from stream spawning brown trout where female age at maturity was more highly influenced by growth rate (and density) differences than males (Jonsson 1989).

The youngest maturing males were, as for the females, among the largest in their age-group. Moreover, those maturing early (age -2) were smaller at maturity than those maturing one year later. Some Arctic charr males matured at a low weight close to the optimal, whereas others matured at double the weight (Forseth et al. 1994). The reason may be that the reproductive success for males is less dependent upon their size, and smaller individuals may adopt alternative strategies such as sneaking (Gross 1984, Sigurjónsdóttir and Gunnarsson 1989; see Introduction). However, we do not know whether or not maturation at optimal size is a strategy or due to chance.

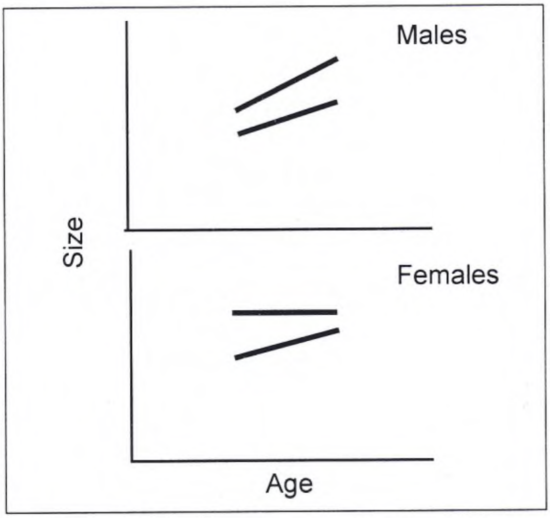

Fig. 4. Relationship between age and size at maturity under good (upper lines) and poor (lower lines) growth conditions illustrated by within cohort reaction norms.

In contrast to females, the relationship between growth and male age and size at maturity did not change across cohorts although growth rates varied considerably (Fig. 4). However, the proportion of mature age -2 males decreased in cohorts where individuals were smaller. Thus, age and size alone did not determine when maturity should occur. The process of maturation seemed also to be highly influenced by growth rate.

The proximate mechanism controlling maturation in fishes may be related to metabolic rate (Metcalfe et al. 1992, Forseth et al. 1994). Studies on otolith micro structures have indicated that a fast growing fish experiences elevated metabolic rates in the embryonic period (Mosegaard et al. 1988, Metcalfe et al. 1992). Fish with high metabolic levels may have an advantage in aggressive encounters (Titus 1990, Titus and Mosegaard 1991, Metcalfe et al. 1992) and tend to be more efficient in converting the food intake into somatic growth (Metcalfe 1986, Abbott and Dill 1989).

What is the energetic consequence for fish having an elevated metabolic level? The energetic needs will increase because of increased maintenance costs. Consequently, these fish require higher food intake to maintain their body mass. When food supply is limited, fish with the largest demands for food are the first to experience a food shortage, and exhibit an inflexion in their growth rate. Furthermore, if the higher metabolism is retained as the fish grow, the relative advantage may diminish or vanish. Fast growers may thus be the first fishes that need to exhibit actions such as a shift niche, or attain sexual maturity (Jonsson and Jonsson 1993, Forseth et al. 1994).

For Arctic charr in Lake Høysjøen, a high metabolic level in early maturing female charr may primarily be advantageous during the first growth season when they have higher growth than later maturing individuals. Although the growth advantage acquired by the early, fast growing fish lasts for one year only, the others (later maturing ones) are unable to catch up in size with the early maturing charr during the juvenile period. The early maturing individuals seem to respond to the decreasing growth advantage by sexual maturation at age -2 (males) and age -3 (females).

Studies on Atlantic salmon (Metcalfe et al. 1989, Metcalfe 1991, Metcalfe et al. 1992), brown trout (Titus and Mosegaard 1991) and Arctic charr (Forseth et al. 1994, this study) now indicate that life-history patterns such as the age at sexual maturity and time of ontogenetic niche shifts, can be determined by early metabolic rate and growth rates in salmonids. At present, however, it is not known to what extent the early metabolic rate is a plastic response and to what extent it is determined by heredity. Allendorf et al. (1983) found a phosphoglucomutase locus (Pgm-1) in the liver of rainbow trout (*Oncorhynchus mykiss*) that correlated with pronounced phenotypic effects. Rainbow trout with liver Pgm-1 expression hatched earlier, grew better during early life and matured younger than those without liver Pgm-1 expression. Allendorf et al. (1983) maintained that the relative success of rainbow trout with and without liver Pgm-1 depended on environmental conditions at the time of hatching. One might expect that similar genetic polymorphism could explain the presence of fish with inherited high or low metabolic rate in Arctic charr and brown trout (cf. Jonsson 1985).

All in all, the present studys show that age and size at maturity in both sexes is flexible and related to the growth rate of the fish. Within cohorts, age and size at maturity decreased with increasing growth rates during the first year of life. This pattern can be recognised as a within cohort reaction norm for age and size at maturity with a positive slope (Fig. 4) assuming that the differences are predominantly phenotypic. Between cohorts, size at maturity decreased with decreasing cohort growth rate. However, the possibility of genotypic variability rather than phenotypic plasticity as an explanation for the observed variation in age and size at maturity could not be ruled out by the present study. Different genotypes for age and size at maturity which differ in fitness under different growth conditions may also explain the observation. Indeed in females, more than in males, maturity was influenced by the age of the fish, indicating a genetic component for maturing at a certain age.

Acknowledgments

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Arctic Charr, *Salvelinus alpinus*, of Lake Annecy: Yield, Growth and Parasitism by *Eubothrium salvelini*

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Abstract

Arctic charr were introduced into Lake Annecy over a century ago and now constitute an important part of the fishery, comprising 25% of the total yield of sport and commercial fisheries in lake. Fishermen demand greater production. The latter is important compared to other lakes. Growth is rapid and it is thought that the total yield should be higher. The efficiency of stocking is lower than in other lakes. Parasitic infection by *Eubothrium salvelini* is thought to reduce the efficiency of stocking with juveniles.

Keywords: Charr, growth, parasitism, *Eubothrium salvelinin*, fishery management.

Introduction

The practice of stocking lakes with Arctic charr juveniles has been used for numerous years in the French and Swiss Alps (Dussart 1954). Recently, the techniques for producing 0+ juveniles were refined to reduce the production costs and allow an increase in the efficiency of stocking. In lake Annecy, the number of juveniles released per hectare of lake is comparatively high. However, the actual charr catch does not satisfy fishermen who demand more intensive stocking. A comparison of actual fish yield with other peri-alpine French and Swiss lakes, places Annecy among the most productive lakes of the region. There are numerous data on Arctic charr growth from lakes in similar geographic regions (Rubin, 1993, Ruhlé 1991). A comparison of these growth curves would show if the population of Lake Annecy presents a satisfactory growth rate which does not translate into an over-population of the lake. If the carrying capacity of the environment is not exceeded, an improvement in production could be envisaged. Nevertheless, the efficiency of stocking is not as good as in Lake Leman (Champigneulle and Gerdeaux, 1993, 1995). The study of Arctic Charr in Lake Annecy has brought to light a high rate of parasitic infection by *Eubothrium salvelini.* As this parasite is passed to the fish by the primary host, a copepod and as the juveniles used for stocking lake Annecy are fed with live plankton, the parasitic infection has been examined to see if this could explain the poor returns of stocking.

In this paper we compare fish yield in lake Annecy with other French and Swiss peri-alpine lakes. We provide information on the Arctic charr stocking program and describe growth of the charr. Data on infections of the cestode *Eubothrium salvelini* are presented together with the results of experiment on the effects of the parasite on growth of cage cultured juveniles.

Materials and methods

Description of Lake Annecy

Lake Annecy has a surface area of 2,800 hectares. It is a lake of glacial origin, with steep banks and a relatively flat bottom at 65 m depth. It has a length of 15 km with a maximum width of 4 km. The lake has benefited from early measures to protect the quality of its water and has always been classed as an oligo-mesotrophic lake. The level of total phosphorus has never exceeded 10 μg l^{-1}.

The initial fish population was poor in terms of the numbers of species. Natural obstacles impeded the colonization of the lake by species which are found in Lakes Leman and Bourget, both situated in the hydrographic basin of the Rhone. At the end of the last century, Arctic charr and coregonids were introduced. The coregonid population is maintained without stocking whereas the Arctic charr was constantly stocked because of the lack of appropriate spawning sites. The present hatchery is close to a pumping station which filters drinking water. Live plankton collected from the filtration process goes directly to the pisciculture site to feed the Arctic charr.

The Fishery and The Stocking Program

Both a professional gill net fishery and an amateur sport fishery co-exist on Lake Annecy. Total data are available from 1948 and since 1974 statistics for each type of fishery are archived separately. The capture of Arctic charr is primarily (90%) by the sport fishermen, and the management of the charr fishery was conceived to give them priority access to this species.

Charr rearing occurs in culture facilities receiving water pumped from a lake depth of approximately 16 m, just beneath the thermocline. Pumped water becames too warm in summer and so the release of the juveniles occurs by mid-July. The juveniles measure 6-9 cm total length.

Growth of Arctic Charr

The study of Arctic charr growth was done using scales, on the one hand by determination of age and therefore length at the end of the growth season for each cohort, and on the other hand by back-calculation of length for each fish. Scales were removed from the dorsal area, between the posterior part of the dorsal fin and the lateral line. The scales were read after cleaning with azote peroxide, using a microscope equipped with a video camera. After image processing by a computer, growth check measurements were taken by cursor and back-calculated lengths determined by a linear model ($Y=aX+b$). For each fish, three scales were read successively. The software calculated the variance between the three measures. Additional readings were made if the variation between the first three measures exceeded a threshold fixed by the operator. Scales were taken from breeding fish in December of each year. To follow the seasonal patterns of growth, sports fishermen collected scales from fish caught during February to September 1993. Data collected from fish previously marked as juveniles and released in July 1988 allowed the validation of the age readings and showed the position of the growth checks.

Catches of spawning fish were made in 1986, 1988, 1990, 1991, 1992 1993. Age determination of these fish allows the allocation of the fish to the year of their birth with a knowledge of their size at the end of the growth year, from 3-6 years. Sexes were not separated for two reasons: the size difference is weak considering the variation between individuals of the same sex and the proportion of females is always low, and the data published for charr rarely distingishes between the sexes. Rubin (1993), working on Lake Leman charr, separated the sexes and found on average 0.5 cm difference in growth each year between males and females.

Parasites

Arctic charr were immediately dissected after capture by net in December 1993 on the spawning grounds. The stomach and digestive tract were examined. The numbers of parasites were indicated using a scale of 0-3: 0 if there were no parasites, 1 if the parasites numbered less than five, 2 if the parasites were more numerous, 3 if the abundance was such that the posterior part of the stomach and caeca were completely filled by parasites, causing stomach wall ulcerations. A sample of charr juveniles was dissected before the release programme to the lake in July 1993 to estimate the prevalence of parasites in this life-stage.

Results

Arctic charr yield and stocking efficiency

Over the past 20 years, annual charr catches have fluctuated from 2.5 tonnes to nearly 8 tonnes (Fig. 1). Over these 20 years, fish production averaged 1.6 kg ha^{-1} and fell below 1kg ha^{-1} only once. Compared to other peri-alpine lakes, the charr production of Lake Annecy is one of the highest (Table 1). This table is given for the period 1981-86. The yield for Arctic charr in Lake Geneva was improved by an intensive stocking. It is actually 1.1 kg ha^{-1} during the last 5 years.

On average, 200,000 juveniles were released annually during this period. Results should reveal on average 6-10 juveniles released for one fish of catchable size (Champigneulle and Gerdeaux 1993). Assuming that all charr are produced as a result of stocking, the efficiency

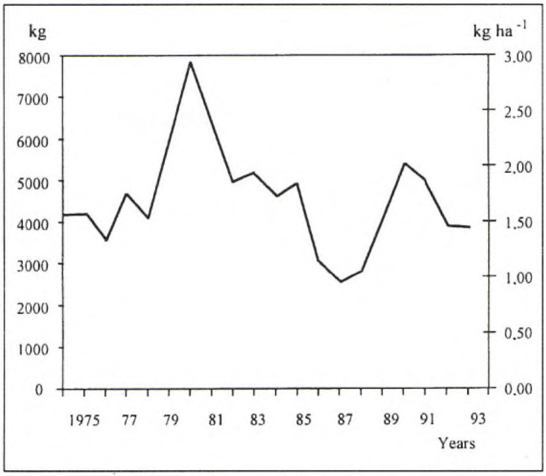

Fig. 1. Annual records of Arctic charr catches in Lake Annecy.

Table 1. Yields (kg ha^{-1}) of different fish species in Swiss and French peri-alpine lakes (Muller 1988, for Swiss lakes; own data for the French Lakes Annecy, Bourget, Leman). Lake surface areas in hectares. Level of eutrophication indicated as *=oligotrophic, **=mesotrophic, ***=eutrophic.

Lake	Surface	Coregone	Charr	Trout	Pike	Perch	Cyprin.
Neuchatel **	21,581	6.7	0.12	0.40	0.30	6.30	10.20
Constance **	17,144	13.3	0.02	0.10	0.30	0.16	4.20
Lucerne **	11,380	23.3	1.85	0.20	0.40	0.01	6.20
Zurich ***	8,852	9.6	0.04	0.30	0.90	6.90	14.06
Thun ***	4,780	8.6	0.25	0.00	0.10	0.10	0.10
Majeur **	4,230	27.6	0.02	0.70	2.90	0.03	5.80
Biel **	3,920	13.3	0.00	0.10	0.80	3.30	11.90
Zug ***	3,830	5.5	0.70	0.10	0.40	0.03	17.40
Lugano ***	3,070	0.0	0.00	0.50	0.10	1.90	7.30
Brienz **	2,918	9.8	0.05	0.10	0.00	0.00	0.10
Walenstadt *	2,423	12.6	0.50	0.50	0.40	1.80	1.20
Murten ***	2,282	0.7	0.00	0.40	1.30	4.60	19.40
Sempach ***	1,450	39.7	0.02	0.10	1.60	3.90	8.00
Hallwill ***	1,020	16.3	0.00	0.00	0.10	1.40	1.40
Joux ***	953	13.9	0.00	0.01	2.80	1.90	2.30
Sarnen *	764	19.3	0.00	0.10	1.10	1.60	10.40
Annecy *	2,800	4.2	1.77	0.30	1.10	0.80	1.20
Bourget ***	4,500	0.1	0.05	0.60	0.40	7.90	7.30
Leman **	58,000	0.7	0.13	0.40	0.10	5.20	4.20

Table 2. Total length (mm) at different ages (3-6) for Arctic charr caught during spawning times in 1986-93. Number of fish examined in parenthesis.

Age	1986	1988	1990	1991	1992	1993
3	278 (44)		290 (53)	282 (25)	277 (12)	
4	331 (64)	309 (28)	336 (77)	334 (99)	319 (86)	317 (27)
5		387 (10)	366 (35)	399 (35)	363 (48)	342 (42)
6					402 (16)	383 (18)

is on average 1 fish caught to 13 juveniles released. However, fisheries statistics show average charr caught to be c. 300g with c. 15,000 fish caught per year.

Growth of Arctic charr in Lake Annecy

Inter-annual variations of the calculated averages for spawning charr captured between 1986 and 1993 were within 3 cm for the same age group (Table 2). Overall average lengths are 283, 319, 367 and 392 mm from the third to the sixth year respectively. The inter-annual differences are of little significance when compared to the variation between the individuals (Fig. 2), which increase with the fish age from the fourth year. The variation can exceed 10 cm. On the other hand, confidence limits remain of the same order.

Small fish in their first two years of growth were not captured and length estimates were determined by back-calculation. These estimates were made using three samples of fish (Table 3, Fig 2). The back-calculations provide results where the Lee-phenomenon is pronounced, due to rapidly growing young fish caught in 52 mm gillnets in December and or at the legal size of 26 cm by sports fishermen. Excluding the figures obtained from fish caught at age 2 or age 3, back-calculated fish length at the end of the first year was on average 103 mm, at the end of the second year 193 mm The estimated length at one year is close to the length of the juveniles released each year. For ages 3 to 5, the average lengths were 269 mm, 309 and 354 mm. These latter results are comparable to those for spawning fish, and equally coincide with the measure-

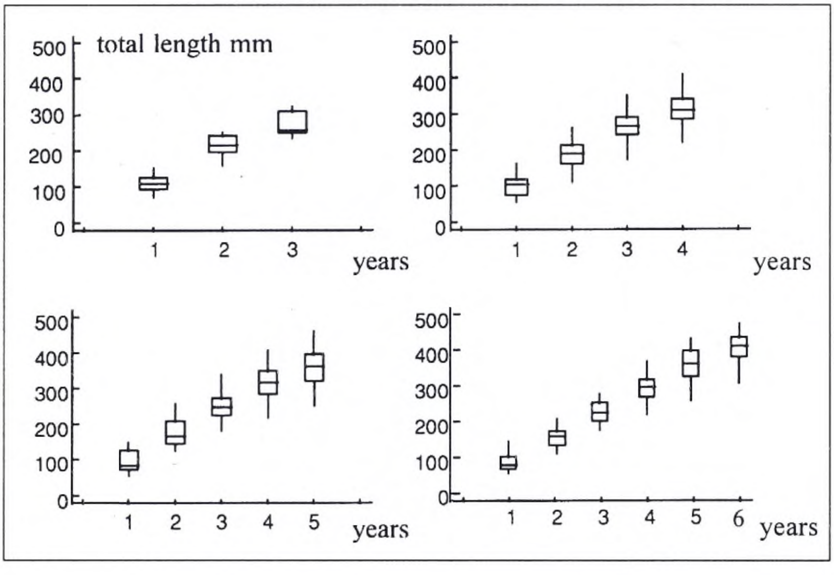

Fig. 2. Results of the back-calculations of length for the Arctic charr caught during spawning time in December 1992 in Lake Annecy. A box-plot is made for each generation between 3-6 years.

Table 3. Results of back-calculation for length of Arctic charr in Lake Annecy. The lengths at time of capture are not given during 1993, because the catches occur during the growth season, not at the end of the season as in December.

Time of sampling	Generation	Number of fish	Length in mm at					Time of capture
			age 1	age 2	age 3	age 4	age 5	
Dec 1992	1987	16	86	155	225	292	355	402
	1988	48	97	176	251	318		363
	1989	87	100	187	270			318
	1990	22	110	216				277
during 1993	1988	11	96	178	248	312	360	
	1989	44	105	187	260	311		
	1990	108	116	217	299			
	1991	30	129	231				
Dec 1993	1988	15	86	152	231	296	348	383
	1989	36	83	161	246	309		342
	1990	36	93	185	275			317
	1991	5	108	207				254

ments for juveniles marked in 1988 and subsequently recaptured (on average 281, 315, 354 and 368 mm from 3-6 years respectively). There were no apparent differences between the rates of the growth in successive generations.

Seasonality of growth

Renewed growth was not visible on the scales until May. Peripheral growth of the scale during the growth season gave an indication of average growth during the fishing season (Fig 3). From April to October, growth is regular. In the spring, charr fed primarily on chironomid larvae and nymphs and switch to young fish of the year later in the season (Van Overmeire, unpub). There was always sufficient food in the lake for charr. This is not necessarily the case for coregonids which show reduced summer growth (Gerdeaux, unpub).

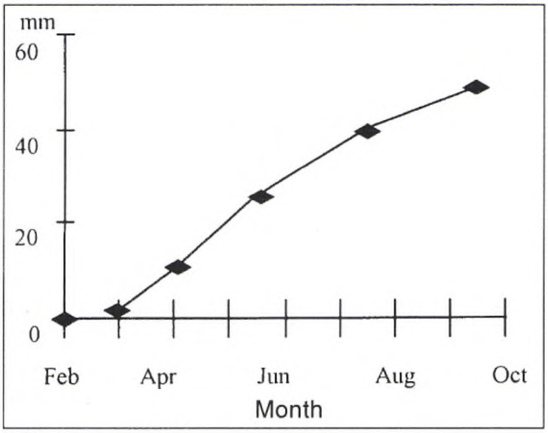

Fig. 3. Cumulative monthly increase of length for the Arctic charr caught during the year 1993. Each point represents the mean for at least 35 fish.

Parasites

Only 6 out 53 adults sampled in December 1993, (11%), did not carry parasites (Table 4). On the other hand, more than a third of individual fish were severely infected. There was no statistical relationship between the length of fish and the parasitic index (P=0.99), nor between the condition factor and parasitic index (P=0.99). There was a weak positive correlation between age and parasitic index (r=0.44) although the sample was small (N=32). Among the female fish, who were on average older, the incidence of parasitism was greater than in males (Table 4). It is difficult to establish if the weak correlation between parasitic index and age is due to inter-annual variations in infection or if fish accumulate parasites with time.

Table 4. Percentages of the parasitic index of *Eubothrium salvelini* in male and female caught in December 1993 in Lake Annecy.

Parasitic index	0	1	2	3	Total
Male	16	26	39	19	31
Female	5	18	18	59	22

Among 200 juveniles examined shortly before release in July, the rate of parasitic infection was already substantial (Fig 4). Of those reared solely on plankton 59% were infected by *Eubothrium salvelini*. Whereas only 42% of fish fed partially on dry feed were infected. The lengths of plankton fed fish with more than 10 parasites were shorter than average. However, there was no correlation between the numbers of parasites and the length of the fish (P=0.999).

Discussion

Lake Annecy is a meso-oligotrophic lake favourable to the development of species such as charr and coregonids. The introduction of these two species proved to be a good choice as they now constitute the main components of the fishery. Fish yields for both species are good, and are higher than yields from comparative peri-alpine lakes. Only in Lake Lucerne, Switzerland, is a higher yield obtained. However, this situation has not satisfied the sports fishermen who demand an increase in the effort of stocking.

The growth curves for Annecy charr are similar to those of the charr in Lake Constance which Ruhlé (1991) compares to those of Lake Lucerne (Fig. 5). A charr of Lake Lucerne attains a length of 25 cm only at the end of its third year whereas the charr of Lake Constance and Annecy attain this length at the start of their third year. The rate of growth of Annecy charr is close to that determined by Rubin (1990) for Lake Geneva charr where the growth curve is linear between the age of 1-6 years. For the first three years of growth, the fish lengths reached in Lake Leman are similar to those of Lake Annecy and Lake Constance, but growth is slower in the fourth year. Such results imply that the charr population of Lake Annecy has sufficient nourishment. This is confirmed by the regular increase in length during the growth season.

A priori, it may be thought that stocking would result in an increase in fish captured. The actual effort is on average 36 juveniles 0+ per hectare of lake. In Lake Leman, the effort is 21 individuals per hectare (Champigneulle and Gerdeaux 1993). These figures are already high and the returns from increased stocking is uncertain. Despite this, the numbers of fish caught are less than could be hoped for compared to Lake Leman, for example.

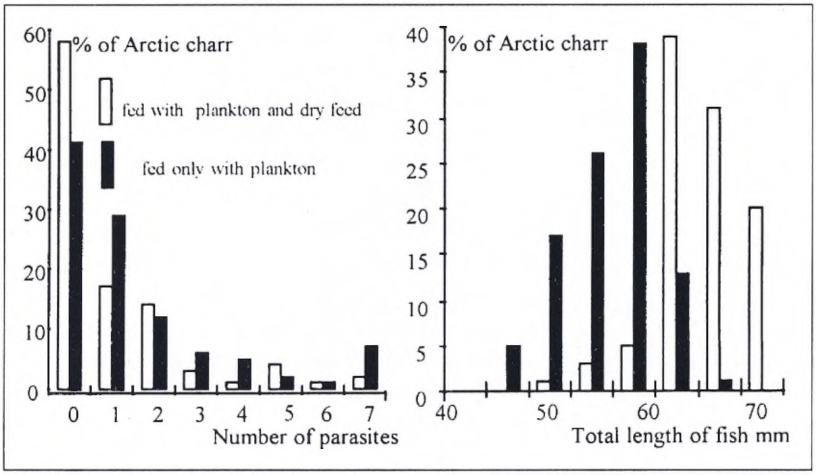

Fig. 4. Frequency distributions of parasites in 100 juvenile Arctic charr fed with living plankton exclusively, and 100 others fed partially with plankton; and, frequency distributions of the total length of these fish.

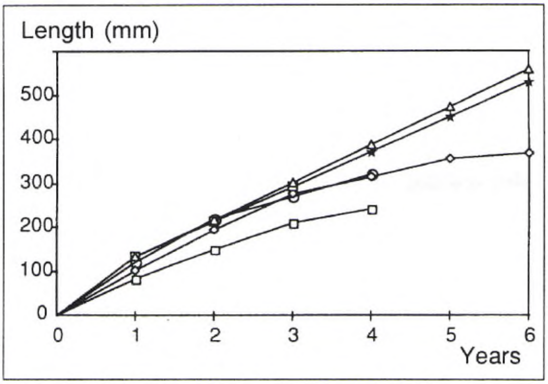

Fig. 5. Growth curves for Arctic charr from Lake Annecy (square), from Lake Geneva (star for male, triangle for female, (Rubin, 1993)), from Lake Constance (circle) and Lake Lucerne (square; Ruhlé, 1991).

In 1988, a high mortality of juveniles occured in the hatchery, due to a heavy infection by *Eubothrium salvelini*. In most years growth of young fed on zooplankton was very good, but the parasite could cause high mortality once the juveniles are released. The parasitism of *Eubothrium salvelini* on sockeye juveniles has a deleterious effect on the growth, survival and swimming performance of the fish (Boyce 1979, Smith 1973). It is also demonstrated that susceptibility of fry of this species to infection diminishes as they exceed a certain size (Boyce 1974). For the atlantic salmon, there is a loss of potential growth in farmed salmon with persistent low-grade infection of *Eubothrium salvelini* (Bristow and Berland 1991). If these results could be applied to arctic charr, the suggestion of feeding with dry-feed could be an easy solution to diminish the rate of infection and in this way to improve the rate of recapture of the fish. Feeding with dry-feed could be an easy solution. This does not satisfy the fishermen who lose the original aspect of their hatchery and increase their expenditure. The study of the seasonality of the *Eubothrium salvelini* may provide some answers. If the zooplankton is not a carrier of the parasite at the start of the season, it could be used at the start of the feeding. Our preliminary studies of adult parasites in winter showed that they have not reached maturity. On the other hand, juveniles fed live plankton are already parasitized in the month of April. It is therefore necessary to observe the annual dynamics of the parasite in order to define the period in which charr juveniles may be fed live plankton.

Acknowledgments

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Egg Development in Hatchery-Reared Arctic Charr (*Salvelinus alpinus*)

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Abstract

Ovaries in Arctic charr broodstock of Lake Geneva strain started to develop in May. Eighty per cent of the increase in oocyte weight occurred from September to December and the relative fecundity of female decreased from the beginning to the end of vitellogenesis. The relationship between body growth and egg weight and fecundity was investigated at different stages of the vitellogenesis. The influence of Arctic charr growth on egg weight and fecundity varied with the stage of ovarian development. Relative fecundity and GSI were positively correlated with growth from April to August (i.e. during the beginning of vitellogenesis) and relative fecundity was negatively correlated with growth from the end of summer to spawning (i.e. during late vitellogenesis). Egg weight was positively correlated with growth from the end of summer to spawning. No significant correlation could be detected neither between egg weight and growth from April to August nor between GSI and growth from the end August to spawning. It is possible to extend the spawning period of Arctic charr by changing the photoperiod. When the spawning period lasted for 4 months or more, mean egg weight increased from the beginning to the end of the spawning period.

Keywords: Reproduction, fecundity, egg weight, gonadal weight, photoperiod.

Introduction

In Arctic charr (*Salvelinus alpinus*), egg size and egg number vary widely between the different populations (Johnson 1980). The present study investigates the relationship between individual growth during the vitellogenesis and egg weight, egg number and gonadal weight in Arctic charr broodfish. The duration of vitellogenesis was also shortened or lengthened by photoperiod manipulations and the consequences on egg weight were examined.

Materials and Methods

In this study, hatchery-reared Arctic charr from the Lake Geneva stock were used. The fish were reared at the Institut national de la recherche agronomique station in Thonon. During the rearing the fish were kept in 4 or 12 m^3 tanks supplied with water pumped from a depth of 36 m in Lake Geneva. In the tanks, the water temperature fluctuated between 5.5°C and 11°C. The fish were fed with dry pellets: trout commercial food, Trouvit, 48% protein, 18% lipid (12% in 1989) distributed during 8 h per day by automatic feeders. They were fed at a ration recommended for rainbow trout.

To measure the increase in gonadosomatic index, total body weight (0.1g) and gonad weight of 20 2-year-old fish were measured monthly between April and December 1989. Gonadosomatic index (GSI) was calculated as: 100 (ovary weight)/total body weight. To determine the mean egg weight and the number of eggs per female, 50 eggs from each female were weighed to the nearest mg, from July to December.

Each month (April, June, July, August, September, November and December), blood samples were taken in 7 females from a caudal vessel with an heparinized syringe and centrifuged for 15 min at 2,000 g. The plasma was frozen until determination of plasma total calcium by flame atomic absorption spectrometry. This parameter is closely related to plasma vitellogenin levels (Nagler et al. 1987). Kruskal-Wallis tests were used to determine significant differences among the monthly samples (GSI, egg weight, egg number and plasma calcium) (Ley 1992).

To measure individual growth, in relation to GSI, relative fecundity and egg weight, 3-year-old females (20 fish), which had spawned during the winter 1991-92, were individually tagged with visible implant tags (Northwest marine technology) injected behind the eye. The fish were weighed to the nearest 0.1 g firstly when they were tagged in April, secondly on 25 August 1992 and thirdly when each female was ripe (ovulated) in winter 1992-93. Individual growth was expressed as: 100(final weight - initial weight)/(initial weight) *N*. *N* is the number of days between two weighings and weight is the total body weight. Growth was estimated from April to 25 August and from 25 August to individual spawning time (December-January).

During the spawning period in winter 1992-93, tagged females were regularly examined twice a week to detect ovulation. Each ovulated female was anaesthetized in 2-phenoxyethanol (0.3 ml L^{-1}) and weighed and the eggs were collected. Ovarian fluid was removed and the eggs were weighed to the nearest 0.1 g. About 50 ova of each female were weighed to the nearest 0.1 mg. Relative fecundity expressed as: number of eggs/body weight (g) was calculated for each female. Correlations were calculated between individual growth (April-25 August and 25 August-spawning time) and GSI, mean egg weight and relative fecundity.

To test the effect of different photoperiods on egg weight, the fish were exposed to different light regimes provided by 60 w, 24 v bulbs controlled by a time switch. Short day experiments were carried out in a tank with a black butyl cover. Different treatments were tested to advanced and to delay spawning in order to extend the spawning period of Arctic charr from fall to spring. Immature fish were subjected to constant long days to induce early sexual development at different seasons. Twenty month old immature fish (50 fish) were subjected to 17h of light and 7h of dark per day (17h L:7h D) from the beginning of October 1988 to 10 May 1989. Afterwards they were kept in refrigerated water at 5°C under a 7h L:17h D light cycle. Fourteen month old immature fish (50 fish) were subjected to a 17h L:7h D light regime from the beginning of April 1990 until spawning time. During the summer 1991 (June-September), fish were kept in refrigerated water to prevent an inhibition of ovulation by warm temperature (Gillet 1991). Three year-old females (190 fish) which have spawned during the winter 1991-92 were randomly allocated into 3 groups: (1) The fish were subjected to a long day treatment (17h L:7h D) in spring followed by a short day treatment (7h L:17h D) from the beginning of summer until spawning time to advance spawning time. (2) The fish were reared in natural day length. (3) The fish were subjected to a long day treatment (17h L:7h D) in fall to delay spawning. Females were examined once a week to detect ovulation and egg mean weight were determined. Day 1 was when the first female was ovulated. During the experiments, furonculosis and fungus disease induced some mortality (always lesser than 20%).

Results

The mean GSI increased ($P<0.001$) during the study period (April to November), but the increase was the highest between August and November ($P<0.01$). From April to July the mean GSI was between 0.68 and 1.68%, and from August to November between 5.5 and 20.0% (Fig 1). The range of variability in the two periods were 35-57% and 11-70% respectively. The development of ovaries was completed in November. The mean egg weight increased 10 times during fall ($P<0.001$), from 5 mg in July to approximately 50 mg in December (range of vari-

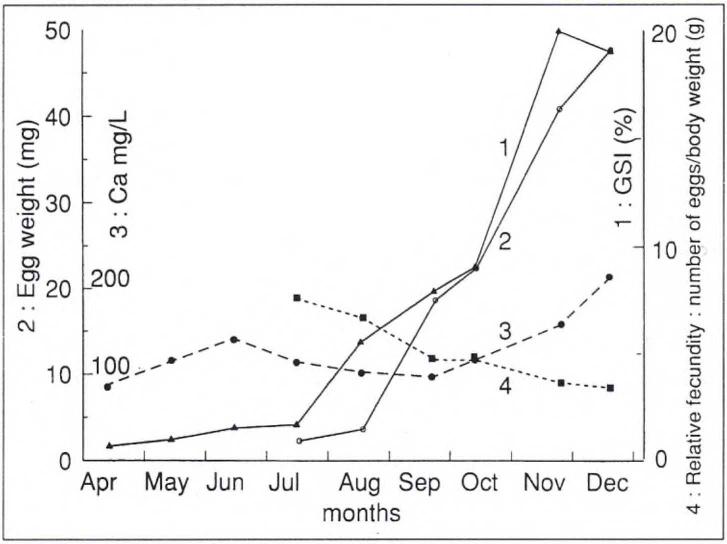

Fig. 1. Gonadosomatic index (GSI) (curve 1), mean egg weight (curve 2), plasma calcium in blood (curve 3) and relative fecundity (curve 4) of hatchery reared Arctic charr from April to December.

ability: 17-78%). The mean number of developed eggs per g of body weight decreased ($P<0.001$) from 7 in July to 3.7 in December (range of variability: 24-38%). Plasma calcium level increased ($P<0.01$) from 96 mg L^{-1} in April to 203 mg L^{-1} in December (range of variability 5-44%). From April to August, plasma calcium level did not increase significantly but it increased ($P<0.05$) between September and November (Fig 1).

GSI ($P<0.05$, $r=0.65$, df 11) and number of eggs per body weight ($P<0.01$, $r=0.73$, df 11) increased with female growth from April to August. However there was no significant relationship between mean egg weight and individual growth during the same period ($P>0.05$, $r=-0.23$, df 11) (Fig 2). Mean egg weight increased ($P<0.01$, $r=0.71$, df 12) and number of egg per body weight decreased ($P<0.05$, $r=-0.51$, df 12) with female growth from 25 August to individual spawning time (Fig 3). No significant correlation was found. (1) Between GSI and female growth during the same period ($P>0.05$, $r=-0.20$, df 12). (2) Between female weight and relative fecundity ($P>0.05$, $r=-0.22$, df 12). (3) Between female weight and mean egg weight ($P>0.05$, $r=0.03$, df 12).

Twenty month old immature fish subjected to long days from October 1989 started to ovulated 8 months after the beginning of the long day

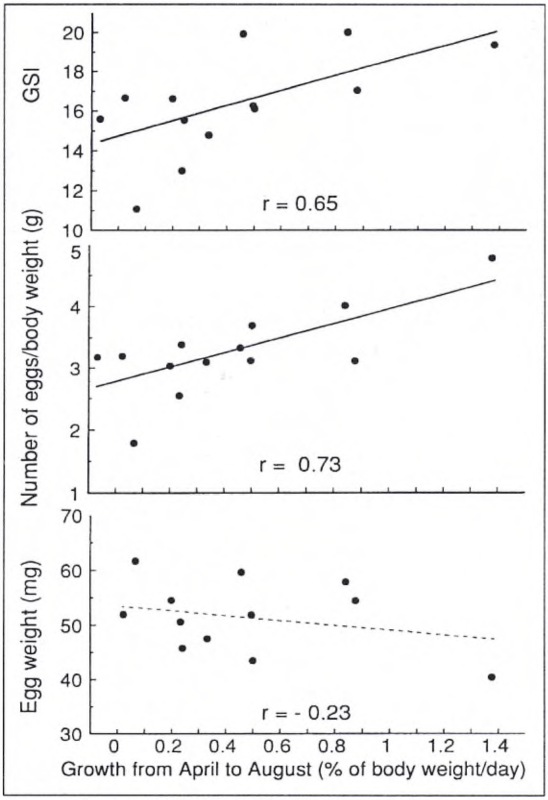

Fig. 2. Correlation between individual growth of females and GSI (top), relative fecundity (middle) and mean egg weight (bottom) during the beginning of vitellogenesis (April to 25 August). 13 females were used.

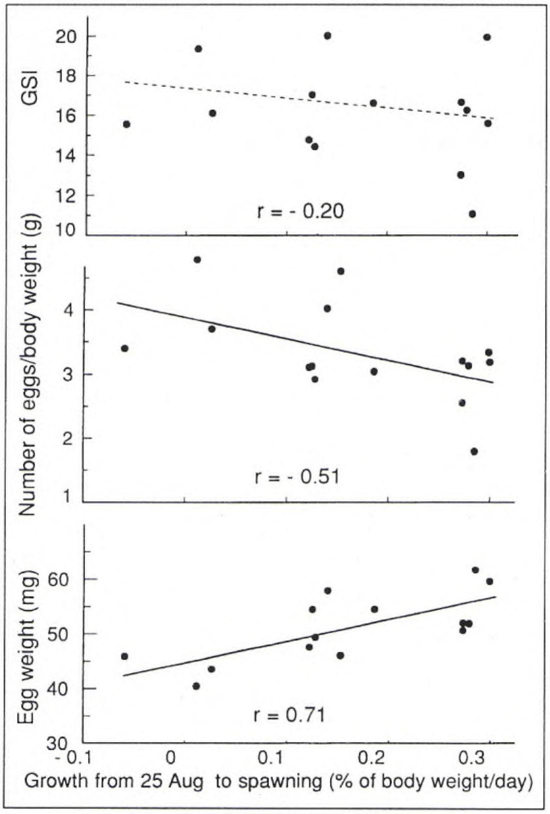

Fig. 3. Correlation between individual growth of females and GSI (top), relative fecundity (middle) and mean egg weight (bottom) during the end of vitellogenesis (25 August to individual spawning time). 14 females were used.

treatment (May 1990), spawning period occurred from May to October. Fourteen month old immature fish subjected to long days from April 1991 started to ovulated 10 months later in February 1992, spawning period occurred from February to September. In 1992-93, advanced females by short days in summer ovulated from the end of October to December, females under natural daylength ovulated from the end of November to January and delayed females by long days in fall ovulated from January to February. Each year, mean egg weight of each females was correlated with the date of ovulation of the corresponding females: 1989 $P<0.05$, $r=0.46$, df 25 (Fig 4a), 1991 $P<0.01$, $r=0.84$, df 22 (Fig 4b), 1992-93 $P<0.01$, $r=0.27$, df 185 (Fig 4c).

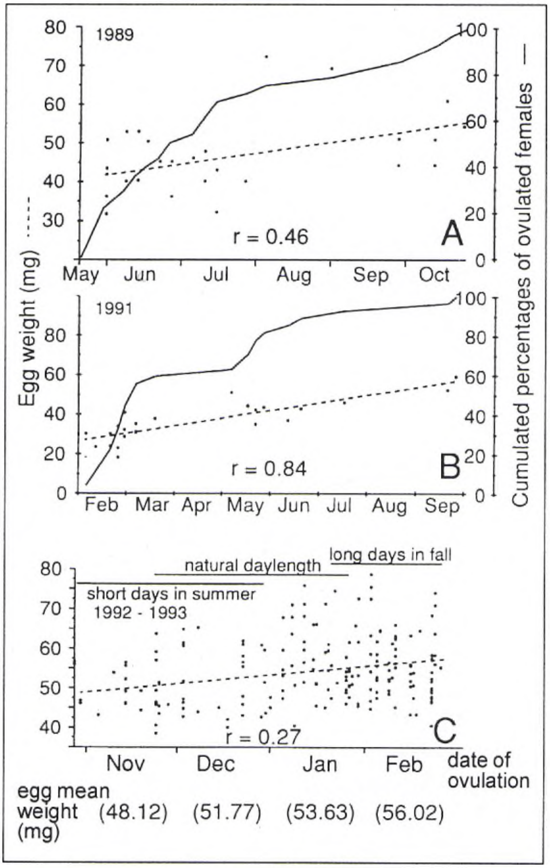

Fig. 4. Effects of photoperiod manipulations on spawning time and mean egg weight. **A:** twenty month old immature fish subjected to long days (17h L:7h D) from October 1988 to 10 May 1989 and afterwards to short days (7h L:17h D) at 5°C until spawning. **B:** Fourteen month old immature fish subjected to long days (17h L:7h D) from the beginning of April 1990 until spawning time. **C:** 3-year old females subjected to long day treatment in spring (advanced spawning), to natural day length all year round or to long day treatment in fall (delayed spawning). Correlation was calculated between the date of ovulation of each female and the mean egg weight of the corresponding female.

Discussion

The development of Arctic charr ovaries from April to December can be divided in two stages: (1) a stage of slow growth of oocytes from April to August, (2) a stage of rapid growth of oocytes from September to November. More than 80% of oocyte growth occurred during the second stage. This was also found in other salmonids, for example brook trout (Mc Cormick and Naiman 1984). Plasma calcium levels which changed parallel to the plasma vitellogenin (Elliott et al. 1984) rose during the second stage of ovary development and remained elevated until spawning. The relative fecundity did not change with body weight of females. In contrast, Määr (1949) reported that relative fecundity decreased with increasing fish weight in Swedish Arctic charr populations. The connection between growth and egg weight and numbers varied with the stage of ovarian development. The number of vitellogenic oocytes was determine in spring as have been found in rainbow trout (Bromage and Cumaranatunga 1988). Improved fish growth at this time of the year increased fecundity and gonadal weight but not egg weight. In autumn, on the other hand, female growth led to increased egg weight and decreased relative fecundity. As a consequence of these opposite changes, gonadal weight was unaffected by female growth during this stage (late vitellogenesis). In August, the formation of new vitellogenic oocytes stopped and the relative fecundity of females decreased due to atresias and body growth. The levels of atresia increased when the food ration was reduced in the rainbow trout (Springate et al. 1985). The positive correlation between female growth from August to spawning and egg weight was probably a consequence of both the cessation of new vitellogenic oocyte formation and the rapid oocyte growth. In many fish species, the ovarian development cycle lasts for more than nine months but the stage of rapid ovary growth lasts only three months. Consequently, measurements of yearly growth was more related to the growth during the stage of oocyte formation than during late vitellogenesis.

Improved feeding opportunities increased female fecundity (Springate et al. 1985). The effect of diet on egg size differed with fish species. Springate et al. (1985) have reported that egg size decreased when ration size was restricted in rainbow trout. In contrast, Bagenal (1969) reported that diet restriction in brown trout resulted in increased egg size, as was later found for roach (Lyagine 1975). Other authors, however have reported that diet restriction have no effect on egg size (reviewed in Springate et al. 1985). Except for Springate and Bromage (1985) few authors have given information on effects of seasonal alterations in food ration on gonadal development. My results indicate that the effect of female growth (i.e. differential ration size) vary with season in accordance with the findings of Springate and Bromage (1985) for rainbow trout. To improve egg size of hatchery reared Arctic charr, it may therefore be advantageous to reduce the food ration of broodfish during the beginning of vitellogenesis and to increase it during late vitellogenesis. Arctic charr have compensatory growth after a period of growth limitation (Mortensen and Damsgard 1993) that may influence the gain in egg size.

The effects of photoperiod manipulations on spawning in Arctic charr appeared similar to that in rainbow trout (Bromage and Duston 1986). Short days in summer advanced spawning. On the one hand, long days in fall delayed spawning, whereas constant long days induced early sexual development, as in the rainbow trout (Skarphédinsson et al. 1985). It is possible to extend the spawning period of Arctic charr from fall to spring by changing the photoperiod. The heterogeneous ovulation period of Arctic charr subjected to constant long days may be explained by a lack of synchronization in the onset of ovarian development caused by constant day length (Bromage et al. 1984). Moreover, photoperiod manipulation influence egg weight. Advancements and delays of spawning produced smaller and larger eggs respectively as found for rainbow trout by Bromage et al. (1984). At the end of the ovarian development in December, plasma vitellogenin levels remained elevated in Arctic charr under natural day length. The vitellogenin incorporation by oocytes was probably prolonged in delayed females whilst it was shortened in advanced females. I hypothesize that the egg size of advanced or delayed females was influenced by the duration of vitellogenesis and by the growth of females during this stage.

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Preliminary Results of the Study on the Sympatric Chars on the Chukotsk Peninsula

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Abstract

Salvelinus malma and *S. taranetzi* are widespread on the Chukchi Peninsula and live sympatrically in most of the water bodies. There is disagreement whether the two are conspecific or different species. Both form resident and anadromous populations in this area, but *S. malma* occurs mainly in running water whereas *S. taranetzi* inhabits lakes. Anadromous char descend to sea for feeding and return to fresh water for spawning in autumn. They spend the winter in fresh water. Contrary to *S. malma*, anadromous *S. taranetzi* do not migrate to sea every year after smolting. Moreover, in the sea, *S. malma* appear to migrate farther away from their river than *S. taranetzi*. Other differences between the two are that *S. malma* grow faster, become larger as adults, and have higher relative fecundity. In anadromous populations of *S. malma*, but not *S. taranetzi*, precociously mature (dwarf) males are found.

Keywords: Migration, age at maturity, growth rate, fecundity, life history, habitat, *Salvelinus malma, Salvelinus taranetzi.*

Introduction

It is known that the morphological and ecological diversity of chars is high in the extreme North-East of Asia (Berg 1948, Savvaitova 1989, Savvaitova et al. 1988, Volobuev et al. 1979, Chereshnev 1982). Two groups of high-Arctic and Pacific chars are common for the Chukotsk Peninsula (Glubokovsky et al. 1979). The taranetz (*Salvelinus taranetzi* Kaganovsky) and Dolly Varden char (*S. malma* (Walbaum)) are the most abundant and widely distributed. There is controversy whether the two chars represent one or two different species. Some authors (Kaganovsky 1955, Chereshnev 1982) refer them to the rank of species, others consider them as forms of the same species, *S. alpinus* (Volobuev et al 1979, Savvaitova 1989).

According to Cherechnev (1982), adult *S. malma* are characterized by the maxillary bones ending well behind the posterior edges of the eyes. Moreover, their caudal fin is broad and has no deep fork. Their sides and backs are sprinkled with small spots. The mouth cavity is dark. Sexual dimorphism is clearly apparent in spawning adults. *S. taranetzi* on the other hand have short maxilla, the caudal fin has a deep fork, the body spots are sparse and large, the mouth cavity is white and sexual dimorphism is not apparent. Furthermore, there is an apparent difference in habitat use. *S. malma* spawn in fast flowing rivers whereas *S. taranetzi* reproduce only in lakes. *S. malma* has a higher fecundity than *S. taranetzi*.

These morphological and ecological differences between the two may be less clear- cut than described by Cherechnev (1982). For instance, based on the criteria, Savvaitova et al. (1988) were unable to differentiate chars from the Chukchi Peninsula. It should be noted, however, that most of the work was based on morphology, and not ecology or genetics. Moreover, field investigations of the chars are difficult due to the adverse climate and the problematic transportation conditions in the area. Therefore new char investigations were performed over the Chukchi Peninsula during 1989-1994, and some new information on these chars is hereby reported.

Study area

Chukchi Peninsula is situated in North-East Asia and separated from the North American continent by the Bering Strait. This is a mountainous area, low land occurs chiefly along the Arctic coast of the peninsula. About 20% of the territory is covered by rocks and the ground has permafrost. There is a moderately continental climate with inclement weather and strong winds up to 70 m s^{-1}. The air is humid and the coastal areas are characterized by fog all year round. About 55% of the peninsula is covered with highland tundra and highland desert (Klukin 1970). Mammal species diversity is low, but there are brown bear, wolverine, wolf, polar fox and fox. Native people (Chukchi and Eskimo) breed reindeer, hunt sea mammals and catch fish. Commercial fishing is mainly based on Pacific salmon (chiefly *Onchorhynchus nerka*) and chars. Amongst chars, *S. taranetzi* from the Ioniveem River and *S. malma* from the Seutakan River are the most abundant populations.

Material and methods

This research was conducted in different parts of the Chukotsk Peninsula in July and October (Fig.1). Sympatric chars were investigated in the Seutakan, Kurupka, Getlangen, Ioniveem and Ieniveem drainages (Table 1). In addition, I report some previously unpublished information on the distribution of sympatric chars in the Achchen Lake drainage.

The fish were caught with gill nets (mesh size 12-65 mm) in lakes and slow flowing rivers. In fast flowing rivers, a weir trap with 18-20 mm mesh size was used. Fork length (mm) and total wet weight (g) were measured. Sex, degree of sexual maturity and stomach contents of fish were identified. Total sample size of *S. malma* and *S. taranetzi* was 1,162 individuals. The fish were aged by use of sacculus otoliths.

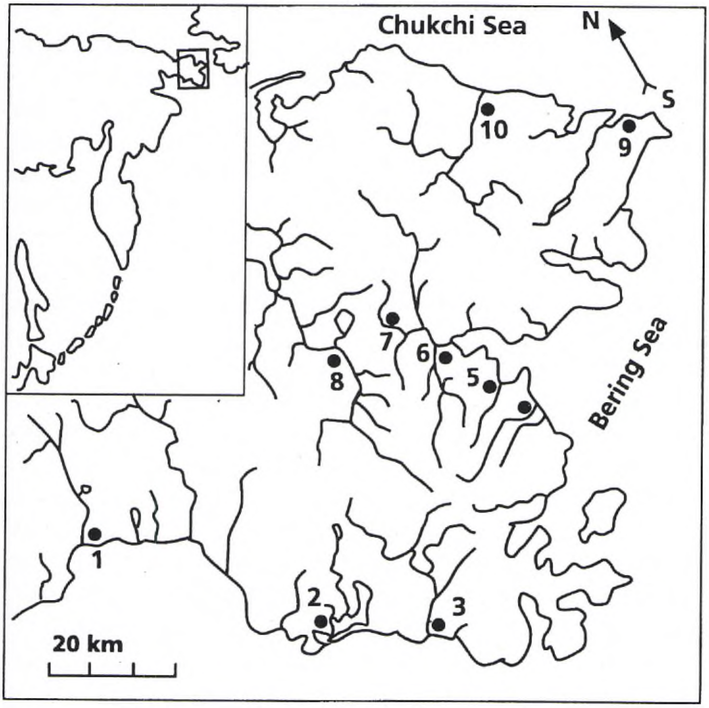

Fig. 1. The study area. The rivers where char samples were collected are indicated by black dots. 1. Seutakan River, 2. Lake - river system Achchen, 3. Kurupka River, 4. Getlyangen River, 5. Utaatap River, 6. Ieniveem River, 7. Igelhveem River, 8. Ioniveem River, 9. Uellen Lagune (Savvaitova at al. 1988), 10. Chegitun River (Cherechnev at al. 1989).

Table 1. Mean fork length (range of variability), mean weight (range of variability), and percentage distribution of *S. malma* and *S. taranetzi* in the sample sizes in the investigated rivers (cf. Fig. 1).

Sample area	*S. malma*			*S. Taranetzi*			Sample Size
	Fork length, mm (Mean range)	Weight, g (Mean range)	%	Fork length, mm (Mean range)	Weight, g (Mean range)	%	(*N*)
Ioniveem River	(320-540)	-	1.5	400(215-655)	745 (87-2,850)	98.5	399
Ioniveem drainage lake	-	-	-	330(148-473)	310 (28- 930)	100	9
Igelhveem River	17 (11-335)	56 (12- 295)	100	-	-	-	39
Ieniveem River	540(315-680)	-	45.8	312(240-469)	-	54.2	48
Utaatap River	595(460-740)	-	100	-	-	-	46
Getlangen River	446(405-520)	-	41.9	331(240-405)	-	58.1	31
Kurupka drainage	435 (9-742)	1,026 (5-2,230)	92.0	380(310-510)	560(340-1,080)	8.0	300
Seutakan River	550(340-920)	1,723(440-4,900)	79.5	453(242-630)	1,073(150-2,920)	20.5	292

Smolt age was determined from the peculiarity of the surface and coloration of the otoliths of anadromous fish (Gudkov and Skopets 1989). The relative female fecundity is given as the total number of eggs divided by body weight in g. "Stat-graphics" was used for statistical calculation.

Results and discussion

Anadromous *S. malma* is widespread in the Bering Sea off the coast of the Chukchi Peninsula (Cherechnev 1990), and was found in all the rivers investigated (Table 1). We found spring resident *S. malma* in the upper tributary of the Igelkhveem River close to hot and salt spring Gilminveem, the largest on the peninsula.

Anadromous *S. taranetzi* occurred in water courses with lakes only. They are the Ioniveem, Ieniveem, Getlangen and Seutakan drainages. Freshwater resident *S. taranetzi* were found in a small, 400 m long, lake of the Kurupka drainage and in some lakes of the main stem of the Ioniveer River. *S. taranetzi* (resident and anadromous) was not found in the Igelhveem, Utaatap, Marich and Pentygney.

Life history

S. malma and *S. taranetzi* occur both as anadromous and non anadromous populations. *S. malma* is more sea-run migratory than *S. taranetzi*. Anadromous *S. malma* migrate to sea every summer (Gudkov 1994) wheras *S. taranetzi* may spend the summer after spawning in the lake as, for example, observed in the Ioniveem River. Some prespawning *S. taranetzi* were found in the Ioneveem drainage in spring and autumn. They were mainly males (70%) and had fork lenghts from 435 to 600 mm and were 5-7 years old. The same was found in the Seutakan River. Immigrating *S. taranetzi* caught in lagunes of the river between 26 July and 10 August were also immature. Most immigrant *S. malma*, however, were in prespawning condition (56%). Immature anadromous *S. taranetzi* from the Inoveem and Getlangen Rivers wintered in fresh water as well. In the ocean, *S. malma* make extensive migrations (Armstrong and Morrow 1980, DeCicco 1992). *S. taranetzi*, on the other hand, tend to stay fairly close to the river mouth as seen from investigations in the Seutakan River.

Most *S. malma* seemed to enter fresh water towards the end of our sampling season in the Seutakan River (Fig. 2). The same was found in the Ieniveem River. In comparison, I found no such increase in number of late entering fish in *S. taranetzi*. Perhaps, some of the *S. taranetzi* feed in large lagunes in the river and do not migrate to sea. Anadromous *S. malma* cease feeding before entering the river. Only 8.4% of the fish caught in the rivers had food in their stomachs. At sea, the fish fed chiefly on invertebrates;

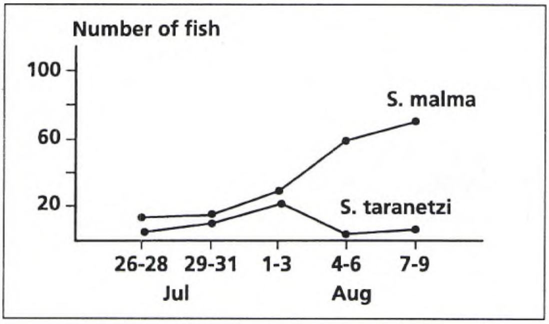

Fig. 2. The number of anadromous *S. malma* and *S. taranetzi* caught at the mouth of the Seutakan River in July and August, 1994.

only 13.8 % had remains of fish in their stomach. Capelin *Mallotus villosus socialis* (Pallas) is most often the food fish. Anadromous *S. taranetzi* fed more intensively in fresh water. In total, 39.5% of the river catch had food in their stomach. Among these, 68.8% ate invertebrates and 46.9% ate fish.

The results of our investigations from the Achchen drainage system confirm Chereshnev's option that *S. malma* spawn only in fast flowing rivers whereas *S. taranetzi* spawn in lakes. In the Achchen Lake, freshwater resident and anadromous *S. tarenetzi* spawn. Anadromous *S. malma*, on the other hand, spawn in the Argitkhin River, a tributary to Achchen Lake. The young of *S. malma* grow up in Achchen Lake together with offspring of *S. taranetzi*.

Parr of chars are not well studied. However, young *S. taranetzi* seem to live in lakes most of the time e.g. Achchen Lake and some lakes in Seutakan, Ioniveem, Kurupka drainages. These young char were not found in rivers. *S. malma* parr seem to be distributed widely within river systems. For instance, parr of *S. malma*, 2 and 3 years of age, leave the Argitkhin River for Achchen Lake to feed. In the Kurupka River, parr were found throughout the various parts of the water course. They were found even in tributaries not used for spawning by *S. malma*. *S. malma* grew larger than *S. taranetzi* in the various rivers investigated (Table 1). However, it is known that in deep mountain lakes *S. taranetzi* can reach lengths and weights of 715 mm and 4 kg

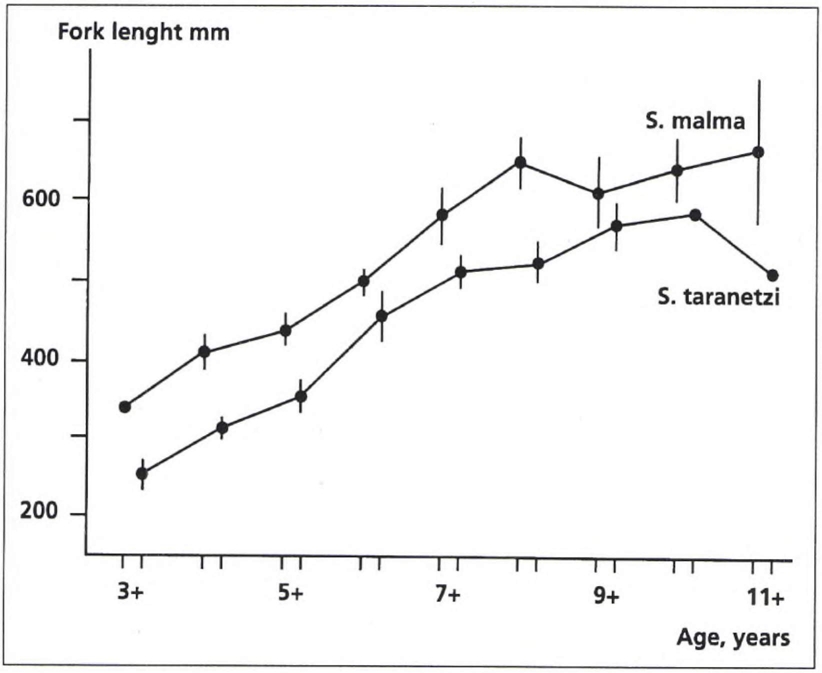

Fig. 3. Mean fork length at different ages of 3-11 years old anadromous *S. malma* and *S. taranetzi* from the Seutakan River. 95% confidence limits of the means are given.

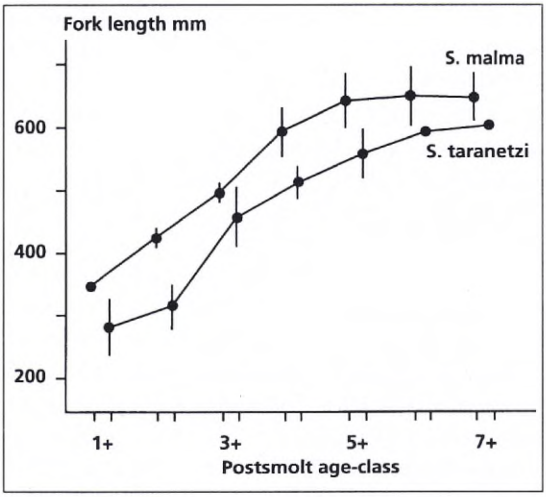

Fig. 4. Mean fork lengths of different sea-ages after the first year at sea of anadromous *S. malma* and *S. taranetzi* from the Seutakan River. 95% confidence limits of the means are given.

(Gudkov 1993). These large lake char are long lived and primarily fish feeding.

In the Sentakan River, *S. malma* grow more rapidly than the sympatric *S. taranetzi*. This difference in growth rates, however, levelled out with age (Fig. 3). Size differences obtained prior to smoltification, remained during sea life (Fig. 4). In parallel *S. malma* grew faster than *S. malma* in the Uellen Lagune (district of Bering Strait) and Svobodni Gulf (Volobuev et al. 1979, Savvaitova et al. 1988).

There was no difference in growth rate between male and female *S. taranetzi*. In the Ioniveem River, body length (y) increased with age:

For males $y=(14.5\pm1.86) + (5.0\pm0.32)\,x$
($r=0.80$)
For females $y=(16.5\pm1.09) + (4.4\pm0.19)\,x$
($r=0.83$)

There is however no significant difference in regression coeffecients between the two sexes (t-test=1.65 with $P>0.05$). Moreover, adult size did not differ significantly between the sexes of *S. taranetzi* from Achchen Lake (Gudkov 1994).

In *S. malma*, on the other hand, males grew faster than females (t-test=6.84 with $P<0.05$). The regression coefficients of the respective sexes were 5.1 (males) and 3.4 (females) ($r=0.90$), and males became larger than females with age (Fig. 5). This sexual dimorphism seems general for North-East Asia (Gudkov 1991). The lenght (x, cm)-weight (y, g) relationship for *S. malma* and *S. taranetzi* were:

$$y\ (malma) = 0.011\ x^{2.95}$$
$$y\ (taranetzi) = 0.002\ x^{3.47}$$

In both cases, the correlation coefficient (r) was equal to 0.97. The exponents in these two equations were significantly different ($P<0.05$), showing that the weight - length relationships of the two species are different.

Smolt age of *S. malma* from the Chukchi Peninsula is usually 2-3 years (Gudkov 1991). In sympatry with *S. taranetzi* in Seutakan River, *S. malma* smolted at 1-4 years of age (mean age=2.7 years). *S. taranetzi* smolted between 2 and 5 years (mean 3.1 years) which is significantly older than *S. malma* ($P<0.05$). In comparison, *S.*

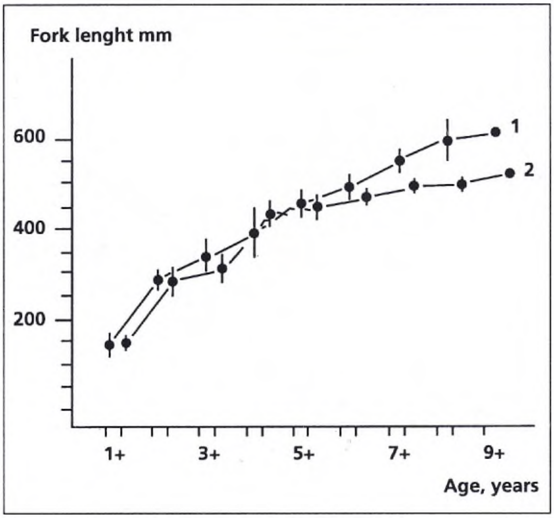

Fig. 5. Mean fork lengths of males (1) and females (2) at ages between 1 and 9 years of anadromous *S. malma* from the Kurupka River. 95% confidence limits of the means are given.

taranetzi from the river Ioniveem smolted at ages between 1 and 7 years with 2-4 years as the most common.

A large part (44%) of the *S. taranetzi* lack sea structure in their otoliths. This indicates that some of the *S. taranetzi* stay as freshwater residents.

The maturing age of *S. malma* varies between the two sexes. Freshwater resident males attain maturity from age-2 onwards, the females mature one year later. Resident fish may live until 10 years of age. Anadromous fish mature later, in the Kurupka river adult males were between 5 and 15 years of age, females from 7 to 17 years, in the Seutakan River males were from 5 to 12 and females from 6 to 14 years of age. Resident fish from the Kurupka River matured from an age of 2+. Sea age at maturity of *S. malma* from the Seutakan River was 2-5 years (11% at age 2).

Freshwater resident *S. taranetzi* from the Ioniveem River attained maturity at age 8+, in the Karupka river they matured at 5+. Anadromous *S. taranetzi* from Ioniveem River matured at 5+. Thus, age at maturity was similar for the two species. According to Chereshnev (1981) the fecundity of *S. malma* excedes that of *S. taranetzi* by about twice. New information confirms this (Table 2).

Conclusions

- Both *S. malma* and *S. taranetzi* occur in a freshwater resident and a sea-run migratory form. The resident *S. malma* live in rivers, *S. taranetzi* live in lakes. Amongst anadromous chars *S. malma* spawn in rivers, *S. taranetzi* spawn in lakes.
- Anadromous fish feed in the sea during summer. The migratory tendency is more pronounced in *S. malma* than in *S. taranetzi*. At sea *S. taranetzi* appears to stay close to the river mouth, whereas *S. malma* may perform long migrations.
- Amongst anadromous char, adult *S. malma* is larger than adult *S. taranetzi*. As young fish,

Table 2. Mean fecundity and relative fecundity (number of eggs per g body weight) with range of variability of anadromous and resident *S. malma* and *S. taranetzi* from the Chukchi Peninsula.

Sample area	Fecundity	Range	Relative Fecundity	Range	*N*
Anadromous *malma* Kurupka River	5,274	3,901- 8,748	3.55	2.45-4.75	33
Resident *malma* Igelhveem River	803	243- 1,160	4.58	3.57-6.18	5
Anadromous *malma* Seutakan River (Cherechnev 1981)	7,800	5,350-13,200	3.4	-	26
Anadromous *malma* Chegitun River (Cherechnev at al. 1989)	-	732- 7,918	-	2.6 -4.2	-
Anadromous *taranetzi* Ioniveem drainage	3,299	2,674- 3,964	1.7	1.5 -2.0	5
Partly anadromous *taranetzi* Achchen Lake (Gudkov 1994)	861	210- 2,278	1.9	1.76-3.5	30
Anadromous *taranetzi* Seutakan River (Cherechnev 1981)	3,830	2,856- 4,763	1.9	-	15

S. malma grows at a faster rate and *S. taranetzi* are never able to catch up in size. In *S. malma* but not *S. taranetzi*, males grow faster than females. The exponent of the length-weight relationship is larger in *S. taranetzi* than *S. malma*.

- Precociously maturing males in anadromous populations and spring resident populations occur in *S. malma* but not in *S. taranetzi* in the Chukchi Peninsula as well as in other regions. Freshwater resident charr of the two species mature at the same age as the anadromous fish. The relative fecundity of *S. malma* is about twice as high as that of *S. taranetzi*.

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DNA Fingerprinting in Arctic Charr, *Salvelinus alpinus* (L.) - Preliminary Analyses with Multi- and Single Locus Minisatellite Probes

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Abstract

DNA fingerprinting techniques using the multilocus probe, bacteriophage M13, and a number of single locus probes isolated from Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., have been used to investigate genetic variability within and between populations of the Arctic charr, *Salvelinus alpinus* (L.). Multilocus DNA fingerprinting revealed genetic variability among individuals in all populations studied. Analysis of allele frequencies from single locus probing revealed significant genetic differentiation between populations. The results show that DNA fingerprinting techniques are powerful additional tools for population genetic analysis in salmonid fishes.

Keywords: Arctic charr, populations, DNA fingerprinting, M13, single-locus probes.

Introduction

Of ten freshwater fish species considered by Maitland and Lyle (1991) to be in need of conservation action in the British Isles, four are salmonids: three species of *Coregonus* and the Arctic charr, *Salvelinus alpinus* (L.). Although there are still over 150 recorded populations of Arctic charr in the British Isles which are all non-anadromous, some are in decline while others may have already disappeared (Maitland and Lyle 1990). Nevertheless the Arctic charr is now being recognized as an aquaculture species in Scotland, particularly in the Highlands and Islands. Recognizing the need for diversification of the aquaculture industry with the implications this has for employment in remote areas and reconciling this need with conservation strategies for threatened populations requires sound knowledge of the diversity present within and between wild populations.

The Arctic charr is morphologically and behaviourally plastic but protein (Ferguson 1981, Kornfield et al. 1981, Andersson et al. 1983, Hindar et al. 1986) and mitochondrial (mt) DNA (Danzmann et al. 1991, Hartley et al. 1992a) studies have revealed little genetic variability within or between populations. However, when a number of different techniques were combined, substantial differences were found between two morphological forms of Arctic charr in Loch Rannoch, Scotland (Hartley et al. 1992b). This suggests that significant genetic variability is present in at least some Arctic charr populations and that this may be revealed if new strategies for assessing this variability are employed.

One such approach is to use DNA fingerprinting techniques (Bruford et al. 1992). Although DNA fingerprinting techniques have been primarily utilized for studies of parentage analysis, they can provide sets of nuclear DNA markers useful for estimating genetic variability within and between populations in organisms where little variabilty has been detected with other genetic techniques. Turner et al. (1990) used oligonucleotide probes to detect genetic heterogeneity in the clonal fish species *Poecilia formosa* and *Rivulus marmoratus*; Hughes and Queller (1993) used microsatellites to demonstrate polymorphism in a social wasp *Polistes annularis*; and Alberte et al. (1994) have demonstrated genetic variation in the seagrass *Zostera marina* with bacteriophage M13 DNA employed as a multilocus fingerprinting probe. All three species showed little or no genetic variability with isozyme analyses.

In this study we assess the ability of minisatellite DNA fingerprinting techniques to detect genetic variability within and between populations of Arctic charr from Scotland and the English Lake District. Both a multilocus approach (using bacteriophage M13 DNA) and locus specific approach (using salmonid derived probes) are considered.

Materials and methods

The populations sampled in this study were Loch Mealt, Isle of Skye; Lochs Clair and Coulin, Wester Ross; Lochs Arkaig and Ness, Highland Region; Lochs Ericht, Garry, Loch and Rannoch (benthic and pelagic morphs), Perthshire; Loch Doon, Dumfriesshire; and Lake Windermere (north and south basins), Cumbria. Their locations are shown in Fig. 1.

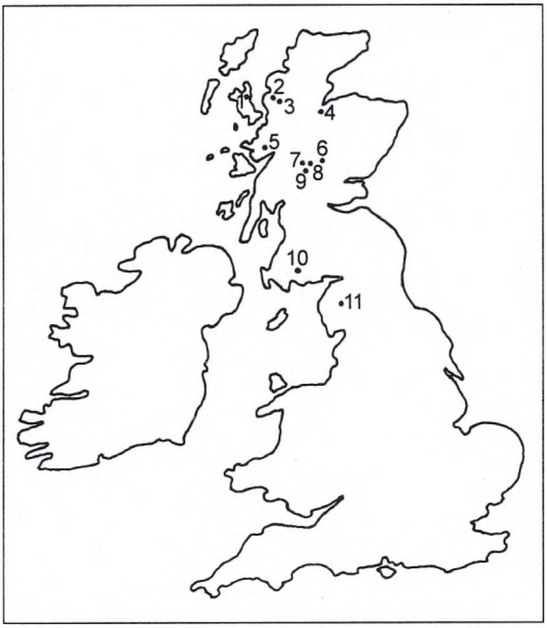

Fig. 1. Map of the British Isles to show the location of the populations sampled. 1) Loch Mealt, 2) L. Clair, 3) L. Coulin, 4) L. Ness, 5) L. Arkaig, 6) L. Loch, 7) L. Ericht, 8) L. Garry, 9) L. Rannoch, 10) L. Doon, 11) Lake Windermere.

DNA was isolated from liver tissue using standard techniques involving proteinase digestion, phenol-chloroform extraction and ethanol precipitation (Sambrook et al. 1989). DNA (3-5 μg) was digested overnight with an excess of the restriction enzyme *Mbo*I for multilocus fingerprinting and with *Hae*III for single locus probing. The fragments were separated by electrophoresis through 20 cm long 1% agarose gels in 1x Tris-borate buffer (TBE) at 35V for either 48 hrs (multilocus) or 24 hrs (single locus probing). Following electrophoresis the DNA fragments were transferred to Hybond N nylon filters (Amersham) by capillary blotting using 0.5M NaCl/0.25M NaOH as the transfer buffer, the gels having first been denatured for 1 hr in 0.5M NaCl/0.5M NaOH.

The multilocus probe (MLP) used was bacteriophage M13 DNA (Vassart et al. 1987). Isotopic labelling of probe by primer extension, together with prehybridization and hybridization conditions were as described by Wells (1988). Post-hybridization washes (all performed at room temperature) were as follows: two washes in 3X SSC, 0.1% SDS (sodium dodecyl sulphate) for 20 min each, followed by a single wash in 2X SSC, 0.1% SDS for 30 min (20X SSC is 3 M NaCl, 0.3M Na_3 citrate). Autoradiography was carried out overnight at -70°C with intensifying screens.

Based on an initial limited survey (Prodöhl 1993) six salmonid derived SLPs were selected for investigation in the present study. These were p*Ssa*-A34 and p*Ssa*-A45/2, isolated from an Atlantic salmon (*Salmo salar*) genomic library, (Taggart and Ferguson 1990, Taggart et al. 1994) and the brown trout (*S. trutta*) derived probes p*Str*-A1, p*Str*-A5, p*Str*-A9 and p*Str*-A22/2 (Prodöhl et al. 1994). Isotopic probe labelling was by random priming using a kit from Gibco-BRL. Prehybridizations (4-5hrs) and hybridizations (overnight) were carried out at 65°C in 3X SSPE pH 7.7 (0.54 M NaCl, 30 mM sodium phosphate, 3 mM EDTA), 0.5% dried milk, 1% SDS, 6% polyethylene glycol (PEG) 8000. Sonicated salmon testis DNA (Sigma) was included as competitor during hybridizations. Post-hybridization washes, also at 65°C, were 30 min in 2X SSC, 0.1% SDS, followed by 2 x 30 min washes in 0.2-0.4X SSC, 0.1% SDS. Autoradiography (1-10 days) was carried out at -70°C with intensifying screens.

Analysis of multilocus DNA fingerprint patterns was carried out directly from autoradiographs. Band sharing coefficients were calculated from adjacent lanes (1-2, 2-3, 3-4 etc.) using the simple similarity statisitic:

$$S=2N_{xy}/(N_x + N_y)$$

where N_x and N_y are the number of fragments in individuals x and y respectively and N_{xy} is the number shared by both (Lynch 1990). Genotypes for the SLPs were scored visually. Genetic statistics were compiled using BIOSYS-1 (Swofford and Selander 1981) and DISPAN (Ota 1993) genetic analysis programmes. Hierarchical gene diversity analysis was performed using a programme supplied by P. Prodöhl, which followed the method of Chakraborty et al. (1982).

Results

Multilocus fingerprinting

A number of restriction enzymes which have 4 base pair recognition sequences generate multibanded DNA fingerprint patterns in Arctic charr when bacteriophage M13 DNA is used as the probe (Hartley, unpublished observation). *Mbo*I was the enzyme of choice for this study as it gave the clearest, most readily scored patterns, examples of which are shown in Fig. 2. Due to the complexity of the patterns only bands greater than 5 kilobase pairs (kbp) were analysed. Furthermore, since some bands of weak intensity were not consistently resolved, probably due to

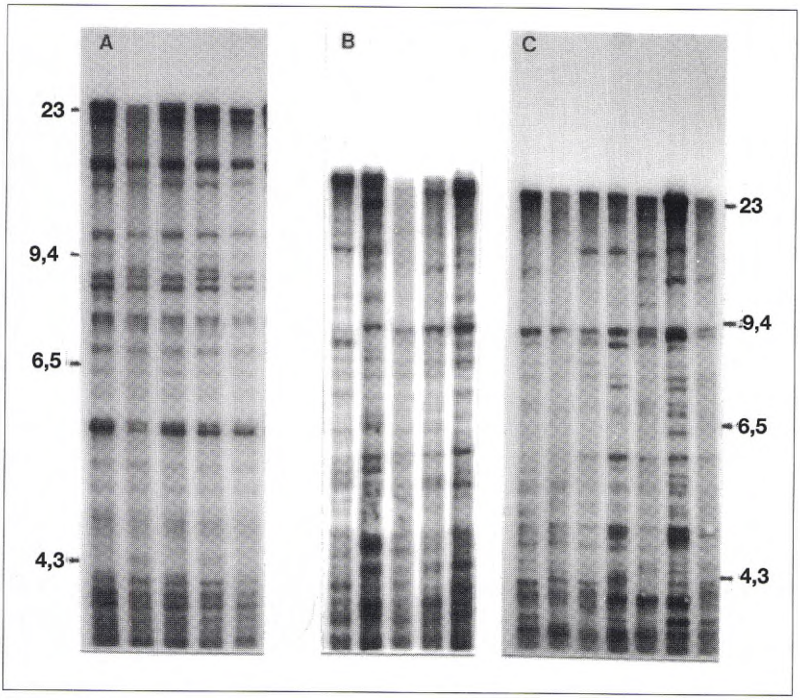

Fig. 2. Examples of multilocus DNA fingerprint patterns obtained with the *Mbo*I/M13 restriction enzyme/probe combination in charr from **A)** Loch Mealt, S=0.86; **B)** Loch Ericht, S=0.48; and **C)** Loch Rannoch, S=0.47. Size markers are from *Hin*dIII digested λ DNA.

Table 1. Means and standard deviations for band sharing coefficients (S) of *Mbo*I / M13 multilocus DNA fingerprint patterns in ten Arctic charr populations.

Population	Mean no. of bands/individual	No. of comparisons	S
Arkaig	15.75 ± 3.86	3	0.59 ± 0.04
Clair	20.08 ± 2.97	11	0.76 ± 0.05
Coulin	11.28 ± 1.98	13	0.87 ± 0.06
Doon	14.70 ± 3.10	5	0.52 ± 0.19
Ericht	18.87 ± 4.63	11	0.48 ± 0.07
Loch	18.59 ± 3.64	5	0.76 ± 0.08
Mealt	16.00 ± 2.76	11	0.86 ± 0.04
Ness	18.67 ± 3.93	6	0.47 ± 0.04
Rannoch 1	9.30 ± 4.32	5	0.47 ± 0.10
Windermere 1	18.17 ± 1.27	7	0.63 ± 0.11

Rannoch 1=benthic morph, Windermere 1=north basin autumn spawners.

minor variations in electrophoretic and probing conditions, comparisons were restricted to individuals run on the same gel. As each gel contained only individuals from a single population, this approach was used to assess within population variability only. The mean number of bands scored per individual on a gel ranged from 9.3 to 20.08 (Table 1). The DNA fingerprint patterns revealed variability in all the populations examined. Mean band sharing coefficients (S) ranged from 0.47 to 0.87 among individuals within populations (Table 1). Four populations (Clair, Coulin, Loch and Mealt) had relatively high values of S (between 0.76 and 0.87) while the other six populations had moderate values between 0.47 and 0.63.

Single-locus profiling

Under the electrophoretic and probing conditions employed three of the six SLPs resolved patterns that could not be readily scored for all samples. p*Ssa*-A45/2 detected a multi-banded pattern while for p*Str*-A9 and p*Str*-A22/2 the number and / or size range of alleles precluded accurate typing. However, the other three SLPs (p*Ssa*-A34, p*Str*-A1 and p*Str*-A5) each detected three to four distinct fragment classes (A-D) in Arctic charr (Fig. 3) which could be confidently typed both within and between gels and these were used in population analyses. While p*Str*-A5 occasionally revealed a weak multilocus pattern in the background, the strength of the single locus bands was sufficient for accurate typing. The observed fragments were classed as single 'alleles' although in some cases they may represent groups of 'isoalleles'. Allele frequencies, together with the mean number of alleles per locus and mean heterozygosities, are detailed in Table 2. Four of the 12 populations (Clair, Coulin, Loch, and Mealt) were monomorphic at all three loci. These are the same four populations that exhibited higher band sharing coefficients by multilocus analyses. In all other populations variability was observed at either one or two of the minisatellite loci. Observed genotype numbers conformed with Hardy-Weinberg expectations in all cases (14 separate χ^2 analyses; lowest P=0.09). Two population specific, fixed alleles were recorded, *Str*-A5 'B' for Loch Doon and *Str*-A1 'A' for Loch Loch (Table 2). Furthermore a high frequency (0.74) diagnosic allele, *Str*-A5 'D', was found in benthic charr from Loch Rannoch. This allele was not observed in any other population screened, including pelagic charr from the same loch. Contingency

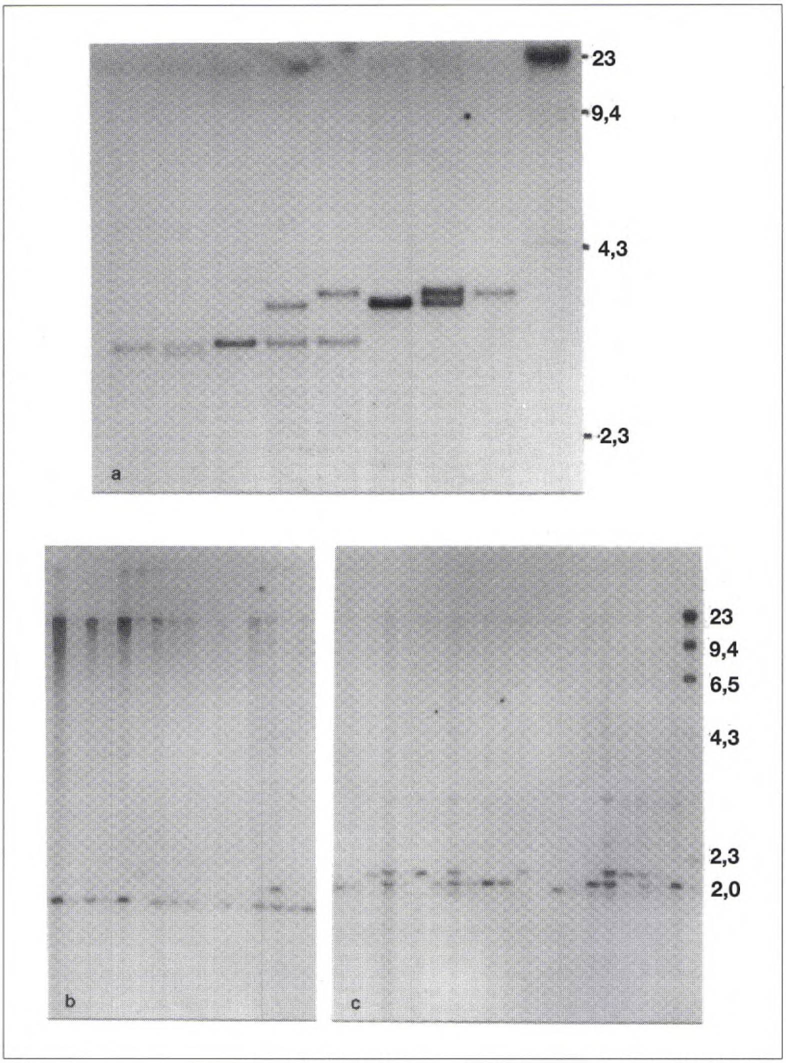

Fig. 3. Examples of single-locus patterns obtained after hybridization with **a)** p*Ssa*-A34, **b)** p*Str*-A1 and **c)** p*Str*-A5. Size markers are from *Hin*dIII digested λ DNA.

χ^2 analysis revealed highly statistically significant genetic differentiation among the twelve populations (Table 3). This was confirmed by computed F_{ST} values (Table 3). The mean F_{ST} over all loci, 0.503, was significantly greater than zero (95% C.I.: = 0.416-0.892). In a hierarchical analysis (Table 4) more than 50% of the total gene diversity was attributable to differentiation between locations. Estimates of D_A (Nei at al. 1983), detailed in Table 5, were used to construct a UPGMA based dendrogram (Fig. 4). Apart from the clustering of the two Windermere and three NW Scotland (Clair, Coulin and Mealt) populations, no strong geographic correlation of groupings was apparent.

Discussion

This preliminary study identifies minisatellite loci as an alternative source for highly polymorphic genetic markers in Arctic charr. In light of the relatively low levels of genetic variability detected by other methods (e.g. Ferguson 1981, Anderson et al. 1983, Hartley et al. 1992a) DNA

Table 2. Allele frequencies and combined heterozygosity values (standard errors in parentheses) for three minisatellite DNA loci in twelve Arctic charr populations. Approximate sizes of the alleles in kilobase pairs are given in square brackets.

Population	*N*	*Ssa*-A34			*Str*-A5				*Str*-A1			Combined		
		A	B	C	A	B	C	D	A	B	C	Mean no.	Heterozygosity	
		[3.7]	[3.5]	[3.1]	[2.2]	[2.1]	[2.0]	[1.9]	[2.1]	[1.9]	[1.7]	of alleles	Obs.	Exp.
Clair	12			1.00			1.00				1.00	1.0 (.0)	.000 (.000)	.000 (.000)
Coulin	19			1.00			1.00				1.00	1.0 (.0)	.000 (.000)	.000 (.000)
Doon	9		0.06	0.94		1.00					1.00	1.3 (.3)	.037 (.037)	.037 (.037)
Ericht	27		0.02	0.98	0.19		0.81				1.00	1.7 (.3)	.136 (.118)	.115 (.097)
Garry	29		0.50	0.50	0.22		0.78				1.00	1.7 (.3)	.253 (.126)	.288 (.151)
Loch	19			1.00			1.00		1.00			1.0 (.0)	.000 (.000)	.000 (.000)
Mealt	12			1.00			1.00				1.00	1.0 (.0)	.000 (.000)	.000 (.000)
Ness	41	0.30		0.70	0.32		0.68				1.00	1.7 (.3)	.301 (.151)	.289 (.145)
Rannoch 1	25	0.58	0.08	0.34			0.26	0.74			1.00	2.0 (.6)	.373 (.188)	.315 (.164)
Rannoch 2	23	0.09	0.67	0.24			1.00				1.00	1.7 (.7)	.188 (.188)	.164 (.164)
Windermere 1	22			1.00	0.45		0.55			0.09	0.91	1.7 (.3)	.212 (.132)	.226 (.149)
Windermere 2	24			1.00	0.35		0.65			0.02	0.98	1.7 (.3)	.167 (.146)	.170 (.149)

Rannoch 1=benthic morph, Rannoch 2=pelagic morph, Windermere 1=north basin autumn spawners, Windermere 2=south basin autumn spawners.

Table 3. Genetic differentiation at three minisatellite DNA loci among twelve Arctic charr populations; contingency chi-square analysis of allele frequencies and F_{ST} values (analysis according to Weir 1990).

Locus	No. of alleles	Chi-square	D.F.	*P*	F_{ST}
Ssa-A34	3	438.13	22	<0.001	0.439
Str-A1	3	559.26	22	<0.001	0.416
Str-A5	4	990.76	33	<0.001	0.892
Over all loci		1,988.15	77	<0.001	0.503

Table 4. Gene diversity analyses from a hierarchical classification of ministellite loci frequency data from 12 charr populations.

	Absolute gene diversity		Relative gene diversity(%)		
	Total	Within samples	Within samples	Between sample within morphotypes	Between locations
Locus					
Ssa-A34	.328	.174	53.105	7.701	39.194
Str-A5	.444	.202	45.402	10.464	44.134
Str-A1	.170	.017	10.142	0.241	89.617
Mean	.314	.131	41.730	7.660	50.610
SE	.080	.057	8.753	2.303	10.573

Table 5. Matrix of D_A genetic distance values (Nei et al. 1983) computed between 12 charr populations, based on three minisatellite loci.

Population	1	2	3	4	5	6	7	8	9	10	11
1 Clair											
2 Coulin	0.0000										
3 Doon	0.3428	0.3428									
4 Ericht	0.0356	0.0356	0.3350								
5 Garry	0.1373	0.1373	0.3819	0.0678							
6 Loch	0.3333	0.3333	0.6761	0.3689	0.4707						
7 Mealt	0.0000	0.0000	0.3428	0.0356	0.1373	0.3333					
8 Ness	0.1133	0.1133	0.3967	0.0620	0.1387	0.4466	0.1133				
9 Rannoch 1	0.3023	0.3023	0.4555	0.3077	0.3128	0.6357	0.3023	0.2240			
10 Rannoch 2	0.1704	0.1704	0.4436	0.1666	0.0643	0.5037	0.1704	0.2010	0.2494		
11 Windermere 1	0.1028	0.1028	0.3583	0.0332	0.1233	0.4206	0.1028	0.0743	0.3624	0.2732	
12 Windermere 2	0.0689	0.0689	0.3463	0.0129	0.1064	0.3988	0.0689	0.0592	0.3392	0.2393	0.0061

Rannoch 1=benthic morph, Rannoch 2=pelagic morph, Windermere 1=north basin autumn spawners, Windermere 2=south basin autumn spawners.

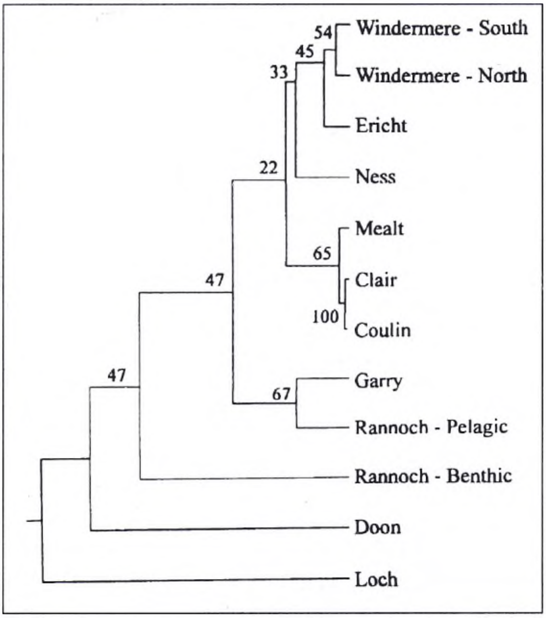

Fig. 4. UPGMA dendrogram of charr populations based on the modified Bhattacharrya's genetic distance D_A (Nei et al. 1983). Numbers on the nodes refer to the percentage of times that node was present in the most parsimonious tree obtained from 1000 bootstrap replicates.

fingerprinting and profiling methodologies are likely to be particularly informative for this salmonid species.

Whereas multilocus DNA fingerprinting can be highly discriminatory, and has been widely used to assign parentage and sibship in animals (e.g. Wetton et al. 1987, Amos et al. 1991) it is less applicable at the population level. Since observed bands cannot be attributed to specific loci, locus specific genotype freqencies cannot be ascertained and thus conventional population analyses are not possible (Lynch 1991). Furthermore, technical difficulties in attaining exactly comparable resolution among gels preclude large scale detailed analyses. Nevertheless a multilocus aproach could provide a relatively rapid, cost effective and sensitive method (cf. a comprehensive isozyme screening) for assessing overall levels of genetic variability in Arctic charr populations. In this regard the analysis suggests that there is considerable variation in heterozygosity levels among the charr populations. Although not directly comparable with other studies it is interesting to note that the lower range of band sharing coefficients (0.47-0.63) is similar to that reported among three wild brown trout populations in Ireland (0.45-0.68) derived from DNA fingerprints detected by the human minisatellite 33.6 probe (Prodöhl et al. 1992).

Single locus minisatellite DNA probes present a more practical method for the detection and population screening of these highly variable loci (Burke et al. 1991). With much less complicated patterns (only one or two bands per lane) allelic fragments can be more consistently resolved and accurately scored among gels, with resultant locus specific data being amenable to standard population genetic analyses. Although generally regarded as being species specific, many isolated SLPs have been shown to hybridize to minisatellite loci in closely related species (e.g. Bentzen et al. 1991, Wolff et al. 1991, Hanotte et al. 1992). Of 12 SLPs isolated from Atlantic salmon and brown trout DNA libraries seven have been found to detect single locus polymorphisms in Arctic charr as well (Prodöhl 1993). This panel of probes should be sufficiently large for most population analyses, without the need to clone and isolate SLPs specifically from Arctic charr DNA. Although three of the six SLPs used to screen the Arctic charr populations were found to be unsuitable, minor alterations to electrophoretic and probing methodologies, together with inclusion of internal DNA standard markers (Taggart and Ferguson 1994), should be sufficient to allow their inclusion in subsequent studies.

No firm conclusions relating to genetic substructuring among the charr populations can be drawn from the limited data obtained to date. However it is clear from the presence of fixed (or at least very high frequency) allele differences that extensive genetic differentiation does exist. At present the pattern of both multi- and single locus results can be most readily reconciled to stochastic events involving relatively small and totally isolated populations.

On a specific note the SLP derived data confirmed the genetic distinctness of two morphs of charr in Loch Rannoch originally reported by Hartley et al. (1992b). However there was no indication of a similar situation regarding the two Lake Windermere populations examined. This is in contrast to the results of Partington and Mills (1988) who found significant differences in the frequencies of the *EST-1** 115 allele and the 130 allele of *MDH*-4,5* between north and south basin autumn spawning charr. The SLP derived data also groups the three populations from the northwest of Scotland together but fixation for a *Hin*dIII mt DNA polymorphism in Lochs Clair and Coulin distinguish these two populations from the Loch Mealt one (Hartley, unpublished observation).

Thus, while DNA fingerprinting techniques can provide additional, powerful genetic markers, their use should not be considered in isolation. It is likely that the full extent of genetic variability and differentiation among Arctic charr populations will only be resolved by utilising a combination of genetic methodologies.

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Current Status and Distribution of Arctic Char *Salvelinus alpinus* (L.) in Norway: The effects of Acidification and Introductions

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Abstract

The community status of 5,666 stocks of Arctic char (*Salvelinus alpinus*) in Norwegian lakes was monitored using interviews. A total of 228 stocks are extinct, and an additional 268 stocks are in differing stages of decline. Acidification is recognized as the most severe threat to Arctic char in Norway, and areas in southernmost Norway are seriously affected. The majority of the stocks in this region were affected after 1960, but the earliest indications of decline occurred in the early 1900s. Stocks in western Norway have experienced the most recent changes. Analyses of principle components, variance, discriminant and regression, indicated that pH and monomeric inorganic aluminium were the water quality parameters most strongly related to char status. However, acid-neutralizing capacity (ANC), alkalinity and calcium were also correlated to char status. Arctic char appear to be more sensitive to acidification than brown trout (*Salmo trutta*) and perch (*Perca fluviatilis*), which occur most commonly in sympatry with Arctic char. The natural distribution of Arctic char in Norway extends along coastal areas throughout the country. However, translocations and introductions over the past 100-120 years have increased the distribution of the species significantly. This is particularly the case in some interior areas in southern Norway and in northern Norway, although exact data from the latter mentioned region are scarce. Most of the introduced stocks cited by Huitfeldt-Kaas (1918), have established self-sustaining populations. A conservation programme for Arctic char in Norwegian lakes is suggested. Unique stocks should be recognized and given priority for conservation. In acidified areas liming may save threatened stocks.

Keywords: Char, threats, acidification, status, distribution, introductions.

Introduction

Arctic char *Salvelinus alpinus* have a northern circumpolar distribution. In Europe the species has been regarded as a glacial relict (Johnson 1980). Char are found in lakes and rivers in Scandinavia and Russia, and in deep alpine lakes in Central Europe. However, in Scandinavia, application of the relict concept to such a widespread species appears misleading.

Arctic char in Norwegian waters were briefly discussed by Collett (1875). Later, Huitfeldt-Kaas (1918) thoroughly outlined char distribution, and discussed possible immigration routes. He suggested that the original colonization of Norwegian watercourses by char was most probably achieved through two different routes; one from the Atlantic in the west, and the other via eastbound rivers from the Ancylus Lake (presently Baltic basin). This general pattern has later been supported by a regional study of genetic variation using enzyme electrophoresis (Hindar et al. 1986). In broad terms, the area reached via natural immigration following the last glaciation, extended from Østfold county in the southeast, along the coast to Finnmark in the northeast and into parts of the interior southeastern region. In mainland Norway, all watercourses below the upper marine limit have been generally accessible for Arctic char, and upstream migration has been possible in rivers with moderate gradients. In some steep rivers in the west, Arctic char are still restricted to lakes below the upper marine limit.

The Arctic char is known for its phenotypic plasticity (Savvaitova 1980), and in Norway sympatric dwarf and normal char are found in several lakes (Aass 1968, Klemetsen and Grotnes 1975, 1980, Hindar and Jonsson 1982, Hindar et al. 1986, Kristoffersen et al. 1994, Hesthagen et al. 1995a). These morphs have been interpreted as species which arrived in Scandinavian waters in repeated immigrations (Nyman et al. 1981). However, recent research has shown that they emerged as a result of local diversification (Hindar et al. 1986, Sandlund et al. 1992, Hindar and Jonsson 1993).

In some watercourses, one morph may be anadromous, performing foraging migrations to the sea during the summer. In Norway, this morph occurs in Spitsbergen, and on the mainland as far south as Bindal in Nordland county (Jensen 1981, Klemetsen 1993).

The distribution of freshwater fishes can change over time due to natural causes (Wheeler 1974). However, in recent decades, man has accelerated these changes considerably through two different processes; various threats may cause deterioration of stocks whereas translocations of indigenous fishes increase the distribution of one species at the expense of another (Wheeler 1977). Species extinctions and range reductions now occur among freshwater fishes all over the world (Moyle and Leidy 1992). Thus, there is a growing concern about protecting the biodiversity and genetic variation of these resources (Lelek 1986, Nyman 1991, Ryman et al. 1994). The status of freshwater fish stocks is a good indicator of the effects of man's influence on aquatic environments (Wheeler 1974). Factors such as habitat alteration through fragmentation or complete destruction, pollution, and overharvesting adversely affect many freshwater fish communities (Miller et al. 1989).

Acid precipitation has been recognized as the most severe threat caused by human activity to freshwater fishes in Norwegian watersheds (Overrein et al. 1980). Severe damages are evident in Atlantic salmon and inland fish stocks (Hesthagen and Hansen 1991, Hesthagen et al. 1994). Field and experimental studies suggest that the Arctic char is highly vulnerable to acidic waters (Almer et al. 1974, Edwards and Hjeldnes 1977, Andersen et al. 1984). Recruitment failure seems to be the main population response of this species to acidification in Norwegian lakes (Andersen et al. 1984, Kleiven and Matzow 1989, Kleiven et al. 1990, Hesthagen et al. 1995a).

Man has been responsible for considerable redistribution of native fish species. This activity confounds the detection of any changes due to natural causes (Wheeler 1974). Due to the high number of undocumented translocations of Arctic char, the natural distribution of the species in Norway is not easily described (cf. Huitfeldt-Kaas 1918). Many introductions were made after techniques for artificial hatching became known in the late 1800s (Helland 1913, Huitfeldt-Kaas 1918, Bleken Rud 1967, Berg 1986).

In the present study, only resident char in mainland lakes in Norway are considered. The aims of the study are two-fold: (i) to document more recent changes in char distribution, and (ii) to identify factors causing deterioration in these stocks, with special reference to the effects of acidification.

Methods

Fish community status

Data on lakes which are or previously were inhabited by fish were obtained through interviews with land owners, local fishermen or others with extensive local knowledge about fish stocks (Hesthagen et al. 1993). Informants were asked to classify the current status for Arctic char as follows: (i) unchanged populations giving satisfactory catches. This group also includes unchanged populations which have never been numerous due to natural factors (unsuitable spawning grounds, competition from other fish species etc.), (ii) populations which have experienced an apparent decline in abundance, and (iii) populations which are apparently extinct. This method has been evaluated through gill net surveys in 230 lakes, of which 42 contained Arctic char (Hesthagen et al. 1993). Agreement between reported fish status and the survey net catches was generally good. Satisfactory catches were obtained in lakes reported to be healthy and only a few or no fish were caught in lakes reported to be barren. However, the reported fish status for affected stocks tends to be too optimistic, as the discriminant analysis classifies a high fraction of these stocks as lost.

Informants were also asked to date the occurrence of damage to a specific decade, and suggest probable reasons for these population changes. Information on potential threats was also obtained from local environmental authorities and various written sources. Such changes might be due to the introduction of non-native fish species or to enviromental changes caused by industrial effluents, agricultural runoff, eutrophication, habitat destruction or hydro power regulation. In this context, changes in population abundance caused by changes in fishing intensity are not considered as damage. When the deterioration of fish stocks could not be related to any local human activity or any other causes, long-range transported air pollutants acting through a degradation of water quality were considered the main reason for the reported damages. In areas where the critical levels of surface waters were not exceeded (cf. Henriksen and Hesthagen 1993), the causes of reported population damages were classified as unknown.

Introductions of Arctic char

The first comprehensive data on the introduction of Arctic char in parts of southern Norway were obtained by Helland (1913). Later, Huitfeldt-Kaas (1918) provided char data for lakes throughout Norway (see also Huitfeldt-Kaas 1927). These lakes were localized on topographical maps, except when localites could not be safely identified by the names given by Huitfeldt-Kaas (1918). Further information has been obtained from the diaries of S.E. Sunde, who was a fishery secretary at the Fishery-inspector of Inland Fisheries between 1919 and 1940. However, most data of Arctic char introductions were obtained from interviews and completed questionnaires from private landowers and local fishermen throughout the country approached in connection with this study.

Information on the accuracy of the timing of these introductions may vary, and five different categories (i-v) are distinguished. Most introductions could be dated to either an exact year (i) or a specific decade (ii). If the time of introduction could be either one of two decades, then the conservative estimate was chosen (iii). For some stocks, particularly those introduced a long time ago, the only certain information is that they were present in a certain decade (iv). Finally, some populations can only be identified as having been introduced without any exact knowledge of when (v). Each category was coded in our database.

Water chemistry

Water samples were taken close to or in the lake outlet at randomly chosen lakes within each county, i.e. not related to fish status or species composition. The samples were collected in late autumn, mainly in September and October between 1986 and 1993. Lakes that were limed or affected by some other human activity were excluded from the sampling programme. The samples were stored and analyzed according to standard methods at the NINA laboratory (cf. Schartau 1991).

The following chemical parameters were included in the analysis: pH, alkalinity, major ions (Ca, Mg, Na, K, Cl, SO_4, NO_3), Al_a (total monomeric aluminium), Al_o (organically bound monomeric aluminium) and Al_i (inorganic monomeric aluminium, Al_i=Al_a-Al_o). Furthermore, ANC (Acid-Neutralizing Capacity) was calculated from the measured variables as ANC= $(Ca+Mg+Na+K)-(Cl+SO_4+NO_3)$. Not all variables were analyzed in each sample (cf. Table 4).

The status of Arctic char was analyzed in relation to the various chemical parameters. Because ANC is a linear combination of seven major ions listed, ANC and these ions were not used together as independent variables in any individual multiple regression analysis as described by Bulger et al. (1993). They analyzed the status of brown trout (*Salmo trutta*) in relation to water chemistry in Norwegian lakes.

All data concerning fish status, time of introduction, causes of damages, liming and water chemical variables were recorded in an Access data base. All lakes were identified from 1:50,000 topographical maps (Statens Kartverk M711-series), and given grid zone designation and sample reference codes in order to recognize each lake and make dataplots possible.

All tests were performed with the statistical package SPSS.

Results

Recent changes in status

The community status of Arctic char was obtained from 5,666 lakes (Table 1). Our data do not represent all char lakes in Norway, but for Nord-Trøndelag and counties further south a dominant fraction is included (Fig. 2). Char occur regularly in Trøndelag and areas further north. Most of the Arctic char stocks are located in Finnmark county, northern Norway.

A total of 228 stocks are reported to be extinct, and an additional 268 stocks are in different stages of decline. The highest fraction of damaged stocks is in Østfold (83%), but this county contains few stocks (*N*=13). Damages are also considerable in Aust-Agder (71%), Vest-Agder (66%) and in Akershus (62%). In Oppland, Hedmark, Telemark and Rogaland, the damage is also relatively high (31-39%).

Table 1. Community status for Arctic char in lakes in different counties. For the location of the different counties, see Figure 2.

County	Total	Unknown	Unchanged	Affected	Extinct
Østfold	13	1	2	4	6
Akershus	41	2	15	6	18
Oslo	22	3	13	0	6
Hedmark	195	19	130	31	15
Oppland	257	7	157	49	44
Buskerud	131	7	89	25	10
Vestfold	6	4	2	0	0
Telemark	122	2	80	22	18
Aust-Agder	60	3	15	16	26
Vest-Agder	40	6	11	9	14
Rogaland	175	7	99	30	39
Hordaland	131	10	107	13	1
Sogn og Fjordane	86	5	72	7	2
Møre og Romsdal	107	7	89	9	2
Sør-Trøndelag	388	46	319	13	10
Nord-Trøndelag	494	25	458	7	4
Nordland	547	40	480	17	10
Troms	562	1	554	7	0
Finnmark	2,289	11	2,272	3	3
Total	5,666	206	4,964	268	228

Table 2. Identification of factors responsible for extinction and reduction of Arctic char stocks in Norwegian lakes. * Introduced stocks in two shallow mountain lakes.

Threats	Status: Extinct *N*	(%)	Reduced *N*	(%)
Acidification	190	(83.3)	198	(73.9)
Eutrophication/Sedimentation	1	(0.4)	10	(3.7)
Hydro power regulation			15	(5.6)
Habitat destruction			1	(0.4)
Introduction of pike	5	(2.2)	4	(1.5)
Introduction of whitefish			8	(3.0)
Introduction of *Mysis relicta*			2	(0.8)
Deoxygenation (shallow lakes)*	2	(0.9)		
Rotenone treatment	1	(0.4)		
Unknown causes	29	(12.7)	30	(11.2)
Total	228		268	

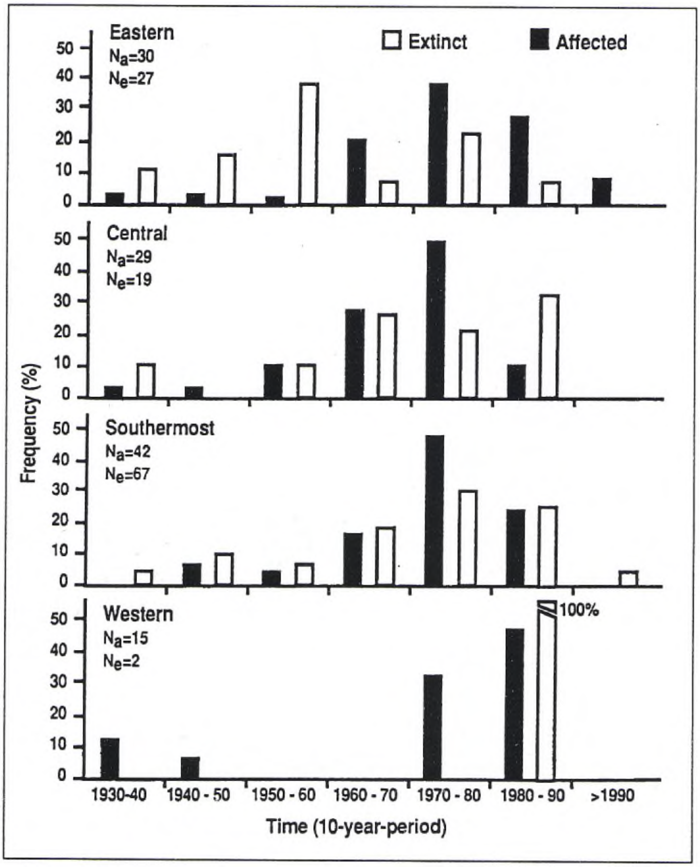

Fig. 1. The time in terms of 10-year-periods when Arctic char stocks in four different regions in lakes in southern Norway became affected and/or extinct. The following counties are included in the different regions; Eastern Norway: Østfold, Akershus and Hedmark, Central Norway: Oppland and Buskerud, Southernmost: Telemark, Aust-Agder, Vest-Agder and Rogaland, and Western Norway: Hordaland and Sogn og Fjordane. N_A and N_E are number of affected and extinct stocks, repectively. For location of different counties, see Fig. 2.

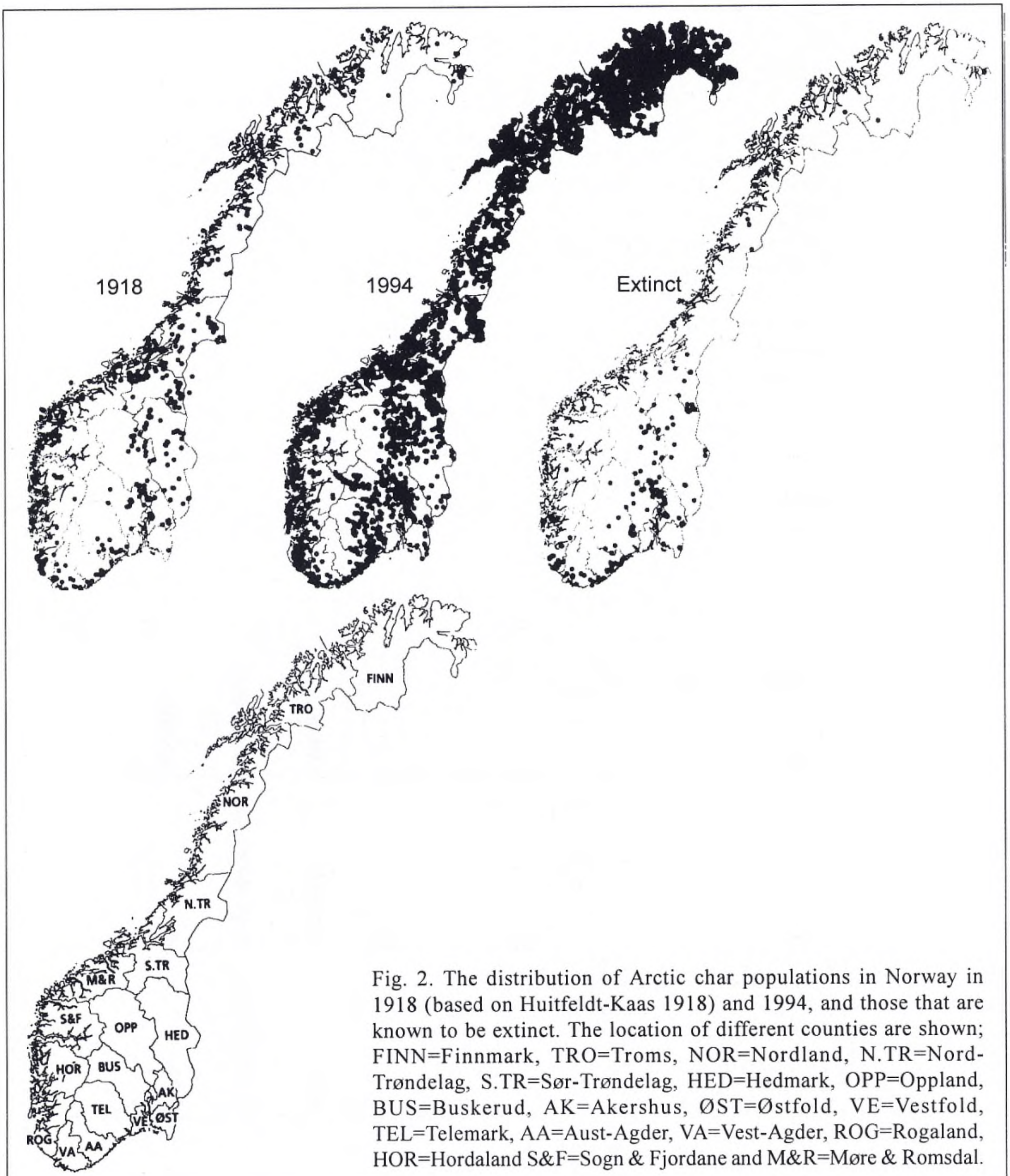

Fig. 2. The distribution of Arctic char populations in Norway in 1918 (based on Huitfeldt-Kaas 1918) and 1994, and those that are known to be extinct. The location of different counties are shown; FINN=Finnmark, TRO=Troms, NOR=Nordland, N.TR=Nord-Trøndelag, S.TR=Sør-Trøndelag, HED=Hedmark, OPP=Oppland, BUS=Buskerud, AK=Akershus, ØST=Østfold, VE=Vestfold, TEL=Telemark, AA=Aust-Agder, VA=Vest-Agder, ROG=Rogaland, HOR=Hordaland S&F=Sogn & Fjordane and M&R=Møre & Romsdal.

Most of the extinctions of char stocks were caused by acidification (83.3%, Table 2). Further, five stocks were wiped out after the introduction of pike (*Esox lucius*). Among stocks which are in different stages of reduction, acidification was also recognized as the most severe threat (73.9%). Some threats were due to introductions of non-native fish species such as whitefish (*Coregonus lavaretus*) and pike, hydro power regulation and eutrophication or sedimentation.

Timing of damage

Damage to Arctic char stocks in eastern parts of Norway (Østfold, Akershus and Hedmark), was first recorded in the 1930s (Fig. 1). However, most stocks became extinct in the 1950s, whereas reductions occurred mainly in the 1960s and 1970s. Char stocks located in acidified regions in southern central Norway were generally damaged (both affected and extinct stocks) later than those in the eastern Norway. However, based on the number of damaged stocks in the ≤1940s, 1950s, 1960s, 1970s and ≥1980s, there was no significant difference in time of damage between these two regions (χ^2-test=6.18, $P>0.05$). In southernmost Norway, the first extinct stocks were also recorded in the 1930s. However, most of the damages occurred during the 1970s and 1980s. In western Norway (i.e. Hordaland and Sogn og Fjordane counties), the effects of acidification on char stocks appeared significantly later than that in other parts of southern Norway (χ^2-test=11.18, $P<0.05$). Although some stocks in Hordaland were reduced before 1950, most population changes in western Norway occurred after 1970.

Changes in distribution

There have been considerable changes in the distribution of Arctic char from the early 1900s (cf. Huitfeldt-Kaas 1918) to the present (Fig. 2). The most pronounced changes are due to translocations (N=233), which have been carried out most intensively in the interior of southern Norway (Fig. 3). In Telemark and Buskerud counties, char originally occurred in only a few lakes near the coast. However, two introductions caused a major increase in the distribution of char in Buskerud: in lakes Breivatn and Ustevatn in 1910, Hol municipality (Aagaard 1915, Dahl 1920). These two lakes are located in two different watersheds, and originally were only inhabited by brown trout. From Breivatn, Arctic char spread downstream to several lakes, reaching lakes Pålsbufjord and Tunhovdfjord, which are located some 35 and 43 km downstream, respectively, after 9 years. By 1919 Arctic char were also translocated into the neighbouring Lake Holtervann, which drains into the Skurdal watershed (Dahl 1920). At present, there are at least 42 lakes in Hol which are inhabited by Arctic char, and this change has occurred within a few decades. In Telemark county, extensive stockings of Arctic char were carried out in the early 1900, based to a large extent on fry from the State Hatchery at Tinn (cf. Landmark 1918)

However, the distribution of char has also increased considerably in other regions which originally only supported brown trout. In the forest area north of Oslo, Arctic char was probably native only to Lake Maridalsvatn (Huitfeldt-Kaas 1918). The first translocation from this lake occurred into Lake Elvatn in Hakadalen around 1800, and later several introductions have been performed in the area (Dahl 1938, Frislid 1987).

In Oppdal municipality in the southernmost part of Sør-Trøndelag county, char were introduced into at least 33 lakes, mainly between 1901 and 1912. In northern Norway, e.g. Nordland, Troms and Finnmark counties, exact data on char introductions have been less easily available. However, considerable redistributions are evident in several areas of all three counties (Berg 1986, Magnus Berg personal communication, see also Annual Reports from the Fishery-inspector of Inland Fisheries).

The rates of establishment of introduced char stocks can be estimated from the data presented by Huitfeldt-Kaas (1918). Of a total 117 introduced stocks cited, 110 stocks (94%) are now self-sustaining (Table 3). The highest number of introductions were reported from Oppland and Sør-Trøndelag counties.

Conversely, the extinction of char stocks have resulted in reduced distribution in parts of southern Norway (Fig. 2). However, there are still some stocks left in most affected areas, causing relatively small reductions in the overall distribution area.

Status of char relative to sympatric stocks of brown trout and perch

Arctic char generally suffered greater damage than brown trout in lakes where these species

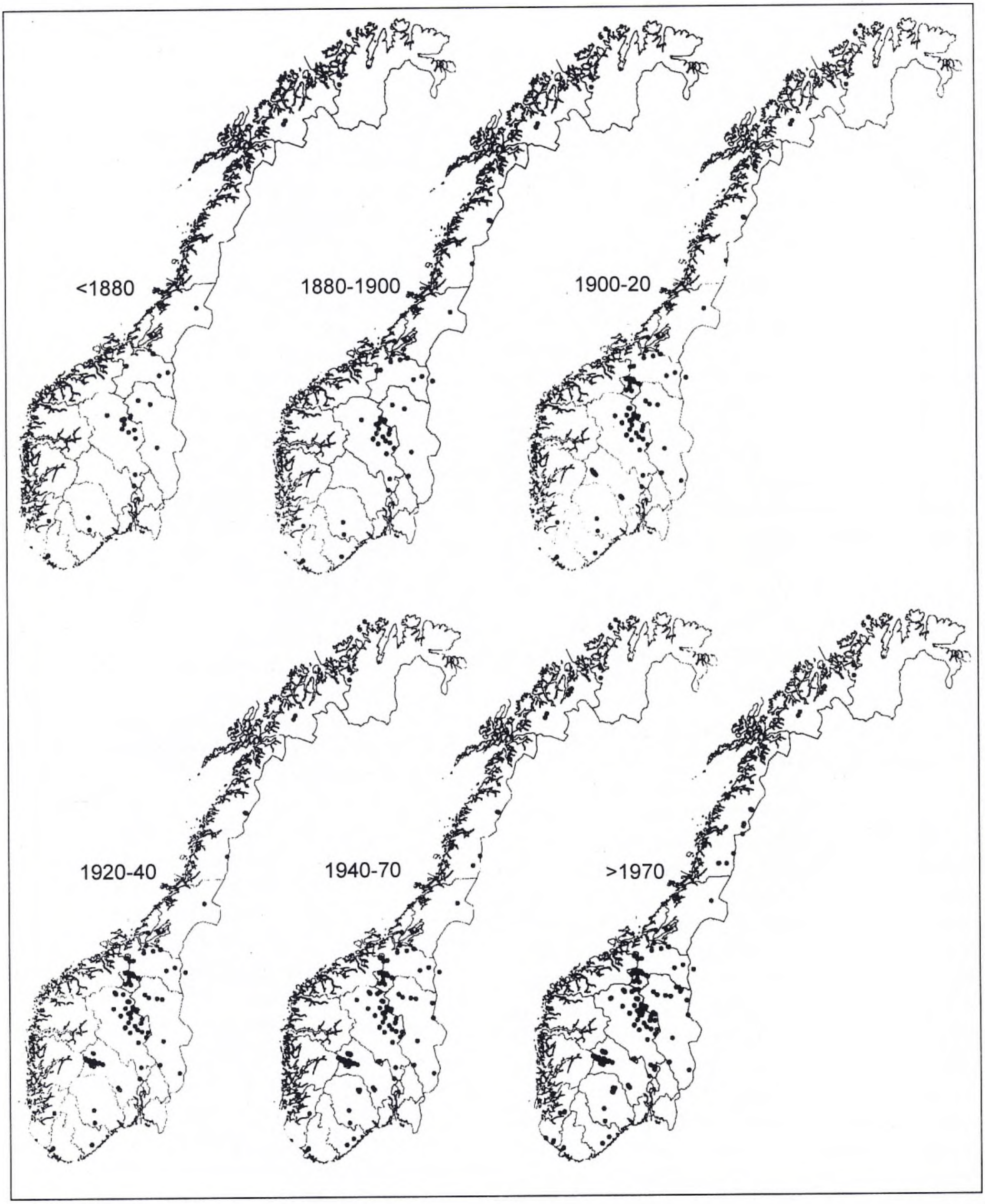

Fig. 3. Cumulative plots of geographical location of Arctic char populations introduced during the periods <1880 to >1970. Only populations where exact information is available were included.

Table 3. Number of Arctic char stocks presented by Huitfeldt-Kaas (1918) in terms of totals, introduced and established of those that were introduced in each county.

County	Total	Introduced	Established
Østfold	3	1	1
Akershus	6	2	2
Oslo	3	1	1
Hedmark	42	9	7
Oppland	35	17	12
Buskerud	16	6	6
Vestfold	4	1	1
Telemark	44	4	4
Aust-Agder	27	4	3
Vest-Agder	18	3	2
Rogaland	39	2	2
Hordaland	106	4	4
Sogn og Fjordane	77	1	1
Møre og Romsdal	56	8	7
Sør-Trøndelag	110	23	23
Nord-Trøndelag	115	10	10
Nordland	107	11	11
Troms	59	6	6
Finnmark	57	4	4
Total	924	117	110

occur in sympatry (Fig. 4). In lakes with unchanged populations of brown trout (N=580), 18% of the Arctic char stocks were damaged (χ^2-test=117.71, $P<0.001$). In lakes where brown trout are affected (N=233), a high fraction of the Arctic char stocks were extinct (31%), χ^2-test=282.81, $P<0.001$. However, in some lakes of this status category, brown trout suffered damage while Arctic char remained unaffected (25%). In lakes where brown trout stocks are extinct (N=55), most Arctic char stocks exhibited the same community status (86%), χ^2-test=8.63, $P<0.05$.

Among sympatric stocks of affected or extinct Arctic char and brown trout, a comparison of time of damage in terms of specific decade was made (Fig. 5). For affected stocks, there was no difference in the time at which they became reduced (sign-test, $P>0.05$), However, among extinct stocks, Arctic char disappeared significantly earlier than brown trout (sign-test, $P<0.05$).

Arctic char also suffered significantly greater damage than perch (*Perca fluviatilis*) (Fig. 4). In lakes with unchanged perch stocks (N=246), 46% of the char stocks were either extinct or reduced (χ^2-test=148.38, $P<0.001$). In lakes where perch are affected (N=31), the majority of Arctic char stocks were extinct (52%), χ^2-test=51.06, $P<0.001$. However, Arctic char were unaffected in a few lakes (N=3) where perch experienced a decline in abundance. In lakes where both species were either affected or extinct, Arctic char responded earlier than perch (Fig. 5, sign-test, $P<0.05$).

Status of Arctic char and water chemical variables

Water quality in different status groups

Study lakes were generally acidic (pH<6.0), low in ionic strength, and consequently low in alkalinity and ANC (Table 4). Lakes that have lost

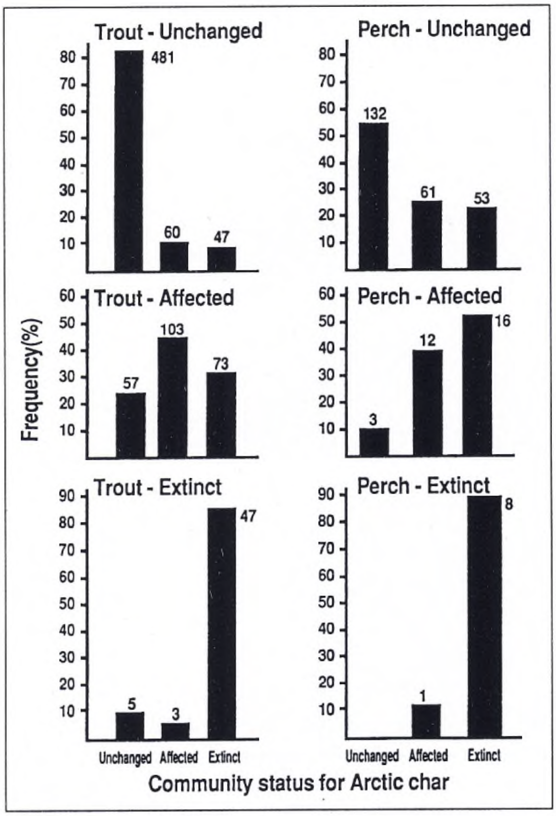

Fig. 4. The precént distribution of community status of Arctic char in location with unchanged, affected and extinct stocks of brown trout and perch in Norwegian lakes. Number of stocks are given above the columns.

their char stocks have poorer water quality than lakes with stocks in different stages of reduction, which on the other hand were more marginal than those sustaining healthy stocks (Table 5). However, there were significant differences in mean values between these three categories only for pH and Al_i (ANOVA, $P<0.05$). Further, for ANC, alkalinity and the calcium concentration, there were significant differences between healthy and damaged (i.e. extinct and affected) stocks.

Principal component analysis (PCA)

PCA can be employed to discover the facets of and the bases for an overall phenomenon

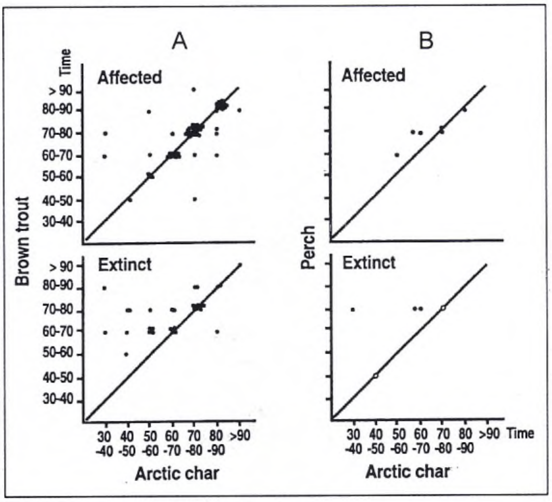

Fig. 5. Analyses of time difference in terms of 10-year-periods when sympatric stocks of (A) Arctic char and brown trout and (B) Arctic char and perch became affected and/or extinct in Norwegian lakes. The 45° line indicates simultaneous effects on the two species.

(Pimentel 1979). Several procedures have been proposed for determining the number of factors to use in a model; one criterion suggests that only factors accounting for variances (eigenvalues) greater than 1 should be included (Norušis 1986). Accordingly, almost 81% of the total variance is attributable to status (37.4%), pH (32.2%) and labile aluminium (11.3%).

Principal component 1 recognizes a lake acidification component; intercorrelation among ANC, alkalinity, pH and calcium (Table 6). Principal component 2 recognizes a positive correlation between magnesium, natrium, nitrate and chloride. This component can to some extent be called the sea salt component, except that sulfate was not included (cf. Bulger et al. 1993). Principal component 3 recognizes a strong positive correlation between status and Al_i, which implies that lakes with high concentrations of labile aluminium are more likely to have damaged char populations.

Discriminant analysis

Discriminant analysis aims to form linear combinations of independent variables for classify-

Table 4. Water chemical data for the study of lakes. N=number of analyses.

Variables	Units	Mean	SD	Minimum	Maximum	N
pH		5.88	0.68	4.45	7.55	349
Alk	μeq L^{-1}	62.74	115.93	0.00	854.00	276
Ca	mg L^{-1}	1.94	2.22	0.18	26.24	349
Mg	mg L^{-1}	0.49	0.43	0.05	3.43	248
Na	mg L^{-1}	2.01	2.28	0.24	15.76	248
K	mg L^{-1}	0.39	0.32	0.01	2.30	248
SO_4	mg L^{-1}	4.22	6.61	8.20	99.00	248
NO_3	μg L^{-1}	86.36	114.38	5.35	534.00	114
Cl	mg L^{-1}	3.26	3.94	0.18	17.65	248
Al_i	μg L^{-1}	27.51	43.52	0.00	218.00	174
ANC	μeq L^{-1}	64.05	130.40	-77.02	748.81	109

ing cases into class membership. This analysis revealed that pH and Al_i were the most significant variables for explaining the fish community status of Arctic char; canonical correlations were 0.58 and 0.56, respectively (Table 7). Calcium, alkalinity and ANC were less important variables for explaining class membership. The percent of grouped cases correctly classified was highest for Al_i (75.9%) with predicted group membership for unaffected and extinct stocks of 89.8 and 59.1%, respectively, as opposed to 59.0% for pH (Table 8). Unchanged and extinct stocks were also the two classes with the greatest classification rate (68-69%).

Regression analysis

In a regression analysis with single independent chemical variables, pH and Al_i yielded the largest R^2-values, explaining 33 and 31% of the variance in Arctic char status, respectively (Table 9). According to this analysis, no other individual variable is a satisfactory predictor, explaining less than 8% of the total variance in char response.

Table 5. Mean values ± standard deviation for 11 chemical variables for lakes with unaffected, declined and extinct char stocks. The mean values were tested by one-way analysis of variance using The Scheffé test ($P<0.05$). Mean values that are not significantly different are given the same superscript letter.

Variable	Unaffected	Declined	Extinct
pH	6.15± 0.58 (237)^{a}	5.44± 0.49 (70)^{b}	5.13± 0.48 (42)^{c}
Alk	81.65± 31.53 (198)^{a}	19.14± 25.65 (49)^{b}	7.28± 10.98 (29)^{bc}
Ca	2.29± 2.58 (237)^{a}	1.29± 0.78 (70)^{b}	1.09± 0.68 (42)^{bc}
Mg	0.51± 0.47 (178)^{a}	0.42± 0.32 (47)^{a}	0.52± 0.34 (28)^{a}
Na	1.89± 2.33 (174)^{a}	2.09± 2.09 (46)^{a}	2.63± 2.28 (28)^{a}
K	0.40± 0.35 (174)^{a}	0.36± 0.23 (46)^{a}	0.35± 0.16 (28)^{a}
SO4	4.14± 7.96 (173)^{a}	4.10± 2.29 (48)^{a}	4.98± 3.10 (26)^{a}
Cl	2.94± 3.79 (172)^{a}	3.55± 3.96 (45)^{a}	4.83± 4.58 (27)^{a}
NO3	72.60±103.17 (88)^{a}	128.30±139.56 (13)^{a}	137.60±142.88 (13)^{a}
ANC	84.69±141.67 (84)^{a}	4.48± 19.94 (13)^{ab}	-15.93± 25.51 (12)^{b}
Al_i	13.84± 20.87 (127)^{a}	48.23± 52.3 (25)^{b}	82.84± 70.80 (22)^{c}

Table 6. Principal component analysis. Eigenvalues, percent variance explained (rotated), and varimax rotated loadings (correlation coefficients) for char status and 11 chemical variables with respect to the three components extracted in the PCA. The highest correlation coefficient for each variable is shown in bold face, and variables having their highest correlations on the same component are boxed.

		Component	
	1	2	3
Eigenvalue:	4.492	3.869	1.352
% variance:	37.4%	32.2%	11.3%
Variable			
ANC (μeq L^{-1})	**0.971**	-0.113	-0.106
Alk (μeq L^{-1})	**0.976**	0.705	0.128
pH	**0.716**	-0.084	-0.551
Ca (mg L^{-1})	**0.975**	0.044	-0.029
Mg (mg L^{-1})	0.583	**0.705**	0.128
Na (mg L^{-1})	-0.084	**0.933**	0.214
NO_3 (μg L^{-1})	-0.070	**0.833**	0.057
Cl (mg L^{-1})	-0.108	**0.924**	0.205
Status	-0.164	0.131	**0.865**
Al_i (μg L^{-1})	0.042	0.209	**0.867**
K (mg L^{-1})	0.583	0.512	-0.117
SO_4 (mg L^{-1})	0.434	0.421	0.218

Table 7. F-statistics of significant variables and P-values for different chemical parameters obtained from discriminant analyses, listed in descending order of magnitude.

Variable	*F*-statistics	*P*-value	Canonical correlation
pH	89.08	<0.00001	0.58
Al_i	38.54	<0.00001	0.56
Alk	10.04	<0.0001	0.26
Ca	9.38	<0.0001	0.23
ANC	5.01	0.0083	0.29
NO_3	2.91	0.0586	0.22
Cl	2.85	0.0599	0.15
Na	1.30	0.2733	0.10
Mg	0.82	0.4416	0.08
K	0.48	0.6194	0.06
SO_4	0.18	0.8350	0.04

A multiple regression analysis using four different variable sets as suggested by Bulger et al. (1993) was performed (Table 10). The first set included physiological variables pH, labile aluminium (Al_i) and calcium. The second variable set comprised the seven main geochemical variables needed to calculate ANC. The third variable set consisted of the seven major ions included in set 2 plus pH. The fourth variable set comprised all independently measured chemical variables (cf. Table 4), except ANC values (cf. Bulger et al. 1993). The results of these multiple regression analyses coincided with those obtained from the other analyses, suggesting again that pH and Al_i are the best predictors of Arctic char status. The fourth data set yielded a small improvement over these two variables compared with that when all measured variables were included (6-7% units). Stepwise multiple regressions only gave minor improvements (7-13% units) compared with pH and Al_i as single variables.

Discussion

According to Huitfeldt-Kaas (1918), the natural distribution of Arctic char in southern Norway was restricted to an area along the coast. However, undocumented human introductions should be considered. Some changes in the original areas of occurrence may also have been due to climatic changes as this species is a cold water salmonidae (cf. Gillet and Breton 1992, Guillard et al. 1992). Harstad (1961) claimed that Arctic char have declined due to increases in water temperature, but also because of competition from other fish species. In southern and central Sweden, Arctic char is regarded as a glacial relict because the species is only found in clear, deep and oligotrophic lakes (Nyberg et al. 1986). Arctic char were generally only caught in water layers with temperatures below 16°C, e.g. only below the thermocline. However, the present distribution of Arctic char in lowland areas of Sweden as well as Norway, may be a result of displacement by fish species that were later immigrants (Huitfeldt-Kaas 1918). We suggest that

Table 8. Classification of char lakes in terms of predicted group membership based on five water chemical variables. Group 1, 2 and 3 comprises lakes with unchanged, declined and extinct stocks, respectively. The percent of grouped cases correctly classified for each variable is indicated.

Variable	Group	*N*	Predicted group membership (%) 1	2	3	Correctly classified
Al_i	1	127	114 (89.8)	7 (5.5)	5 (4.7)	
	2	25	13 (52.0)	5 (20.0	7 (28.0)	
	3	22	8 (36.4)	1 (4.5)	13 (59.1)	
						75.9
pH	1	237	162 (68.4)	59 (24.9)	16 (6.8)	
	2	70	20 (28.6)	15 (21.4)	35 (50.0)	
	3	42	6 (14.3)	7 (16.7)	29 (69.0)	
						59.0
ANC	1	84	44 (52.4)	33 (39.3)	7 (8.3)	
	2	13	1 (7.7)	8 (61.5)	4 (30.8)	
	3	12	0 (0.0)	3 (25.0)	9 (75.0)	
						56.0
Alk	1	198	94 (47.5)	64 (32.3)	40 (20.2)	
	2	49	7 (14.3)	16 (32.7)	26 (53.1)	
	3	29	0 (0.0)	8 (27.6)	21 (72.4)	
						47.5
Ca	1	237	119 (50.2)	45 (19.0)	73 (30.8)	
	2	70	16 (22.9)	18 (25.7)	36 (51.4)	
	3	42	6 (14.3)	11 (26.2)	25 (59.5)	
						46.4

Table 9. Simple linear regression analysis between different chemical parameters and char status as independent variable exhibiting regression coefficient (R^2), *F*-value and significant level.

Variable	R^2	*F*-value	*P*
pH	0.33	169.28	<0.00001
Al_i	0.31	77.54	<0.00001
Alk	0.06	18.35	<0.00001
Ca	0.05	17.17	<0.00001
ANC	0.08	9.50	<0.005
Cl	0.02	5.48	<0.05
NO_3	0.05	5.42	<0.05
Na	<0.01	2.43	>0.05
K	<0.01	0.85	>0.05
SO_4	<0.01	0.22	>0.05
Mg	<0.01	0.18	>0.05

Table 10. Stepwise linear regression analyses with R^2-values between char status and different chemical variables. Only significant regressions ($P<0.05$) are listed.

Variables	R^2
Physiological variables (pH, Ca, Al_i)	
Step 1: Al_i	0.31
Step 2: pH	0.40
Major ions	
Step 1: Na	0.07
Step 2: K	0.12
Major ions + pH	
Step 1: pH	0.28
Step 2: SO_4	0.38
All measured variables	
Step 1: Al_i	0.38
Step 2: pH	0.46
Step 3: SO_4	0.51

this might have been the case in Østfold which has the highest fish diversity in Norway, and where Arctic char now inhabit only a few lakes.

There have been considerable translocations and introductions of Arctic char in Norway, especially during the past 100-120 years. However, man-made alterations of the distribution of freshwater fishes have probably occurred in Norway since the first human settlement following the last glacial period (Huitfeldt-Kaas 1918). Arctic char probably occur in the mountains of central and northern Scandinavia because of natural immigration via the Ancylus lake through eastbound rivers (cf. Behnke 1972). Introductions of char by man have probably been quite common in this area (Ekman 1910, Klemetsen and Grotnes 1980).

Of the introduced Arctic char populations mentioned by Huitfeldt-Kaas (1918), 94% are now self-sustaining. A similarly high rate of establishment of char populations has also been found elsewhere (Jagoe et al. 1984). However, introductions of Arctic char into Swedish lakes resulted in a much lower percent of established self-sustaining populations (Alm 1920, Brundin 1939). Arctic char have been introduced in lakes in different European countries, and the success of these introductions has been attributed to physical, chemical and biological habitat characteristics (Brenner 1984). There are at least three reasons for high establishment rates of char in Norwegian lakes. Firstly, because the brown trout was, with very few exceptions, the only native fish species present prior to these introductions (cf. Dahl and Sømme 1942), char were subjected to low interspecific competition. Arctic char is generally competitively superior to brown trout because of selective differences like higher activity rates at lower temperature and better ability to locate prey items in poorer light conditions (Langeland et al. 1991). Secondly, most introductions probably involved a relatively large number of specimens, as hatchery-reared fry were used for stockings. Between 1876 and 1900, at least 5,778,100 Arctic char fry were stocked in lakes in southern Norway, which previously did not contain char (Landmark 1904). Thirdly, physical conditions in the lakes, being oligotrophic, cold water localities, were probably optimal for Arctic char (cf. Johnson 1980, Nyberg et al. 1986).

Our study suggests that acidification is the most serious threat to Arctic char in Norwegian lakes; causing losses or reductions in nearly 400 stocks. Arctic char populations in southernmost Norway are most seriously damaged, as 69% of all stocks in the Agder counties are affected. This damage is more severe than in the most affected areas in southern Sweden, where about 30% of the Arctic char stocks are now extinct (Nyberg et al. 1986). In northern Norway, only a few Arctic char stocks at Jarfjordfjellet (Sør-Varanger) near the Russian border are damaged (Hesthagen et al. 1995b). High emissions of SO_2 from the Kola Peninsula in recent years have caused acidification of the surface water in this area (Traaen 1987, Henriksen et al. 1988).

Some stocks of Arctic char in southern Norway were reported to be extinct in the 1930s. However, the first negative effect of acid deposition on Arctic char was probably evident in the early 1900s. The first fish status surveys in this area were carried out during the 1970s (Snekvik 1974, 1977, Muniz et al. 1976, Sevaldrud and Muniz 1980). However, these studies did not record Arctic char in all of the lakes they were found in the early 1900s (Huitfeldt-Kaas 1918). This probably means that these stocks were lost early in this century; information which was not readily available from interviews carried out 60-80 years later. According to Huitfeldt-Kaas (1918), all these char stocks were native. Hence, their disappearance was not due to their failure to become established after introductions. Damage to Arctic char in early 1900s is probably due to acidification. During this period, several brown trout stocks were reduced or wiped out in the same area, and Atlantic salmon suffered from episodes of fish kills (cf. Jensen and Snekvik 1972, Hesthagen et al. 1994).

The concentration of labile aluminium (Al_i) and pH are the chemical parameters most strongly related to Arctic char status. Both variables are considered toxic to fish (Baker and Schofield 1980, Driscoll et al. 1980, Schofield and Trojnar 1980, Rosseland et al. 1990). Hence, our data on char verify that factors usually responsible for losses of fishes in acid, soft waters are a combination of increased H+ ion concentration and the presence of toxic aluminium (cf. Sayer et al. 1991). The decline and extinction of fish in acidic, aluminium-rich water is explained by ionoregulatory failure (Muniz and Leivestad 1980, Wood 1989, Rosseland et al. 1990, Rosseland and Staurnes 1994).

We found that calcium explained little of the variation in char status. Calcium is considered to be of importance for fish status because it acts directly to ameliorate the toxic effects of low pHs and high concentations of labile aluminium (Brown 1983). Regression analyses conducted by Muniz and Walløe (1990), supported a conclusion that the concentration of calcium had no influence on the status of brown trout populations in Norwegian lakes. However, contributions made by an independent variable to a multiple regression are very much dependent on the other variables in the model presented by Bulger et al. (1993). They also focused on the role of calcium in determining ANC and pH, and hence labile aluminium concentration.

In lakes that had lost or reduced stocks of char, mean pHs values were 5.13 and 5.44, respectively. In different regions in Sweden, Arctic char became extinct in lakes with pHs between 4.5-5.2 (Almer and Hanson 1980, Degerman et al. 1992). In acidified lakes which have lost their char stocks, liming to a pH of 5.5-5.6 seems necessary for successful re-establishment (Lindström et al. 1984). Similarly, Arctic char kept at pH 5.5 did not exhibit any mortality, whereas there was a 10% mortality among specimens exposed to pH 4.8-5.0 for a period of 3½ months (Edwards and Hjeldnes 1977). However, it is a combination of the effects of low pH and high levels of toxic aluminium which are toxic to Arctic char. The mean concentration of Al_i in lakes with unaffected char stocks was 13.84 µg L^{-1} , compared with 82.84 µg L^{-1} in locatities where stocks were extinct.

Stress behaviour might also be partly responsible for the disappearance of char from acidic waters (Jones et al. 1985). Behavioural and physiological stress responses of Arctic char to acidification are rapid, however, fish may take several days to recover (Jones et al. 1987). These authors claimed that this interpretation does not contradict earlier suggestions concerning populations which become extinct through reproductive or recruitment failure, but rather that acid-stress behaviour would be expected to contribute to these failures. It has also been suggested that a low length/weight ratio in char in a lake reclaimed by liming is due to physiological disturbance (Lindström et al. 1982).

The present study indicates that the Arctic char is more sensitive to acidification than brown trout and perch. Similar differences in sensitivity to acidic waters between these three species have also been documented through test-fishing (Almer et al. 1974, Andersen et al. 1984, Linløkken 1985, Kleiven et al. 1990). However, perch may also disappear before Arctic char (Kleiven and Matzow 1989).

These differences in sensitivity are also in accordance with the results obtained by Edwards and Hjeldnes (1977) who noted that when exposed to lethally low pH, survival was highest in brown trout, intermediate in Arctic char and lowest in rainbow trout (*Oncorhynchus mykiss*). A similar result was also found by Bua and Snekvik (1972), based on hatching experiments with brown trout and Arctic char. Other experimental studies with char in combination with other species and tabulation of relative susceptability, indicate that char are highly sensitive to acidic soft water (Spry et al. 1981, Jagoe et al. 1984, Rosseland and Skogheim 1984).

However, from comparing ANC values (lake outlet samples) and fish status, it has been concluded that brown trout are less tolerant to acidification than Arctic char (Lien et al. 1992, Lydersen et al. 1994). This conclusion might merely be due to the fact that lake-spawning char are generally exposed to better water quality than stream-spawning brown trout (cf. Nyberg et al. 1986). The adult populations of brown trout may persist for years if a lake is less influenced by acidic events than its headwater streams (Bulger et al. 1993). The lake-spawning behaviour of Arctic char in southern Norway (cf. Aass 1968), provides protection against these acidic episodes. However, in northern regions of Scandinavia, river spawning by Arctic char might be more common (Curry-Lindahl 1957, Guldseth and Heggberget 1977), and such char stocks may be more vulnerable to acidification.

Eutrophication and sedimentation have threatened several char stocks in Norway. Destruction of spawning sites caused by sedimentation of humic substances have been claimed as one reason for the disappearence of the char stock in Lake Osensjøen in the late 1800s (Nysæther 1977). Lake enrichment followed by lower concentrations of oxygen and siltation of spawning sites, might represent a threat to Arctic char stocks (cf. Mills et al. 1990). However, changes in trophic status occur gradually, and the causality to any changes in char status might be difficult to detect. Moreover, there might also be some influence of climate changes (cf. Mills et al. 1990). However, the effect of this factor may be difficult to isolate.

The distribution and abundance of Arctic char may be affected by the introduction of other fish species such as whitefish and pike. However, pike might not be a serious threat to Arctic char in larger, deeper lakes because the two species occupy different habitats (Dahl 1914, Nyberg et al. 1986, Degerman and Nyberg 1987). Several introductions of whitefish have also affected char stocks negatively. In Finland, Arctic char was threatened in lakes after extensive stockings of whitefish (Kallio-Nyberg and Koljonen 1991). Whitefish was a more effective zooplankton-feeder that Arctic char, and are therefore considered competitively superior (Svärdson 1976).

A high fraction of Norwegian watersheds are now regulated for hydro power production. Fluctuating water level might cause drying out and freezing of char eggs (Aass 1961). The development of Arctic char in regulated lakes may therefore depend on the extent of the lowering of the water level and changes in the water temperature regime. Sixteen years after impoundment in a Norwegian reservoir, the abundance of Arctic char was reduced by 70% (Aass 1972). Reproduction of Arctic char in hydroelectric reservoirs might also be indirectly affected by changing water temperature regime through an increase in algal growth on the bottom substrate (cf. Mills et al. 1990).

Increased water levels in regulated lakes may have removed migration barriers and facilitated further penetration (Aass 1961). Another aspect of watershed regulation is the creation of tunnels which Arctic char may use to further penetrate into new lakes. This has occurred in connection with the regulations in Uste- Hol and Hjartdal in Telemark county (Aass 1961, 1991). Arctic char reached the eastern part of Nordmarka near Oslo through a tunnel between Hakadal and Akerselva watershed constructed in 1906 (Dahl 1938, Aass 1961).

Arctic char may also be accidentally introduced into hydroelectric reservoirs during stockings of other species. Most Norwegian reservoirs are inhabited by brown trout, and regular stockings of this species are generally carried out to compensate for reduced natural recruitment. An accidental introduction of Arctic char was evident in Lake Tesse Reservoir in Oppland county in the late 1950s (Løkensgard 1963). However, this introduction failed, probably due to the low number of fish introduced and drying out of spawning grounds during winter.

Arctic char may also be negatively affected by introductions of *Mysis relicta* which have been carried out in several Norwegian lakes (Langeland and Moen 1992, see also Nesler and Bergersen 1991).

Conservation

Arctic char seem to be highly vulnerable to acidification. Hence, this species is an important indicator organism for detecting the first effects of acidification on freshwater fish communities. Further, stocks with unique genetic properties (e.g. river spawners or polymorphic stocks), cf. Hindar and Jonsson (1982), Hindar et al. (1986), Hesthagen et al. (1995a), should be identified and given priority regarding protection and conservation measures (see also Maitland et al. 1991). Localities containing unique populations might also be protected as nature reserves (cf. Hammar and Filipsson 1988).

Due to acidification, the reduction and extinction of Arctic char in Norway is likely to continue. Liming is now the main local measure to prevent further losses of fish populations and restore acidified lakes. In Sweden, liming has been undertaken over a longer time and to a greater extent than in Norwegian waters (Nyberg 1984, 1988, Appelberg et al. 1989, 1992). A Swedish study demonstrated that most of the fish species recolonized between 25-50% of the lakes where they had been extinct, but Arctic char did not (Bergquist 1991). The same will probably also occur in Norwegian lakes, because Arctic char are completely wiped out in several acidified watercourses. Therefore, re-introductions of Arctic char in lakes which originally supported this species should be considered. Such restocking has been successful in several Swedish lakes (cf. Hasselrot et al. 1984, Nyberg et al. 1986). Although there appears to be little genetic variation between Arctic char populations, restocked fish should preferably be taken from the same watershed or the same geographical area (cf. Hindar et al. 1986, Hartley et al. 1992). In any breeding programme, it is necessary to study the magnitude of the genotype-environmental interaction in specific locations (Gjedrem 1992).

In Norway, few data are thus far available to evaluate the effect of liming on Arctic char stocks. Preliminary results indicate that strongly reduced char stocks may need many years to recover in spite of a significant improvement of water quality (Saksgård and Hesthagen 1995). The reason for this is unknown, but may be related to reduced hatching success caused by a lack of clean gravel on the spawning grounds (cf. Frost 1965, Rubin and Buttiker 1992).

Action should also be taken to prevent further translocation of Arctic char due to its harmful effect on native species like brown trout (Dahl and Sømme 1942). In several areas, Arctic char inhabit lakes where they can move to other lakes or be easily transferred by man to near-by localities which do not support char. Introduction of new species as well as foreign genotypes of species already present may have a detrimental effect on native fish stocks (Achieng 1990, Hindar et al. 1991, Ryman 1991).

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Responses of Wild Juvenile Arctic Char to Cover, Light and Predator Threat

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Abstract

Experiments on wild juvenile Arctic char, *Salvelinus alpinus*, were conducted in a stream tank installed at the Koroc River, 58°49'N, 65°45'W, northern Québec. Diurnal responses of fish to texture of substrata and overhead cover showed that cover was used most during the brightest daylight hours. We were unable to demonstrate this response was related to avoidance of UV radiation. At reduced ambient light levels, the diurnal pattern of cover use was weakened. Feeding activity was higher over sand than more complex substrata, suggesting that in open habitats prey are more visible and stimulate feeding. Substratum complexity did not affect either initial or secondary responses of juvenile char to threat by a model avian predator nor the latency period before resuming activity. Over sand, threatened char were less active than unthreatened fish, but this was not true over cobble. This suggests that juvenile char perceive less risk of predation when associated with complex stream bed materials offering good hiding places. These stream tank observations were generally supported by field data on habitat use by juvenile char in the Koroc River.

Keywords: Habitat selection, parr behaviour, avian threat, stream tank.

Introduction

Knowledge of the ecology of juvenile Arctic char, *Salvelinus alpinus*, is required to understand the production dynamics of anadromous stocks. In Canada the fry and parr stages of the life cycle have proved especially difficult to study and there is little detailed information (Johnson 1980; Dempson and Green 1985; Stenzel and Power 1991). In studies conducted at Koroc River, Québec, Stenzel and Power (1991) reported juvenile Arctic char were rarely observed by day but were visible by lantern light in low numbers along the shore at night. In a stream tank, in June, parr were mostly hidden in coarse rubble during daylight hours and emerged at night (Adams et al. 1988). This diel pattern of activity tended to break down in August. Such behaviour explains the difficulty observing and sampling juvenile Arctic char in shallow streams.

There are clearly a number of factors which could account for the cryptic behaviour of char living in clear, shallow, lotic environments. There is extensive evidence that UV radiation can damage fish (Bell and Hoar 1950; Allison 1960; Bullock 1982) and that some fish are visually sensitive to near UV wavelengths (Muntz and Northmore 1970; Avery et al. 1983; Hawryshyn and Beauchamp 1985; Hawryshyn et al. 1989). In pure water UV transmittance is reduced 5% m^{-1} (Clarke and James 1939). In natural waters, containing particles and dissolved organic materials, penetration is less and, at high latitudes, surface intensity is reduced. Nevertheless, with depletion of the ozone layer, exposure to UV radiation is likely to increase, especially in clear shallow streams. This raises the critical question, do juvenile char detect and avoid exposure to damaging radiation? Parr living in shallow water during daylight hours are also exposed to bird predation. In particular, gulls

(Laridae), mergansers (Anatidae) and loons (Gavidae) prey on young Arctic char (Johnson 1980). Assuming that shallow water offers protection from piscivorous fish (Schlosser 1987), is the cryptic behaviour a response to threat of avian predation? If either of the above considerations are important, then char are likely to select habitats offering suitable cover. In addition, the physical structure of the stream habitat is likely to modulate responses of juvenile Arctic char to light radiation and threat of avian predation because available shade and distances to hiding places will vary. In Arctic rivers, cover is almost entirely provided by the stream bed but, in general, both overhead and instream cover should serve similar ends.

In addressing the above questions and trying to understand what habitat factors might control the productive capacity of riverine habitats for juvenile Arctic char, a stream tank was constructed in a tributary of the Koroc River. Experiments focused on the effects of stream bed composition (substratum), overhead cover, light and simulated threat of avian predation on the behaviour of juvenile Arctic char.

Material and Methods

The stream tank was of modular construction, using prefabricated pieces small enough for transport by small aircraft and boat, and assembled on site using basic hand tools. The tank consisted of eight trapezoidal units surrounding a roofed observation area supported on a gravel pad (Fig. 1). The dimensions of each unit were: inner 114 cm, outer 177 cm, width 76.5 cm and depth 37.5 cm. The inner wall consisted of clear 0.64 cm thick plexiglass. Each unit could be isolated by removable 9 mm mesh screens. The tank was gravity fed from a tributary stream via 34 m

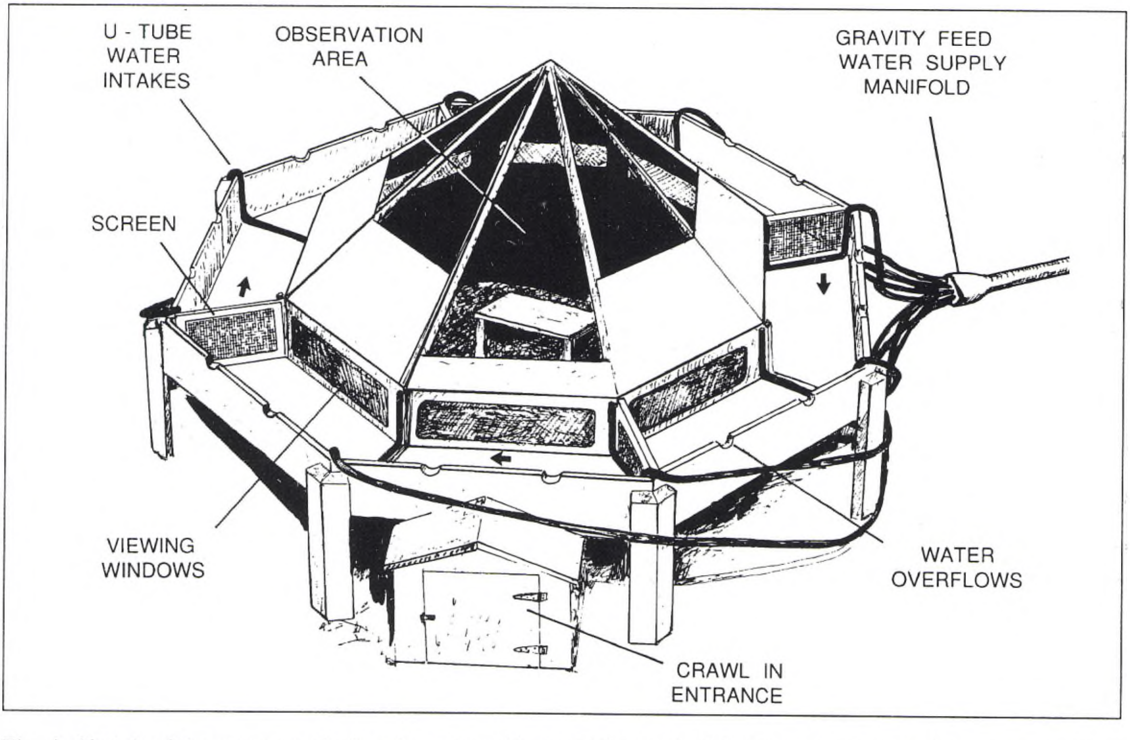

Fig. 1. Sketch of the stream tank showing general layout. The roof of the observation area is cut-away to give an impression of the interior and there are four screens in place. Dimensions are given in the text.

of 10.2 cm diameter ABS pipe. The stream supported juvenile Arctic char and water quality was similar to that of the Koroc River. Water entered each unit through a 3.8 cm diameter supply pipe, feeding a U tube set in behind the screen holder. The vertical sections had ten 4 mm orifices directed downstream. Water overflowed through two screened surface notches in each unit. This produced a slow flow with small eddies through each unit. Velocity varied from 1.5 to 3.6 cm s^{-1} (2 cm s^{-1} at the surface). Observations were made from the black darkened observation area through viewing slits in black side blinds which limited the chance of fish detecting observers.

Arctic char used in the experiments were captured at night with a hand seine and lantern along the shore (Stenzel and Power, 1991). They were held in an enclosure in the river, usually for 12-36 h (range 0-168 h) before transfer to the stream tank. Fish were allowed 12±2 h to acclimate. Acclimation time was assessed by counting feeding strikes by individual fish for 2 min every 2 h. It was assumed 'normal' activity had resumed if the strike rate was not significantly different during two consecutive 24 h periods following acclimation. Since no differences were detected, Wilcoxon signed-ranks test (Zar 1984), four replicates (P=0.46 to 1.00), it was concluded fish resumed 'normal' activity within 12 h. All time is given as eastern daylight saving time. Distinctive parr markings on the right side of each fish allowed individual identification (Bachman 1984).

Experimental design

Habitat use

Habitat use was examined between 11 and 24 July, 1987 by dividing the tank into two experimental areas, each extending over four units (Fig. 2A). Each unit in each area had a different substratum: sand (<0.4 cm^3); gravel (0.4-20 cm^3); cobble (200-1,000 cm^3); boulder (2,000-6,000 cm^3). The order was randomly selected. Use of overhead cover was tested by randomly placing a black plastic cover above either the upstream or downstream half of each unit. Eight possible habitats were therefore available to each fish. Four small fish (<8.5 cm fork length; 6.6±0.8 cm, mean ±SD) were randomly assigned to one area and four large fish (≥8.5 cm; 11.1±1.6 cm) were placed in the other. There were few fish 7.5-9.5 cm so the same size groups were used in all experiments. Examination of otoliths showed small fish ranged from 0+ to 3+ years old, large fish frorm 1+ to 4+ years old. Following acclimation, individual fish were observed at 2 h intervals for 48 h using the instantaneous-scan-sampling method (ISSM) (Altmann 1974). The habitat occupied was recorded at 15 s intervals for 5 min. Observations were divided into day and night to see if habit use varied over 24 h. Night was defined as the period when light intensity was <50 lux and varied during replicates. It was between 00:00 and 02:00 in the first experiment and at 22:00, 00:00 and 02:00 for other replicates. Due to the large number of observations in which fish were hidden, data were combined for each individual to produce an observation index for day and night. This was the number of times a fish was seen in any of the eight habitats divided by the number of possible observations and is a measure of habitat use. Four replicates of the experiment, using different fish, resulted in observations on 25 fish. Seven fish were never seen.

Ultraviolet light

Experiments were carried out on the effect of reducing the UV component of ambient light on use of overhead cover and on selection of habitats with reduced UV when no overhead cover was available. Four pairs of adjacent units were used in these experiments (Fig. 2B). Sand substratum was used throughout to minimize stream bed cover and maximize fish visibility. Three pairs of units had overhead cover placed over either the upstream or downstream half of each unit and the other part was open as a control in one pair, covered in UV filtering plexiglass[1] in

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[1] Rohm and Haas UF-1, 0.32 cm thick, reduces transmission of light sigmoidally <400 nm and blocks it completely at 350 nm.

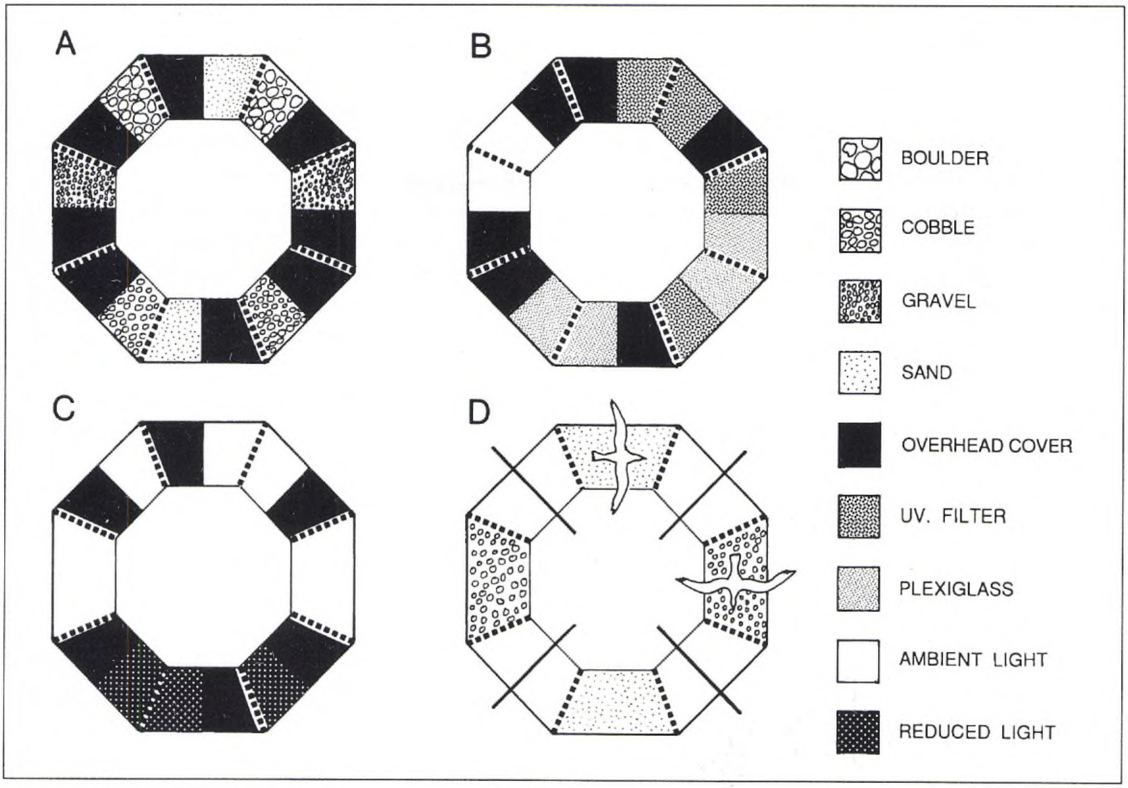

Fig. 2. Stream tank experimental designs. The positions of screens separating units or larger areas are shown by the broken lines. **A.** Layout for habitat selection, half of the tank contained small fish, the other half larger fish. **B.** Arrangement for UV sensitivity experiments, the substratum was sand in all units. **C.** Set-up to test the effect of a 90% reduction in illumination. Only fish <8.5 cm were observed, sand was the substratum. **D.** Arrangement for predator threat experiments. Positions of the vision screens preventing control fish sighting the 'gull' are indicated by a solid line.

a second pair and covered in regular UV transmitting plexiglass[2] in the third pair. In the fourth pair of units, UV filtering plexiglass was placed over one half and UV transmitting plexiglass over the other half of each unit.

In the overhead cover experiments, two fish (small 6.9±0.8 cm, large 10.0±1.0 cm) were placed in each unit of the paired treatments. The position of each fish was noted every 15 s for 5 min each hour between 09:00 and 17:00 over 2 d. Four replicates were run between 8 and 17 July, 1988. Data were obtained from 44 of 48 experimental fish.

In the UV light sensitivity experiment (fourth pair of units) the size range of fish (small 6.8±0.9 cm, large 9.8±1.1 cm) and observational protocol was the same. Five replicates were run between 11 and 17 July, and 23 and 26 August, 1988.

Light intensity

The effect of light intensity was studied by reducing it in three adjacent units and maintaining natural levels in the opposite three units (Fig. 2C). The single units between served as buffer

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[2] Rohm and Haas 0.32 cm thick regular transmitting plexiglass (a control for the UF-1 plexiglass).

zones. The three reduced light units were covered with RoscoSun N9 (Rosco Laboratories Ltd.), diminishing ambient light above 380 nm by 90%. Overhead cover was placed in random order on half of each unit and sand was used as the substratum throughout. Two small fish (7.3±0.7 cm) were placed in each unit. Four daytime observations were made at 2 h intervals between 09:00 and 17:00 for 2 d. The same protocol was used as for the UV experiments except that after each 5 min observation period the number of feeding strikes during the next 2 min was recorded. Three replicates were completed between 13 and 21 August, 1988. Data were obtained from 33 out of a possible 48 fish.

Night observations were made over 4 h between 22:00 and 02:00 in the same experiment. Due to inadequate visibility, individual fish could not be identified. Their positions were discerned every 15 min using a diffuse pin-hole light source similar to that used by Nunan and Noakes (1985) so that 2 fish • 2 positions • 16 observations = 64 possible records per night for each treatment area.

Avian predator threat

Four alternating units were used, two containing sand and two cobble substrata in random order. Cobble covered 40-45% of the floor of these units; stones were evenly placed and three small rock covers provided. This arrangement kept fish visible while offering hiding places. No cover was available in the sand units. One sand and one cobble unit were selected randomly for 'gull' threat treatment in each experiment, the other units served as controls. A black plastic screen was placed in the unused buffer units to ensure fish in the control units could not see the threat (Fig. 2D). A white, wooden model of a gliding gull was 'flown' above the threat treatment units. It was attached to a rod which was rotated by hand at approximately 0.8 m sec^{-1}, 0.5 m above the water surface. Two fish were placed in each unit so that there were both large (10.9±1.7 cm) and small (7.2±0.6 cm) threatened and control fish for each substratum. Fish in treatment units were 'threatened' 5 times d^{-1} at 1.5 h intervals, starting at 11:00 for 2 d. Four replicates were carried out between July 21 and August 10 1988. Observations were recorded for 51 fish.

Fish reaction to threat was described and the latency period until a fish resumed its previous activity or a normal non-threatened behaviour was recorded. Fifteen minutes after the threat, activity was recorded for 5 min using the ISSM. Every 15 s behaviour was categorized as either swimming, hovering, feeding or agonistic (grouped active behaviours), under cover, resting or hiding (grouped non-active behaviours). Using the same protocol, the behaviour of fish in control units was recorded 5-30 min after the threat treatment.

Statistical analysis

Assumptions of normality and homogeneity of variance were verified for all data sets prior to the application of parametric tests. Normal probability plots were visually examined to assess the normality of the residuals, whereas homogeneity of variance was examined graphically by plotting the residuals against the predicted values (Montgomery 1984). Where these parametric assumptions were violated, a square-root transformation was successful in achieving normality and constant variance. The maximum probability of a Type-1 error was set at 0.05.

Habitat use

The data were transformed with a square root transformation, consequently the indices of habitat use cannot be treated as percentages. These data were analyzed with a repeated measures, multifactorial ANOVA (SAS Institute Inc. 1982). The repeated measures were time (day or night), substrata (sand, gravel, cobble or boulder) and cover (presence or absence of overhead cover) (i.e. 4 replicates • 2 size classes • 2 times • 4 substrata • 2 cover states). Individuals were treated as subsamples in this model. Multiple-means comparisons were carried out using a Tukey test (Zar 1984) and both Tukey's test and a modified *t*-test were used when interactions involved repeated measures (Steel and Torrie 1960).

Ultraviolet light

For each fish, data were combined to calculate the percentage of time the fish was seen under cover. The data were then subjected to a split plot ANOVA, blocking on replicates. UV treatment was randomized within each replicate and data were split into large and small fish to determine the effects of fish size and the presence of UV light on the use of cover. A *t*-test was used to determine whether the mean use of overhead cover was significantly greater than 50%.

Data from the UV sensitivity experiment were combined over time to yield the percentage of times an individual was under UV filtering or UV transmitting plexiglass. For each size class, a Wilcoxon test was performed (Zar 1984) in which the percentage of times individuals were recorded in each habitat was compared.

Light intensity

Illumination data were analyzed in three ways. For daytime data, a comparison was made between use of cover in reduced and ambient light environments. For each individual, the percentage of times this individual was under cover during the daytime was determined. A two-way ANOVA model (3 replicates • 2 treatments) was used to examine the effect of illumination on the use of cover.

Secondly, the average number of feeding strikes was calculated for each individual for each replicate. The same ANOVA model was fitted to these data to determine whether diminished light affected feeding activity.

In the third analysis, diurnal patterns of cover use were examined. Data for each chamber were combined separately for day and night to give the percentage of the number of observations the fish in each chamber were under cover. A repeated-measures ANOVA was carried out with day and night observations being the repeated measures. To determine whether fish were distributed randomly in the units, a *t*-test was carried out to examine whether use of cover during the day and night was significantly different from 50 percent.

Avian predator threat

The latency times to resume activity for treatments subjected to threat were examined to determine whether substrate affected this behaviour. The average latency for each individual was calculated and, after a square-root transformation, a two-way, split plot ANOVA was used (4 replicates • 2 sizes • 2 substrates) (SAS Institute Inc. 1982).

Secondly, measures of activity were obtained by categorizing all behaviourial activity frequencies into either active or non-active. These data were combined for each individual to calculate a measure of activity, that is, the proportion of all scan observations in which the fish was active. This data set was subjected to a three-way, split plot ANOVA. Four replicates of each size category of fish were conducted with each replicate being subdivided into substrate type and bird treatment (4 replicates • 2 sizes • 2 substrates • 2 bird treatments). The nature of significant interactions was examined using a Tukey test for comparisons of multiple means (Zar 1984).

Results

Habitat use

Results are summarised in Fig. 3A. There were differences in uses of overhead cover between day and night (F=13.85, P=0.0005). During day, overhead cover and open areas were equally used (q=0.90, P>0.50) but at night open areas were preferred (q=7.44, P<0.001). Overhead cover was used significantly more by day than by night (t=3.37, P<0.05) but no significant diurnal preferences for uncovered areas was found (t=2.02, 0.05<P<0.10) (Fig. 3B).

Juvenile Arctic char exhibited substratum preferences (F=6.92, P=0.0009). Boulder was used significantly more than gravel (q=5.70, 0.001<P<0.005) or sand (q=5.00, 0.005<P<0.01) (Fig. 3C). There were a large number of hidden fish (53% of all observations). Since fish were generally visible in sand and gravel units, most of the missing fish were probably using coarse substrates and preference for these was underestimated.

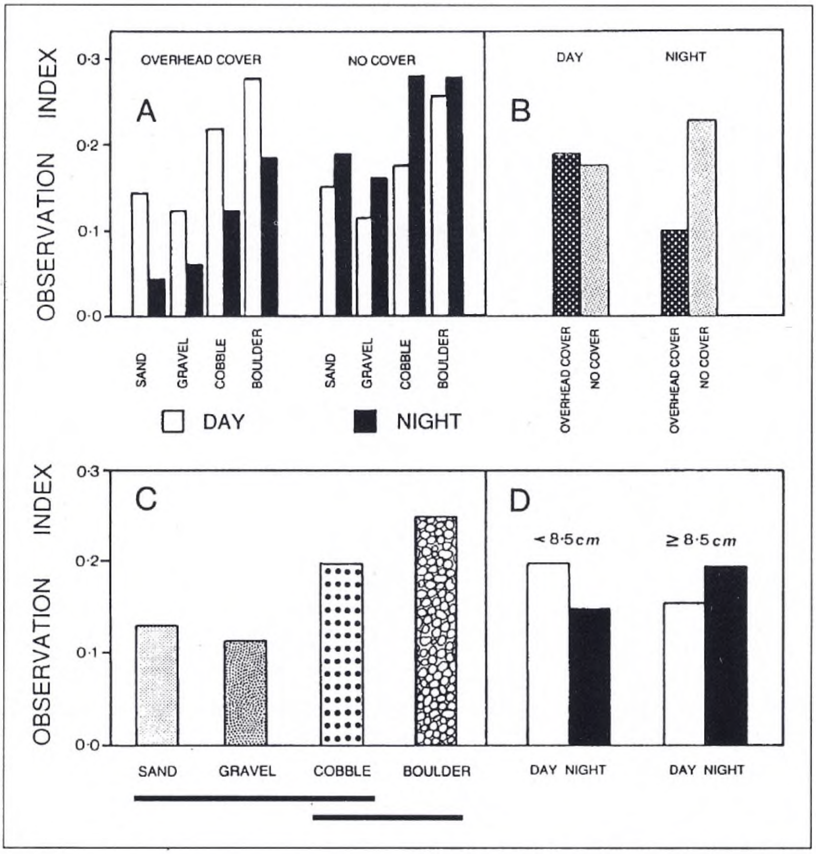

Fig. 3. Habitat use by juvenile Arctic char. The observation index is the number of observations of an individual in each habitat divided by the total observations possible. **A.** Overall use of all habitats by both small and large fish. **B.** Diurnal pattern of overhead cover use by all fish. **C.** Substrata use by all fish. Coarse substrata are used significantly more than fine. **D.** Diurnal patterns of visibility for both small and large juvenile Arctic char. The differences are not significant.

Size did not appear to influence choice of substratum, although there was an indication that the two size classes may exhibit different diurnal patterns of activity (*F*=5.28, *P*=0.0612) (Fig. 3D). Habitat visibility indices suggest that small fish tended to be more active by day (mean index 0.20 compared to 0.16) and large fish by night (0.20 compared to 0.15).

Ultraviolet light

No significant difference was found between the percentage of fish using overhead cover in the ambient light control compared with units covered by regular or UV filtering plexiglass (77%, 65% and 59%, respectively) (*F*=2.09, *P*=0.21) (Fig. 4A). There was a tendency to use overhead cover less when UV radiation was blocked. However, when no overhead cover was available, juvenile Arctic char of both size groups showed no preference for the UV protected habitat (<8.5 cm: *P*=0.92; ≥8.5 cm: *P*=0.76).

Light intensity

Reduction in illumination had no significant effect on the use of overhead cover by juvenile Arctic char by day (*F*=0.33, *P*=0.57) and no effect on their daytime feeding activity (*F*=1.92, *P*=0.19). Reducing the illumination did not significantly alter the overall use of overhead cover (*F*=1.01, *P*=0.33) but there was a significant diurnal pattern of use. Juvenile Arctic char were observed under overhead cover 63% of the time by day and only 47% by night. Overhead cover was selected by day (*t*=2.30, *P*=0.02) but at night distribution was random (*t*=0.55, *P*=0.29). Although the interaction of treatments and day and

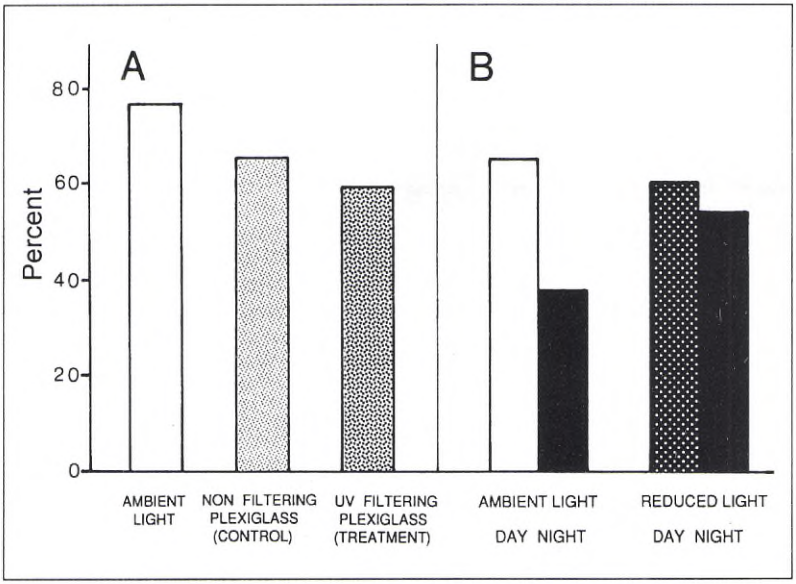

Fig. 4. **A.** Daytime use of overhead cover by juvenile Arctic char when the alternatives are ambient light, normal light transmitting plexiglass and UV filtering plexiglass. **B.** Effect of a 90% reduction in ambient light by a neutral density film (RoscoSun N9) on use of overhead cover by small (<8.5 cm) juvenile Arctic char. Percent is the mean percentage of observations in which individual fish were beneath overhead cover.

night was not significant (*F*=3.03, *P*=0.09), the diurnal pattern of overhead cover use was stronger in the ambient light units. In ambient light, overhead cover was used 66% by day and 38% by night, whereas in reduced light units the values were 61% and 55%, respectively (Fig. 4B).

Avian predator threat

Juvenile Arctic char threatened by the model gull did not always react (Table 1). Forty-one percent of the time there was no response, generally when the fish was not active. During the majority (62%) of these cases, the fish were already resting and in 28% they were hidden and may not have seen the threat. A few resting fish simply raised then lowered their dorsal fins.

Table 1. Occurrence (%) of initial predator-avoidance responses exhibited by juvenile Arctic char (July 21-August 10, 1988)

	Initial predator-avoidance responses (%)					
	no reaction	motion-less	slow sink	swim	dart	zig-zag
Sand	43	4	8	11	10	24
Cobble	39	1	16	16	14	14
Total	41	3	12	13	12	19

Active fish seldom (10%) failed to react but the responses were quite varied. Ceasing activity and remaining motionless was the rarest response (Table 1). Usually fish moved to the bottom either by remaining still and slowly sinking, swimming to the substratum or to cover, darting very quickly forward or darting in a zigzag direction. Darting and zigzagging were very vigorous responses which often stirred up the substratum. The type of response was not influenced by the substratum with the exception of zigzagging which was observed in 24% of responses over sand but only 14% over cobble.

Subsequent responses were either non-active or active. The majority of fish remained motionless on the bottom (46% of all threats or 78% of all active initial responses), generally in corners, along edges or, when available, under rock covers or beside cobble. Fish occasionally rested in the open. In 13% of observations the fish alternated between periods of hovering, swimming or feeding and resting. This pattern of activity was interpreted as 'cautious' behaviour.

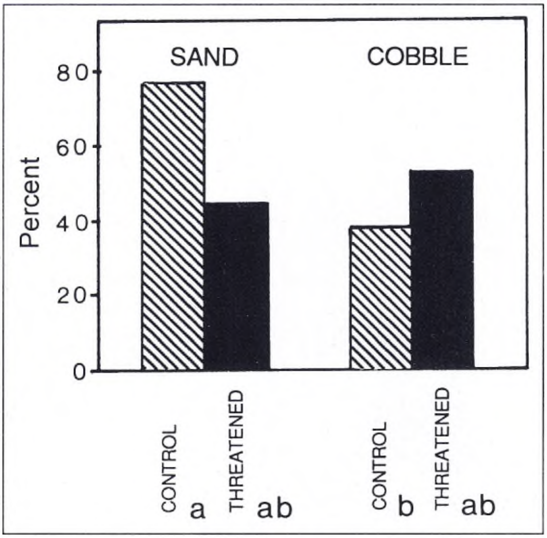

Fig. 5. Percent frequency of observations in which fish were engaged in active behaviour over two substrata. Controls are compared to fish threatened by a model 'gull' flown overhead. Columns designated with different letters are significantly different (Tukey's test $P<0.05$).

Fish which responded to the predator threat remained inactive for very different periods of time. The mean interval to resume activity for all fish was 364 s. It was 324 s for small fish and 407 s for large fish although these were not significantly different (F=0.15, P=0.71). Neither substrata (F=0.53, P=0.49) nor the interaction of fish size and substrata (F=2.25, P=1.18) were found to be significant.

Activity measured 15 min after the threat was compared between threatened and control fish. The effects of substratum, sand versus cobble, and fish size were tested as well as any interactions between these factors. The threat-substratum interaction was the only significant effect (F=6.15, P=0.02) (Fig. 5). The activity of control fish over sand was significantly different from that of those over cobble (77% and 32%, respectively; q=4.53, $0.01<P$=0.025).

Discussion

This work was carried out to elucidate some of the determinants of productivity of riverine anadromous Arctic char stocks. Juveniles have proved extremely difficult to study, in part because of their cryptic behaviour in summer. Carefully designed experiments in a stream tank offer a solution but attention must be paid to keeping conditions close to natural. This was our approach and explains why the density of parr was kept low in our experiments. Natural densities of juvenile Arctic char are very low along the shores of the lower Koroc River. Conventional methods, including snorkeling, baited traps and electrofishing revealed few or no fish, highest numbers (>10 per 100 m^2) were recorded in near shore habitats by lantern at night (Stenzel and Power 1991). An advantage of using few fish is that individuals can be identified without marking, but there are fewer observations. This complicated some experiments as a few char were never seen during an experiment. Other benefits include results not influenced by density induced agonistic behaviour or other effects of crowding (Huntingford et al. 1993). Data were obtained on wild fish observed under close to natural conditions, including prey availability, and, as such, provide valid insights into wild char behaviour.

Our results are entirely consistent with the descriptions of summer time habitat use by juvenile Arctic char in the Koroc River provided by Adams et al. (1988) and Stenzel and Power (1991). Once juveniles reach the parr stage they select areas offering daytime hiding places and use open areas within a few m of these for foraging at night. We extended these observations by offering overhead cover, a habit attribute which has been shown to be important in many salmonid studies (Scruton and Gibson, 1993; Fausch 1993) but is not often available in Arctic streams. Addition of overhead cover may explain why the diurnal pattern of substrata use reported by Adams et al. (1988) was not seen in our results. Parr were never far from overhead cover and tended to remain more active by day. In this respect they may have responded to overhead cover in much the same way brook trout and Atlantic salmon parr use deeper water for cover (Gibson and Power 1975). By night, the juvenile Arctic char avoided the overhead cover and were most active in open habitats. These results suggest that foraging time may be reduced in summer in streams lacking overhead cover and that this limitation should be more severe at higher latitudes. If true, this implies arctic streams may be more difficult environments for fish than generally believed.

One suggestion we investigated was that hiding in the stream bed provided protection against exposure to damaging UV radiation (Jokiel 1980). In our experiments we were unable to demonstrate that juvenile Arctic char responded to reduced UV levels or that they were capable of detecting these wavelengths. Since UV irradiance levels fluctuate seasonally, daily and with the weather, and we had some problems with condensation on the plexiglass tank covers, our results can only be accepted as preliminary. Further controlled experiments are needed to address this question. A second reason for daytime hiding could be avoiding too intense light or, conversely, reduced levels of illumination act as a cue for foraging. Reducing the level of visible light by 90% did not alter the use of overhead cover or feeding strikes in young Arctic char by day. We reduced light by one logarithmic unit but this may have been within the range the eye could easily accommodate (Blaxter 1975). Young Atlantic salmon and brook trout feed most at dawn and dusk (Hoar 1942), as do Pacific salmon, at light intensities close to their cone threshold levels (Ali 1959). Even on cloudy days, light intensity is >3 orders of magnitude greater than at dawn or dusk, hence light reduction by one order of magnitude was probably insufficient to illicit a response.

Reduced light did not appreciably modify the use of overhead cover in our experiments, nor did variations in cloud cover or weather appear to have any effect. Gibson (1966) found no effect between cloudy and sunny days on use of cover by brook trout or Atlantic salmon. However, other authors report both light intensity and cloud cover can alter use of overhead cover by fish (Jones 1956; McCrimmon and Kwain 1966).

The advantage of overhead cover may be that it increases visual acuity. Helfman (1981) reported that sunlit prey can be seen by a shaded observer at 2.5 • the distance a sunlit observer can see shaded prey. This was attributed to 'veiling brightness' and the incremental threshold. The position of juvenile Arctic char in our experiments, hovering at the edge of the shadow formed by the overhead cover, darting out to strike potential prey, then quickly retreating, suggests they were using the cover to enhance feeding. This advantage is lost at night. Between the rod and cone thresholds, both visual acuity (Nakamura 1968; Northmore 1977) and feeding activity (Ali 1959; Brett and Groot 1963) improve with increasing illumination. Moving into a brighter open habitat at night should facilitate feeding since the retinal structure of Arctic char is well suited to both photopic and scotopic (dark-adapted) vision (Ali 1965).

A final reason why cryptic behaviour might be important is to avoid predation. The gull silhouette elicited a variety of 'flight and fright' reactions in juvenile Arctic char. In preliminary experiments an oval shape worked equally well so recognition of a particular shape was not necessary. Responses were similar over sand or cobble, except the zigzag occurred slightly more often over the fine substratum. A zigzag reaction was reported by Hoar (1958) in Pacific salmon and has been described in other fish species. It occurs most frequently in the absence of immediate cover and is termed 'protean' behaviour (Keenleyside 1979). It may appear inappropriate in initially attracting attention. However, parr are difficult to follow through the movement and the stream bed is often disturbed, decreasing visibility. It may also seem energetically costly but Webb (1975) suggested that the faster a fish accelerates the less energy is used to reach a given speed and location. Over cobble, where there are more hiding places, young Arctic char do not need this strategy as often as over sand. The raising of the dorsal fin when fish were resting on the tank bottom is a low-key threat posture (Noakes 1978) and may be a displacement behaviour.

Remaining motionless was the most common secondary response and is one way fish avoid detection, even in the pelagic zone (Sandlund et al. 1987). Visibility is reduced by an ability to slowly match the colour of their background and parr markings (Hailman 1977; Noakes 1980).

The latency to resume activity was extremely variable, ranging from seconds to over 20 min. Although Grant and Noakes (1987) found that latency increased with size in young-of-the-year (YOY) brook trout, we noted no difference between our small and large size groups of Arctic char. We were not experimenting with YOY fish, our small group were at least 1+. Since YOY Arctic char can be seen by day amongst flooded vegetation and along stream edges near upstream spawning areas, it is probable that wariness develops as the fry develop during the first year.

Many authors have commented on the importance of cover in predator-avoidance responses (Hoar 1958, Kalleberg 1958, Gibson 1966, Chapman and Bjornn 1969, Fausch 1993). DeVore and White (1978) noted that brown trout sought physical contact with cover when frightened. Arctic char did likewise, using the tank corners when nothing else was available.

The cost of responding to predator threat is diminished activity and loss of foraging time (Grant and Noakes 1987). Over sand, threatened fish were less active and this may have been the optimal strategy for hiding. Over cobble, Arctic char displayed similar activity to control fish. Since cover was close, the risk of predation was apparently reduced and there was no need for extra precaution.

In the open sand habitat, feeding strikes and general activity were highest in non-threatened fish. This supports the idea that open habitats can be profitable feeding areas because prey are more visible. Wilzbach et al. (1986) found that 'simplifying' an environment increased feeding activity. However, more complex habitats are safer for small fish (Werner et al. 1983). This suggests that trade offs exist between maximizing foraging efficiency and risk of predation. Young Arctic char in the Koroc River in summer exemplify this: they hide in the stream bed by day and forage in open areas in very shallow water at night. This should protect them from bird predation by day and large piscivores at night, while permitting unobstructed views for feeding. In winter, habitat use must be quite different, as it is in many species of stream salmonids (Power et al. 1993, Vondracek and Longanecker 1993). There may also be marked differences between stocks of Arctic char (Olsén and Karlsson 1991).

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Growth and Smoltification of Anadromous Arctic Char Presmolts in Lentic and Lotic Habitats

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Abstract

Presmolt growth rate, smolt age and size were studied in three anadromous populations of Arctic char *Salvelinus alpinus* in northern Norway. All populations live sympatrically with Atlantic salmon *Salmo salar* and anadromous brown trout *Salmo trutta*. Beiar Arctic char inhabit the main river (the River Beiarelva) in running water, without access to any lake. Saltdal Arctic char mainly spawn, and their young remain until smoltification, in a lake on a tributary of the River Saltdalselva. This is the only lake in the watercourse accessible for anadromous fish. Arctic char in the Hals watercourse mainly inhabit the lake Storvatnet and the main tributary of this lake, while the main river downstream from Storvatnet (the River Halselva) is less utilized by char. Smolts of Beiar char were youngest and smallest, and annual growth rates were higher than in the two other populations. Variation in smolt age and annual growth rates was largest in Hals char. Arctic char presmolts living in lotic habitats grow faster, smoltify at a lower age and at a smaller size than char living in lentic habitats. Freshwater temperature in summer seems to be important for the utilization of running waters in the way that Arctic char presmolts appear to avoid warmer river stretches.

Keywords: Arctic char, growth, smolt age, lentic habitat, lotic habitat.

Introduction

The Arctic char has a circumpolar distribution, and there seems to be no northern limit to anadromous stocks (Johnson 1980). In northern Europe, warmed by the North Atlantic drift, the southern limit of anadromy is in the southern part of Nordland county in Norway at a latitude of 65 °N (Huitfeldt-Kaas 1924, Nordeng 1961). On the western side of the North Atlantic, influenced by the southerly flow of the Labrador Current, anadromous stocks have been reported from the northeast coast of Newfoundland at about 49 °N latitude (Bigelow 1963). On both sides of the Atlantic, the southern limit seems to be associated with mean January air temperatures between -1 and -6 °C, and July means of about 12 °C (Huitfeldt-Kaas 1924, Johnson 1980). Anadromous Arctic char often migrate to lakes in late summer, where they spawn and remain during the winter. Young Arctic char usually remain in the lakes until they smoltify. However, some populations also utilize running water as spawning and nursery areas, and in some rivers they have no access to any lake. These populations stay in running water throughout the freshwater periods of their lives. Jensen (1994) compared growth and age distribution of a river-dwelling and a lake-dwelling population of anadromous Arctic char, and observed that river-dwelling fish grow better and smoltify at a lower age and at a smaller size than lake-dwelling fish. The aim of the present study is to compare presmolt growth rate, smolt age and smolt size of these two populations with similar data for a third one. In the third watercourse, the river passes through a lake 3 km above the outlet to the sea, and the Arctic char population is numerous both in running water and in the lake, and hence is a mixture of river-dwelling and lake-dwelling fish.

Also, possible reasons why the majority of Arctic char may stay in lentic water even though they grow more slowly and smoltify at later ages than cohorts in running water are discussed.

Study sites

The three Arctic char populations are all situated in northern Norway. Beiar and Saltdal are two neighbouring watercourses situated at 67 °N, 15 °E in the county of Nordland, while Hals watercourse is situated at 70 °N, 23 °E in the county of Finnmark (Fig. 1). The Rivers Beiarelva and Saltdalselva both flow to the north from Saltfjellet mountain region. Their outlets are 90 km apart. Drainage areas of these rivers mainly consist of high mountains, birch forests, and in lower regions some farmland. The Hals watercourse is less mountainous. Below the treeline it is mainly covered with birch forest.

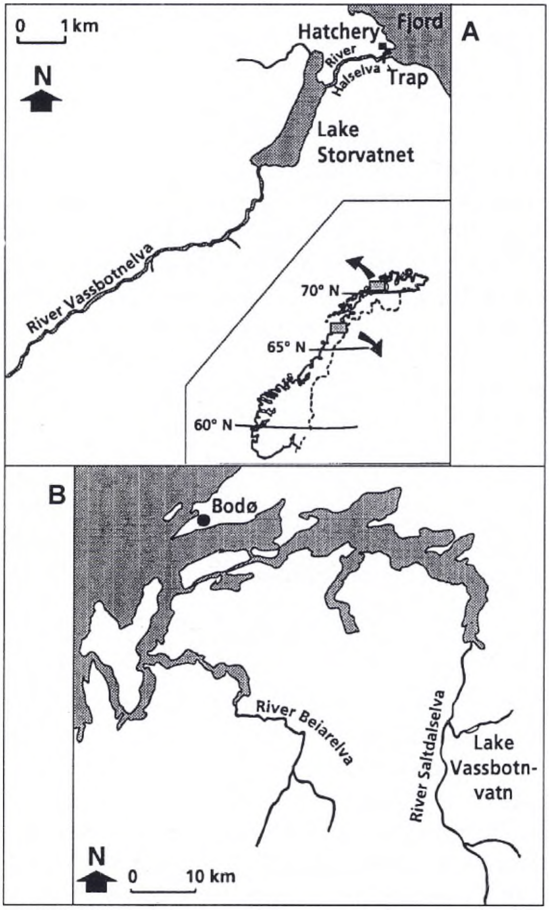

Fig. 1. Map of the study sites. **A.** The Hals watershed, and **B.** the Beiar and Saltdal watersheds.

River stretches accessible to anadromous salmonids are 31, 65 and 20 km long in the Beiar, Saltdal and Hals watercourse, respectively. The Beiar Arctic char population is river-dwelling, without access to any lake. Char stay in running water in the main river throughout the freshwater periods of their lives. The majority of the char living in the Saltdal watercourse migrate to lake Vassbotnvatn (0.6 km^2, 76 m a.s.l.), which is the only lake available to them. The lake is located on a tributary of the River Saltdalselva, 6 km from the main river, and 20 km from the sea (Fig. 1). Arctic char presmolts inhabiting the Hals watercourse are found in the lake Storvatnet (1.2 km^2, 30 m a.s.l., 3 km from the sea), as well as in running water, but are more numerous in the river upstream from the lake (the River Vassbotnelva) than in the river downstream from the lake (the River Halselva). Atlantic salmon and anadromous brown trout are also present, as well as threespined sticklebacks *Gasterosteus aculeatus* L., European eel *Anguilla anguilla* L., and flounder *Platichthys flesus* (L.) in all three watercourses.

All of the rivers are rather cold, with a water temperature of about 12 °C in August in the Rivers Saltdalselva and Halselva, and about 9 °C in the River Beiarelva. The water temperature in the River Vassbotnelva reaches about 10 °C in August (Fig. 2). The rivers are usually covered by ice from November/December to April. The mean annual water flow is 41, 55, and 5 m^{3}s^{-1} in the Rivers Beiarelva, Saltdalselva, and Halselva, respectively. Peak spring flow occurs in June in all three watercourses.

Material and methods

Scale and otolith samples and data on total length, sex and gonad maturation of migrating anadromous Arctic char were collected by anglers in the main river in the Beiar and Saltdal watercourses each year from 1976 to 1988. In addition, some anadromous Arctic char were

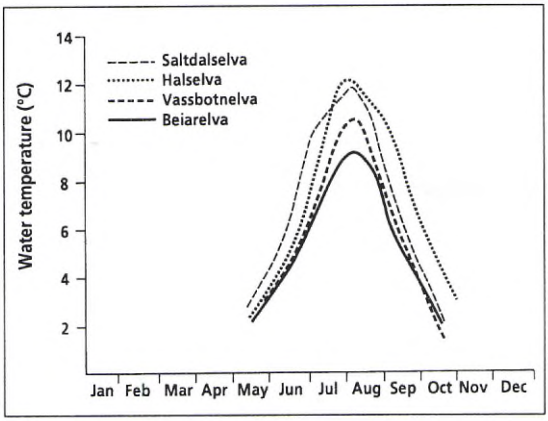

Fig. 2. Average water temperatures in the Rivers Beiarelva and Saltdalselva, and in two sections of the Hals watershed (the Rivers Halselva and Vassbotnelva).

collected with nets of mesh size 26 to 39 mm in the River Saltdalselva each summer from 1976 to 1984. Analyses of smolt age and size were carried out on 233 samples from the Beiar watercourse (length range 22-50 cm) and 200 specimens from the Saltdal watercourse (length range 22-48 cm).

Decending smolts from the Hals watercourse were sampled in a trap catching all migrating fish of lengths greater than 10 cm. The trap is located in the lowermost part of the main river (Halselva), about 200 m upstream from the river mouth (Fig. 1). The material used in this study (550 Arctic char smolts) was collected between 1987 and 1990, and represents 6% of the total number of descending smolts in that period. Natural tip length (Ricker 1979) of smolts was measured to the nearest mm.

The age of Arctic char smolts from the trap in the Hals watercourse was determined from otoliths. Scales and otoliths were used in combination when determining smolt age as well as total age of adult char from the two other watercourses. Otoliths are assumed to yield the most accurate age, as some individuals may lack the first winter zone in their scales due to slow growth (Nordeng 1961, Gullestad 1974, Jensen and Johnsen 1982), and because winter zones of spawning fish may be difficult to observe on scales (Nordeng 1961). In the presmolt period of Saltdal char, one more year was observed in otoliths than in scales in 4.1% of the samples, while the opposite was noticed in 1.6% of the samples. Among the Beiar char this discrepancy was smaller. The growth increment at first migration to sea is easiest to detect in scales (Nordeng 1961). Therefore, smolt sizes of adult fish were analysed by back-calculating from scales. Jensen (1994) back-calculated smolt lengths of Beiar and Saltdal char according to the Lea-Dahl method (Lea 1910), but was aware that this method most probably overestimated smolt size. In the present paper the discrepancy has been quantified, and the estimated smolt sizes were adjusted accordingly to compare with Hals Arctic char smolts. This was achieved independently in two different ways; 1) by analysing the relationship between scale size and fish length, and 2) through back-calculation of scales of fish with known smolt size.

The relationship between scale radius and fish length was examined using 68 presmolts and 264 adult char of the Beiar stock, and 8 presmolt and 200 adults from the Saltdal stock (Fig. 3). The presmolts were caught in running water in the main rivers using electrical fishing gear. None of the presmolts 48 mm or less had developed scales, while scales were present on all larger fish. Hence, presmolts less than 48 mm were excluded from Fig. 3. The linear regression between scale radius (x, mm) and fish length (y, mm) was described by the equation:

$$y=-1.435+332.41x\ (r^2=0.889,\ P<0.0001). \quad (1)$$

However, Fig. 3 indicates that the relationship is curvilinear, and not a straight line. Small fish (<60 mm) had smaller scales than estimated from equation (1), while the opposite was the case for fish between 60 and 300 mm. Smolt lengths (9-27 cm) are therefore overestimated by equation (1), and according to Fig. 3 this overestimation seems to be 10-18 mm. A power function ($y=330.5 \cdot x$ (exp 1.083), $r^2=0.947$, $P<0.0001$) gave the best fit to the data, but from this function smolt lengths were underestimated.

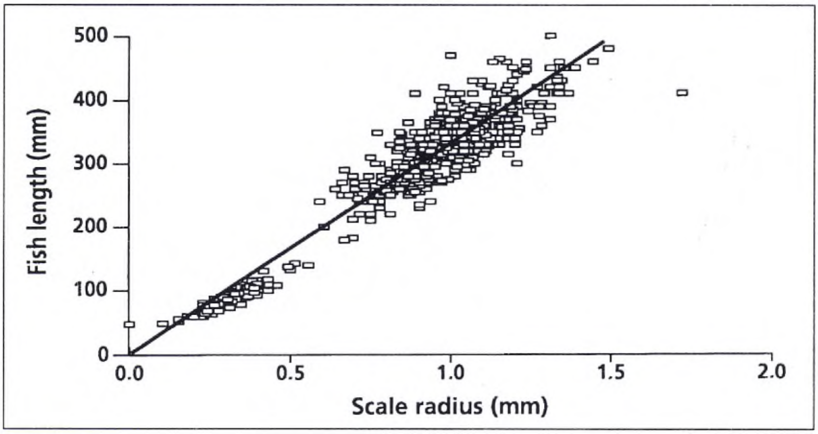

Fig. 3. Relationship between scale radius (x, mm) and fish length (y, mm) of Arctic char from the Saltdal and Beiar populations (regression line: $y=-1.435+332.41x$, $r^2=0.889$).

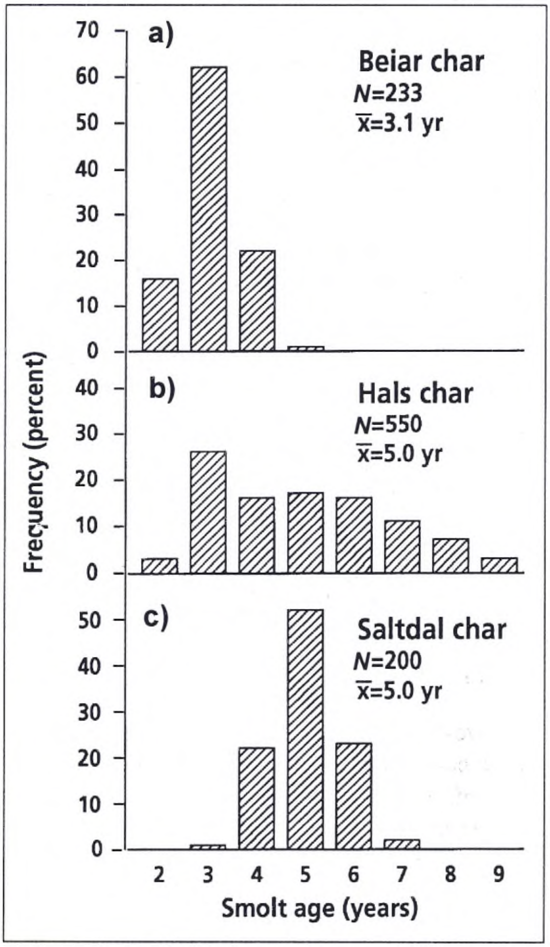

Fig. 4. Smolt ages (x=mean age) of anadromous Arctic char of **(a)** the river-dwelling (Beiar) population, **(b)** the mixed (Hals) population, and **(c)** the lake-dwelling (Saltdal) population.

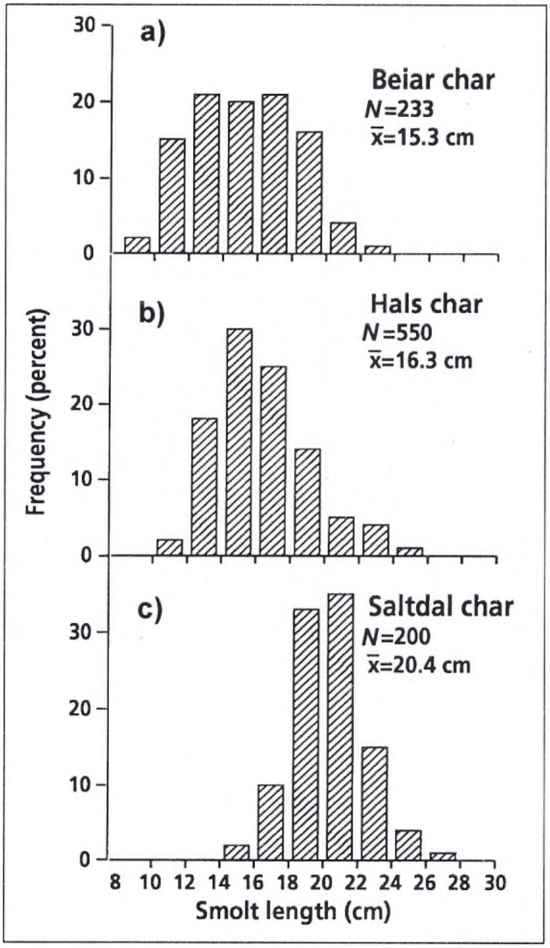

Fig. 5. Smolt lengths (x=mean length) of anadromous Arctic char of **(a)** the river-dwelling (Beiar) population, **(b)** the mixed (Hals) population, and **(c)** the lake-dwelling (Saltdal) population.

I concluded that smolt lengths of Arctic char were overestimated by linear back-calculation of scales by the Lea-Dahl method, but did not succeed in constructing an equation which satisfactorily estimated smolt lengths.

Scales of 29 adult Arctic char with known smolt size were analysed, using the second method. At smolt decent through the trap in the River Halselva, these fish had been tagged with individually numbered Carlin tags. One or several years later they were recaptured in the same trap and collected. When back-calculating smolt size from their scales, the back-calculated smolt lengths by the Lea-Dahl method were always larger than the real values, with an average overestimation of 14.4 mm (7.6%). This discrepancy did not significantly change for adult fish length or smolt length ($P>0.05$).

Hence, both methods gave similar results. Therefore, by estimating smolt lengths of Beiar and Saltdal char, back-calculated values were reduced by 14.4 mm.

Quantitative electrofishing for presmolt salmonids was carried out annually at six sites in each of the Rivers Beiarelva and Saltdalselva in early August from 1975 to 1992, by three successive fishings according to the removal method (Zippin 1958). Arctic char stay in areas with lower water velocities than do Atlantic salmon and brown trout (Heggberget 1984). The rate of water flow at most of the localities used during the density estimates was usually higher than ideal for young Arctic char, and therefore this species is most probably underrepresented in these samples. However, the results revealed that Atlantic salmon and brown trout were the predominant species in fluvial habitats (Johnsen and Jensen 1986, Jensen and Johnsen 1988, and unpublished), while catches of 112 and 2 presmolt Arctic char (34-139 mm) were made in the Beiarelva and Saltdalselva, respectively. A similar programme in the Hals watercourse during late August in 1992 and early September in 1993 resulted in a total catch of 104 char at six sites in the River Vassbygdelva, and 12 char at four sites in the River Halselva. In the Rivers Beiarelva and Saltdalselva, salmonid presmolts were also sampled annually in late April/early May from 1978 to 1992, with a total catch of 66 and 18 Arctic char, respectively.

Results

Smolt ages were considerably lower in river-dwelling (Beiar) than the lake-dwelling (Saltdal) populations (Mann-Whitney U-test, $P<0.001$). In the former population, smolt ages varied between 2 and 5 years, with a mean (± SD) of 3.1

Table 1. Average length (x ± SD, mm) of Arctic char smolts of different smolt ages in the Beiar, Saltdal and Hals populations. The Beiar and Saltdal smolt lengths are back-calculated from scales of adult fish, and then adjusted as described in Material and methods, while the Hals smolt lengths are measured during their outward migratation. Sample sizes (*N*) are also given.

Smolt age (years)	Beiar char		Saltdal char		Hals char	
	length ± SD	*N*	length ± SD	*N*	length ± SD	*N*
2	119 ± 20.1	37			126 ± 12.6	15
3	153 ± 26.6	144	155 ± 0.7	2	140 ± 14.0	145
4	175 ± 25.2	51	199 ± 20.3	43	157 ± 20.6	89
5	197	1	204 ± 19.7	104	167 ± 22.1	92
6			209 ± 19.3	47	177 ± 27.1	90
7			226 ± 27.5	4	187 ± 26.7	62
8					188 ± 30.6	40
9					175 ± 14.7	17
Mean	153 ± 30.6	233	204 ± 20.8	200	163 ± 28.4	550

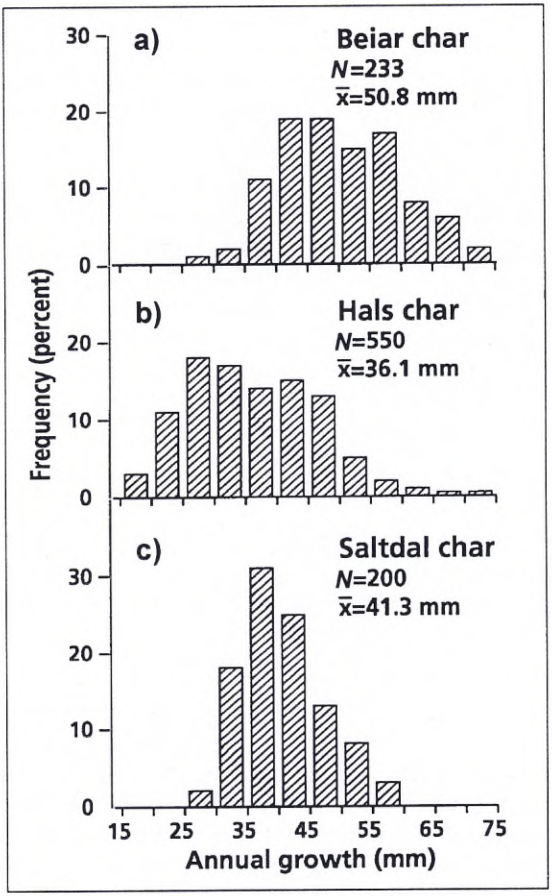

Fig. 6. Mean annual growth of Arctic char presmolts of **(a)** the river-dwelling (Beiar) population, **(b)** the mixed (Hals) population, and **(c)** the lake-dwelling (Saltdal) population.

± 0.63 years, while in the lake-dwelling population, smolt ages were 3-7 years, with a mean of 5.0 ± 0.76 years (Fig. 4). In the Hals watercourse, containing both river-dwelling and lake-dwelling Arctic char, variation in smolt age was larger (2-9 years), with a mean of 5.0 ± 1.80 years, which was significantly different only from the river-dwelling population (P<0.001).

Estimated smolt sizes from the population in running water (the Beiar stock) were smaller than those from the lake-dwelling population (the Saltdal stock), with mean lengths of 153 ± 30.6 mm (variation 88-221 mm) and 204 ± 20.8 mm (variation 153-271 mm), respectively (Kolmogorov-Smirnov (K-S) test, P<0.001, Fig. 5). The mean length of smolts descending the trap in the River Halselva was 163 ± 28.4 mm (106-250 mm), which is intermediate between, and significantly different from, those of the Beiar and Saltdal watercourses (Scheffé multiple tests, P<0.05). Smolt length increased with smolt age in all three populations (one-way ANOVA, P<0.001, Table 1). Smolts from the Saltdal population were larger than smolts of the same age (except age=2) from the two other populations (K-S tests, P<0.001). Three- and four-year-old smolts from the Hals population were on the average smaller than smolts of the same age from the Beiar population (K-S tests, P<0.001), while two-year-old smolts from these two populations were the same size (K-S test, P>0.05).

Table 2. Average annual growth rate (g, mm ± SD) (length at smolting divided by age at smolting) for Arctic char smolts of different ages of the Beiar, Saltdal and Hals populations. *N*=sample size.

Smolt age	Beiar char		Saltdal char		Hals char	
(years)	g ± SD	*N*	g ± SD	*N*	g ± SD	*N*
2	59.3 ± 10.0	37			63.1 ± 6.32	15
3	51.1 ± 8.85	144	51.7 ± 0.24	2	46.7 ± 4.68	145
4	43.7 ± 6.31	51	49.6 ± 5.07	43	39.2 ± 5.16	89
5	39.3 ±	1	40.9 ± 3.94	104	33.4 ± 4.42	92
6			34.8 ± 3.22	47	29.5 ± 4.51	90
7			32.3 ± 3.93	4	26.8 ± 3.81	62
8					23.5 ± 3.82	40
9					19.4 ± 1.64	17

Table 3. Densities of Arctic char presmolts (per 100 m²) caught in running water during quantitative electrofishing in the Rivers Beiarelva and Saltdalselva, and in two sections of the Hals watershed (the Rivers Halselva and Vassbotnelva). The numbers represent total catch after three successive fishings at six, six, four and six sites in the four rivers, respectively. Data for the first two rivers are average numbers for the years 1975-92, while those from the Hals watercourse are for the years 1992-93.

River	Fry (0+)	Older fish
Beiarelva	0.6	0.6
Saltdalselva	0	0
Halselva	0.7	0.5
Vassbotnelva	2.9	1.7

Average annual growth of presmolts (length at smolting divided by age at smolting) of the Beiar, Saltdal, and Hals char populations was estimated to be 50.8 ± 9.8, 41.3 ± 6.6, and 36.1 ± 10.5 mm, respectively, and was significantly different for all watercourses (Scheffé multiple test, $P<0.001$, Fig. 6). The annual growth rate decreased with increasing smolt age in all three populations ($P<0.001$, Table 2).

In spite of very low numbers of presmolt Arctic char in the River Saltdalselva (Table 3), 18 individuals were caught in running water during field work carried out in late April/early May between 1978 and 1992. Their size was not significantly different from Beiar char of the same age (K-S test, $P>0.05$, Table 4). In spite of some differences in sampling time, Table 5 indicates that Arctic char presmolts from the River Vassbotnelva also grow at rates similar to the Beiar char. Comparable data are lacking from the River Halselva.

Table 4. Mean length (mm, ± SD) of presmolts of Arctic char caught in late April/early May in running water in the Rivers Beiarelva and Saltdalselva. Sample sizes in parentheses.

Age (year)	River Beiarelva	River Saltdalselva
1	55.3 ± 8.2 (32)	57.5 ± 6.4 (14)
2	93.4 ± 14.5 (30)	93.8 ± 14.3 (4)

Table 5. Mean length (mm, ± SD) of presmolts of Arctic char caught in running water in early August in the River Beiarelva and in early September in the River Vassbotnelva. Sample sizes are given in parentheses.

Age (year)	River Beiarelva	River Vassbotnelva
0+	40.3 ± 3.1 (58)	45.8 ± 2.9 (73)
1+	72.8 ± 7.8 (49)	78.0 ± 4.6 (20)

Annual density estimates of salmonid presmolts in running water in the River Saltdalselva between 1975 and 1992, gave a total catch of only two Arctic char presmolts. The corresponding catch in the River Beiarelva was 112. Densities of Arctic char were very low compared to brown trout and Atlantic salmon in both rivers (Table 3, Table 6). Similar densities of Arctic char to those in the River Beiarelva were also found in the River Halselva, while Arctic char presmolts were more numerous in the River Vassbotnelva (Table 3). Atlantic salmon and brown trout were both found to be most abundant in the River Halselva, and least numerous in the River Vassbotnelva (Table 6).

Table 6. Average densities of Atlantic salmon and brown trout parr (per 100 m²) in the Rivers Beiarelva and Saltdalselva, and in two sections in the Hals watershed (Halselva and Vassbotnelva), estimated by the successive removal method (Zippin 1958, Bohlin 1984). Fry (0+) are not included in the estimates. Data from Johnsen and Jensen (1986), Jensen and Johnsen (1988), and unpublished.

River	Atlantic salmon	Brown trout	Sampling period
Beiarelva	10.6	26.1	1975-85
Saltdalselva	15.9	24.6	1975-86
Halselva	40.5	34.4	1992-93
Vassbotnelva	1.0	6.1	1992-93

Discussion

Arctic char presmolt growth rates were higher in running water than in lakes in the present study. In the Saltdal watercourse, the majority of Arctic char migrate to the only lake accessible to them, where they spawn, and where the young remain until smoltification. Beiar Arctic char, which spend their entire freshwater life in running water, grew faster in the presmolt period, and smoltified earlier and at a smaller size than Saltdal char. However, the few Arctic char which were caught in running water in the River Saltdalselva exhibited a growth rate similar to that observed in the river-dwelling population in the River Beiarelva (Table 4).

In the Hals population, containing both river-dwelling and lake-dwelling fish, average smolt age and smolt size were intermediate, but average annual growth rates were lower than in the other two populations. However, smolt ages and smolt sizes were within larger ranges. Although lower than in the two other populations, annual growth rates demonstrated considerable differences in growth within the Hals watercourse. Among the Hals Arctic char presmolts which were caught in running water, growth rates were similar to that of the Beiar char (Table 5), and higher annual growth rates were observed in running water than the average for descending smolts from that watercourse. In contrast, Arctic char presmolts caught in fish traps in the profundal areas of the lake Storvatnet by Strand (1991), grew significantly slower than the average for descending smolts ($P<0.001$). As far as presmolts are concerned, the lake-dwelling Arctic char probably experience lower nutrient conditions and lower water temperature than the river-dwelling Arctic char, as young Arctic char in lakes usually select benthic and deep-pelagic habitats (Frost 1965, Johnson 1980, Hindar and Jonsson 1982, Riget et al. 1986, Sandlund et al. 1987).

These observations are in contrast to results from studies of Atlantic salmon parr. Atlantic salmon parr occupying lacustrine habitats grow faster than those in fluvial habitats in the same river system (Pepper 1976, Hutchings 1986, O'Connell and Ash 1993). The differences may be explained by the habitat preferences of the two species. In lakes, Atlantic salmon parr are mainly found in the epilimnion, experiencing higher water temperatures and more abundant food resources than Arctic char staying in benthic and deep pelagic habitats. Hutchings (1986) suggested that more abundant food resources, reduced energy requirements for maintaining position, and reduced competitive interactions in the lacustrine habitat were probably the main factors contributing to enhanced growth of Atlantic salmon. He concluded that such movements have an adaptive basis, in the context of an evolutionarily stable reproductive tactic. Better growth in lacustrine habitat relative to fluvial habitat was considered to be of adaptive significance.

The smaller average smolt size in the Beiar than the Saltdal Arctic char population may be caused by a stronger motivation for seaward migration in individuals experiencing running water, or a delay in descending from the lake because of problems with locating the outlet. O'Connell and Ash (1993) observed larger Atlantic salmon smolts in river systems in Newfoundland where lacustrine rather than fluvial habitats predominated. In stocking experiments with Atlantic salmon in lakes, smolts often descended after the normal smolting period, or did not leave the lakes at all (Munro 1965, Berg 1967, Frantsi et al. 1972, Rimmer and Power 1978, Hansen et al. 1984).

Differences in growth rate may also explain the smaller smolt sizes in river-dwelling than lake-dwelling char. Fast growing individuals often migrate at younger ages and smaller sizes than slow growers (Økland et al. 1993). This may be because of inherited intraspecific variation in growth rate as well as variation in metabolic requirements, i.e. fast growers need more energy than similar-sized slow growers. Thus, fast growers will be constrained by food limitations in the habitat sooner and at a smaller size than slow growers, and should gain at an earlier age and smaller size by switching to richer feeding opportunities (Jonsson and Jonsson 1993). However, both increased and decreased growth rate may induce maturity. When feeding intensity increases, the proportion of early maturing fish (residents) will usually increase (Thorpe 1986). On the other hand, fish may also attain maturity when growth rate decreases suddenly. Arctic char living in lakes to a larger extent mature before they smoltify than their counterparts in rivers. According to well-definable spawning zones in otoliths, some resident char in the Salangen watershed in northern Norway transformed into anadromous char after spawning 1-3 times. This applied to both sexes and accounted for about 9% of anadromous char (Nordeng 1961, 1983).

Some potential explanations of why juvenile densities of Arctic char are considerably higher in the River Beiarelva than in the River Saltdalselva, could be differences in water velocities, water temperature (Fig. 2), or densities of presmolt Atlantic salmon and brown trout in the two rivers (Table 6). In the Ungava Bay region of Canada, anadromous Arctic char are only found in streams with average gradients of less than 70 m/km from the lake to the sea (Power and Barton 1987). However, the gradients of those parts of the Rivers Beiarelva and Saltdalselva which are accessible to anadromous salmonids are only 1.2 and 1.4 m/km, respectively, indicating that fish experience about the same water velocity in both rivers. The average gradients in the Rivers Halselva (10 m/km) and Vassbotnelva (14 m/km) in the Hals watershed are somewhat higher, but are below the critical level for the Ungava Bay region. In running water, competition with Atlantic salmon and brown trout parr may be severe for Arctic char presmolts. Preferences for water velocity, depth, shelter as well as substrate vary among the three species (Heggberget 1984, Heggenes and Saltveit 1990). Temperature preferences also differ in such a way that Arctic char are adapted to the coldest water. Lowest temperature and optimum temperature for growth are lowest for Arctic char and highest for Atlantic salmon, while brown trout are intermediate. Arctic char may grow at temperatures as low as 3 °C (Wandsvik and Jobling 1982), while the lowest temperatures for growth of brown trout and Atlantic salmon are 4 °C and about 7 °C, respectively (Allen 1940, Elliott 1975, 1991, Jensen and Johnsen 1986). Optimum temperatures for growth are about 12-14 °C for Arctic char (Swift 1964, Jensen 1985), 13-15 °C for brown trout (Elliott 1975, Jensen 1990), and 16-17 °C for Atlantic salmon (Siginevich 1967, Dwyer and Piper 1987). River stretches with the highest temperatures may therefore be disadvantageous for Arctic char in competition with Atlantic salmon and brown trout. Average water temperatures in the Rivers Saltdalselva and Halselva are higher than in the Rivers Vassbygdelva and Beiarelva (Fig. 2), but below the optimum temperature of 12-14 °C for growth of Arctic char. However, temperatures vary between years, and years warmer than the average may be decisive for the survival of Arctic char.

Densities of other salmonids reflect interspecific competition, which is greatest in the Rivers Halselva and Saltdalselva, and smallest in the Vassbotnelva (Table 6). In warmer river systems, Arctic char probably fall behind in competition with Atlantic salmon and brown trout in running water, but survive by seeking cooler water in the profundal zone of lakes. Temperature regimes like that in the River Saltdalselva are probably similar to those experienced when Arctic char avoid running water, but still survive in lentic habitats.

Non-anadromous populations of river-dwelling Arctic char are common in the arctic. Such populations also exist in arctic and high boreal areas in Scandinavia (Curry-Lindahl 1957, Aass 1984) as well as in the French Alps (Roule 1925). At lower altitudes and in southern Scandinavia, the species is only found in lentic habitats. Temperature regimes at which lotic populations of resident char are present are unknown, but a clear parallel to anadromous char is obvious. One major difference from anadromous populations is the lack of Atlantic salmon as a competitor, while brown trout is usually present in lower regions.

A climate change associated with the so called "green-house effects" has been hypothesized by a number of authors. A warmer climate in northern Scandinavia will most probably reduce the distribution area of anadromous Arctic char in such a way that populations in the southern part will be extinct or reduced. River-dwelling populations will probably be the most vulnerable to the climate change. Also lotic parts of mixed populations may be lost, while lentic populations may be more tolerant to temperature increases.

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The Palatability of Free Amino Acids and Classical Taste Substances in Frolich Char, *Salvelinus alpinus erythrinus* (Georgi)

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Abstract

The palatability of 21 free L-amino acids (1-100 mM) and 4 classical taste substances (5-10%) was tested in frolich char, Salvelinus alpinus erythrinus. The fish were one year of age and 7-9 cm in length. The tests were performed by offering the fish agar pellets containing the substances at the desired concentration. Of the substances tested, only aspartic acid,glutamic acid, cysteine, histidine and citric acid significantly increased the consumption of pellets by the fish. Lysine had a strong deterrent effect on palatability. The remaining amino acids, sodium chloride, calcium chloride or sucrose did not give a significant change in pellets acceptance. The possibility of creating the mixture of highly effective feeding stimulants for Arctic char is discussed.

Keywords: frolich char, taste perception, free amino acids, classical taste stimuli, feeding stimulants.

Introduction

Arctic char, like other salmonids, have well developed chemosensory systems. The receptor cells of the olfactory organ differentiate in the early life stage (Olsen 1993) and their olfactory sensitivity to chemical signals is extremely high (Døving et al. 1973; Belghaug and Døving 1977; Døving et al. 1980). The Arctic char detects odours released by aquatic food organisms and demonstrate a remarkable capacity to discriminate between many interspecific odours released by sibling, nonsibling and conspecific fish from different populations (Døving et al. 1974, Olsen 1986, 1992; Olsen et al. 1986). In addition it is probable that the olfactory sense plays an important role in guiding the Arctic char during their anadromous migration (Nordeng 1971; Døving 1989).

The taste system of Arctic char is not as well studied. Nevertheless, it has been shown that there are numerous taste buds in the mouth of these fish (Hara et al. 1993). The spectrum of effective amino acids is narrow as shown by electrophysiological studies of the gustatory responses to these compounds (Hara et al. 1993). Furthermore, the behavioral responses to taste stimuli in char have not been studied. In the present paper we describe the palatability of 21 free L-amino acids and 4 classical taste stimuli for frolich charr *Salvelinus alpinus erythrinus.*

Materials and methods

Fish

Frolich char aged 1 year with a length of 7-9 cm were used. The juveniles specimens were reared from eggs under artificial conditions. The living eggs were collected and fertilized by adult fishes in Lake Davatchan before they arrived at the Department of Ichthyology, Moscow State University.

Determination of palatability

The methods developed by Mearns et al. (1987) were used to determine the palatability of chemical substances. Experiments were performed by offering the fish one agar pellet at a time. During the next minute, consumability of the pellet was registered.

The order in which the pellets with different chemical quality were introduced to the fish was performed in random sequence and alternated with the introduction of control (blank) pellets and pellets containing water extract of chironomid larvae.

During the experimental work, the fishes were fed ad libitum with chironomid larvae once daily after the completion of the experiments.

Preparation of agar pellets

The pellets were prepared from agar-agar gel (2%, Reanal). A dye solution (Ponceau 4R 0.5 mM, Aldrich) was added to the gel with one of the chemical substances in the appropriate concentration. The blank gels contained the dye only. The diameter of the pellets was 1.3 mm and the length was 2.0 mm.

Substances

The list of 21 L-isomers of free amino acids (0.1-100 mM; Fluka, NBC, Calbiochem) and 4 classical substances (5-10%; Reachim) are shown in Table 1 and Table 2.

The differences between responses of fish to control and flavoured pellets were assessed using the *t*-test.

Results

Amino acids

Only 5 of the free amino acids used for testing had any influence on pellet consumption. The palatability of pellets containing aspartic acid, glutamic acid and cysteine was high and similar to the pellets that contained chironomid larvae extract (Table 1). The pellets containing histidine were swallowed by the fish at a rate 2.2 times more frequently than blanks. One of the amino acids, lysine, significantly decreased pellets consumption and its acceptance value was 9 times less than that of the control. Thus, lysine had a significant deterrent effect. The remaining 16 amino acids had no significant effect on the pellets palatability for fish at the concentrations used.

Classical taste stimuli

Of the classical taste stimuli, only citric acid (5%) had a significant effect on the palatability (Table 2). Fish swallowed pellets with this substance 3.3 times more often than the control pellets but 1.2 times less frequently than the pellets containing extract of chironomid larvae. The responses of fish to pellets containing calcium chloride, sodium chloride and sucrose were the same as the blank pellets.

Discussion

The results of this bioassay with frolich char clearly indicate that only a few substances give a positive palatability. In an electrophysiological study on the gustatory responses of Arctic char, *Salvelinus alpinus*, it was also shown that only a limited number of amino acids had an effect (Hara et al. 1993). However, amino acids giving responses in this behavioural study and in those of the electrophysiological experiments are not the same. The absence of a strong correlation between the potent amino acids determined by these two methods has also been indicated in rainbow trout, *Oncorhynchus mykiss*. In non-salmonid fish, however, there is a close correlation between gustatory activity of free amino acids in behavioral and electrophysiological tests (see reviews by Caprio 1984; Marui and Caprio 1992).

We suspect that the observed discrepancy between earlier reported electrophysiological data (Hara et al. 1993) and the behavioural data reported here may be determined by one or several different causes. Arctic char and frolich char are different at the subspecies level (Savvaitova 1993). There is not any information about subspecies specificity of teleosts in the spectra of effective taste stimuli. But a number of studies have shown conclusively that different fish species may have very different rank orders of effective taste stimuli (Marui and Caprio 1992). It is quite possible that this discrepancy may be

Table 1. Palatability of agar pellets containing free amino acids for frolich charr juveniles. The ***, ** and * indicate that the values are significantly different from the control $P<0.001$, $P<0.01$ and 0.05, respectively.

Substances	Concentration (mM)	Gel consumption (%)	Number of pellets
Extract of chironomids	75 g l^{-1}	93.8±3.5***	48
Control	-	18.8±5.7	48
L-Aspartic acid	10	90.5±3.2***	48
L-Glutamic acid	10	89.3±3.4***	48
L-Cysteine	100	83.3±3.4***	48
L-Histidine	100	41.7±7.2*	48
L-Leucine	10	33.3±6.9	48
L-Tryptophan	10	27.1±6.5	48
L-Phenilalanine	100	25.0±6.3	48
L-Arginine	100	22.9±6.1	48
L-Proline	100	22.9±6.1	48
L-Norvaline	100	20.8±5.9	48
L-Alanine	100	20.8±5.9	48
Glycine	100	18.8±5.7	48
L-Methionine	100	18.8±5.7	48
L-Serine	100	18.8±5.7	48
L-Tyrosine	1	18.8±5.7	48
L-Glutamine	100	16.7±5.4	48
L-Isoleucine	10	16.7±5.4	48
L-Asparagine	100	16.7±5.4	48
L-Threonine	100	16.7±5.4	48
L-Valine	100	14.6±5.2	48
L-Lysine	100	2.1±2.1**	48

Table 2. Palatability of agar pellets containing classical taste stimuli for frolich charr juveniles. The *** indicate that the values are significantly different from the control ($P<0.001$).

Substances	Concentration (%)	Gel consumption (%)	Number of pellets
Extract of chironomids	75 g l^{-1}	95.0±2.8***	60
Control	-	23.3±5.5	60
Citric acid	5	76.7±5.5***	60
Calcium chloride	10	33.3±6.1	60
Sodium chloride	10	30.0±6.0	60
Sucrose	10	28.3±5.8	60

connected with the different food experience of fish used in electrophysiological and behavioural trials. It should also be noted that the fish used in our experiments were 7-9 cm while the fish studied by Hara et al. (1993) were 20-35 cm and adults of 3+ years age. As it has been shown in sturgeons, the free amino acids gustatory spectra was extending in fish ontogeny (Kasumyan 1992; Kasumyan et al. 1992).

Arctic char are important for fish farming and sport fishing in the northern hemisphere. The results of our study demonstrate that it is possible to create highly effective additives to both the fodder and artificial baits for Arctic char. It should be noted that the feeding stimulants are species-specific and that the fish have an excellent capability to perceive and distinguish different taste substances.

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Disruption of the Ontogenetic Habitat Shift Pattern in a Population of Arctic Charr *Salvelinus alpinus* as a Result of Intensive Fishing

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Abstract

The stunted charr *Salvelinus alpinus* of Lake Takvatn, North Norway used all major habitats of the lake in the icefree season. Charr in the profundal, the pelagic and the littoral habitats differed with respect to age and size and the population displayed a regular pattern of ontogenetic habitat shifts in the lake. From 1984-89, 666,000 charr (31.3 mt) were removed by intensive fishing with funnel traps. The result was a substantial catch per unit effort (CPUE) reduction of charr. The fish left the pelagic zone completely and the littoral CPUE decreased markedly. The profundal CPUE did not change but young fish started to appear in the littoral zone. Brown trout *Salmo trutta* CPUE increased from 1991. We conclude that the intensive fishing programme reduced the density of charr in the lake significantly, and that decreased intraspecific competition led to a disruption of the regular ontogenetic habitat shift pattern observed in the pre-experiment situation.

Keywords: Arctic charr, ontogenetic habitat shifts, intensive fishing.

Introduction

Lacustrine, landlocked populations of Arctic charr display a multitude of life history strategies and ontogenetic habitat use. Some lakes have dimorphic or even polymorphic populations with distinct differences in habitat and food (Frost 1965, Klemetsen and Grotnes 1975, Hindar and Jonsson 1982, Hammar 1984, Klemetsen et al. 1985, Sandlund et al. 1992). There are also large differences in life histories and habitat use in monomorphic Arctic charr populations. In many lakes, the charr grow old and large and feed mainly on benthos and fish, as cannibals if allopatric. Other lakes have dense populations of stunted charr.

This was the situation in Takvatn, an oligotrophic lake in northern Norway. The stunted charr displayed very clear ontogenetic habitat shifts in the icefree season (Klemetsen et al. 1989). Young, immature parr lived in the profundal areas of the lake and mainly fed on chironomids and some plankton (Klemetsen et al. 1992). Only few parr were caught in the littoral region. As 3+ and 4+ fish they left the deep regions and shifted to the pelagic zone where they fed on plankton and surface insects. This shift was coupled with a change to silvery body colours and schooling behaviour. We interpreted the shift to the pelagic region as a relict smoltification. Mature fish dominated the littoral region of the lake. The fish density was high and the littoral charr were stationary (Svenning and Grotnes 1991).

In Lake Takvatn, there was a clear-cut coupling between the major life history stages of parr, smolt and adult fish and the three major habitats of the lake (Klemetsen et al. 1989). We concluded that the slowgrowing Takvatn charr exploited the production of all habitats of the lake maximally by adopting this ontogenetic pattern, and that the driving force was intraspecific competition caused by high fish density.

In 1984-89, Takvatn was fished intensively with baited funnel traps in order to remove large numbers of charr. The traps fished selectively for charr and a total of 666,000 fishes (31.3 metric tons) were removed in the six year period (Amundsen et al. 1993). In essence, this was an experimental mass removal of charr with a whole lake approach. If the habitat segregation of parr, smolt and adult charr was a result of high intraspecific competition, a change in the regular pattern of ontogenetic habitat use should occur if a reduction of fish density was obtained during the experiment. We expected to find a marked reduction of charr density in the less productive profundal and pelagic habitats and a mixture of charr of all sizes and all ontogenetic stages in the littoral zone of the lake.

Methods

Lake Takvatn is a 14.2 km^2 dimictic, oligotrophic and 80 m deep lake situated at 214 m a.s.l. and 69° N in the Målselv river system, North Norway. The fishes of the lake are Arctic charr, brown trout and threespined stickleback *Gasterosteus aculeatus*. A closer description of the lake is given by Klemetsen et al. (1989). Amundsen et al. (1993) describe the traps and their use and give annual yields for 1986-89. The trap yields were 25,000 charr in 1990 and 1991 and the trap fishing was stopped in 1992.

Test fishing was done with gillnets in the three major lake habitats, i.e the littoral, profundal and pelagic zones. The littoral zone is defined as being shallower than 15 m (above the lower edge of submerged macrophytes, mostly *Nitella* sp.) and the profundal zone as deeper than 25 m. Experience had shown that almost no fish is caught deeper than 50 m. Consequently the profundal sampling was restricted to 25-50 m. In 1990, we also sampled the sublittoral, defined as 15-25 m. The pelagic zone was defined as offshore epipelagic waters. The mesh sizes were always chosen to give representative samples. Prior to 1989, nets with bar mesh sizes ranging from 6 to 52 mm were used (for details, see Klemetsen et al. 1989 and Amundsen et al. 1993). From 1989, we changed to multimesh test nets with 5 m panels ranging from 6 to 45 mm. Bottom nets used in the profundal and littoral zones were 1.5 m deep. Floated nets used in the pelagic zone were 6 m deep. Catch per unit effort (CPUE) values are given as number of fish per 100 m^2 net per night. The CPUE values were adjusted to correct for the changes of nets in 1989.

The present contribution concentrates on the development in the three major habitats by comparing time series samples from the years before, during and after the intensive fishing programme. We focus on the length distributions of charr because the habitat shift pattern is related to size. Age is certainly also important, but for the young stages age and size were strongly correlated. This was also the case for older fish after the intensive fishing (Amundsen et al. 1993). The behaviour of the young and small fishes were of special interest and we defined small fish to be below 15 cm fork length. The annual trends were expressed by comparing the total samples of the different years. They represent sampling from the whole ice-free season, normally at least three times from June to October. We compared the total annual samples with the samples from August, which represents a stable summer situation in Takvatn, and found no important differences. We therefore present the total annual samples in order to increase the sample sizes. The seasonal development in the post-experiment situation was studied in 1990 with parallel sampling in the littoral, sublittoral and profundal zones in late June, early July, late July, early August, late August, late September and late October.

Results

The charr CPUE decreased dramatically in the pelagic zone of Takvatn in the period 1984-89 (Fig. 1). No charr were caught in the offshore open waters after 1990. A steady and pronounced CPUE decrease was also observed in the littoral

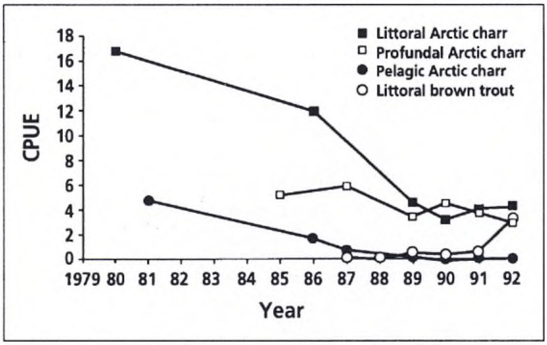

Fig. 1. Catches per unit effort (CPUE, number of fish per 100 m^2 net area per night) of Arctic charr (whole season) and brown trout (August) in Lake Takvatn before, during (1984-89) and after mass removal of charr.

catches. As with the pelagic catches, the steepest decrease occurred from 1986 to 1989. After that, the littoral CPUE values remained low, with the lowest observation in 1990.

The profundal CPUE values showed little variation from 1985 to 1992, and there was no clear temporal trend. The values were below the littoral values before 1989. After that, the differences between littoral and profundal CPUE values were small.

Brown trout were only caught in the littoral zone of Takvatn. Prior to 1990, the catches were very low, with CPUE values close to zero. After 1990, the catches of trout increased and CPUE reached the level of littoral charr in 1992.

Before the intensive fishing programme, the sizes of the charr from the littoral zone reflected the dominance of stunted, mature fish in the 18-22 cm range (Fig. 2). Young fish below 15 cm were rare in that habitat, and there were very few fish above 23 cm in the population. During the period of mass removal (1986-89), the length distributions of charr in littoral samples changed substantially. Small fish below 15 cm became regular components of the littoral samples from 1986. Large fish above 25 cm also appeared regularily from 1986. The small fish were mostly immature, and both parr and smolt types occurred in the littoral samples.

The trend in the profundal samples was different. Small charr dominated completely in 1985, before the fish removal was effective (Fig. 3). Small charr of the parr type prevailed in the profundal samples all the time but, in addition, larger charr started to appear in the profundal nets from 1986.

The charr disappeared completely from the pelagic zone after 1990 (Fig. 1). The catches decreased in the years before that, and the last year with a relatively good sample was 1987 (Fig. 4). Compared to the situation before the mass removal, the sizes of the pelagic charr seemed to increase during the period of intensive fishing.

The seasonal trends of the size distributions in the post-experiment situation (1990) were different in the three benthic habitats (Fig. 5). In the littoral zone, large charr dominated completely in the early part of the season. Small fish below 15 cm started to appear in late July/early August. This trend lasted for the rest of the season.

In the profundal zone, small fish dominated at all times, from late June to late October (Fig. 5). The small profundal charr were of the parr type, with finger marks and dark body colours. A few large charr (>30 cm) were also found in the profundal zone. The seasonal development of the sublittoral zone resembled the profundal trend closely, with a strong component of small fish at all sampling times.

Brown trout were very few in Takvatn in the years prior to the mass removal of charr. After 1990 the trout CPUE increased markedly in the littoral zone (Fig. 1) and the samples of 1991-93 were dominated by young and small fish (Fig. 6).

Discussion

Our hypothesis was that the pattern of ontogenetic habitat shifts of the Takvatn charr should change if the mass removal reduced the fish density in the lake. The results clearly indicate that the regular pattern we observed before the mass removal programme was disrupted during the programme.

We could not be sure that even a substantial mass removal of charr would result in a reduc-

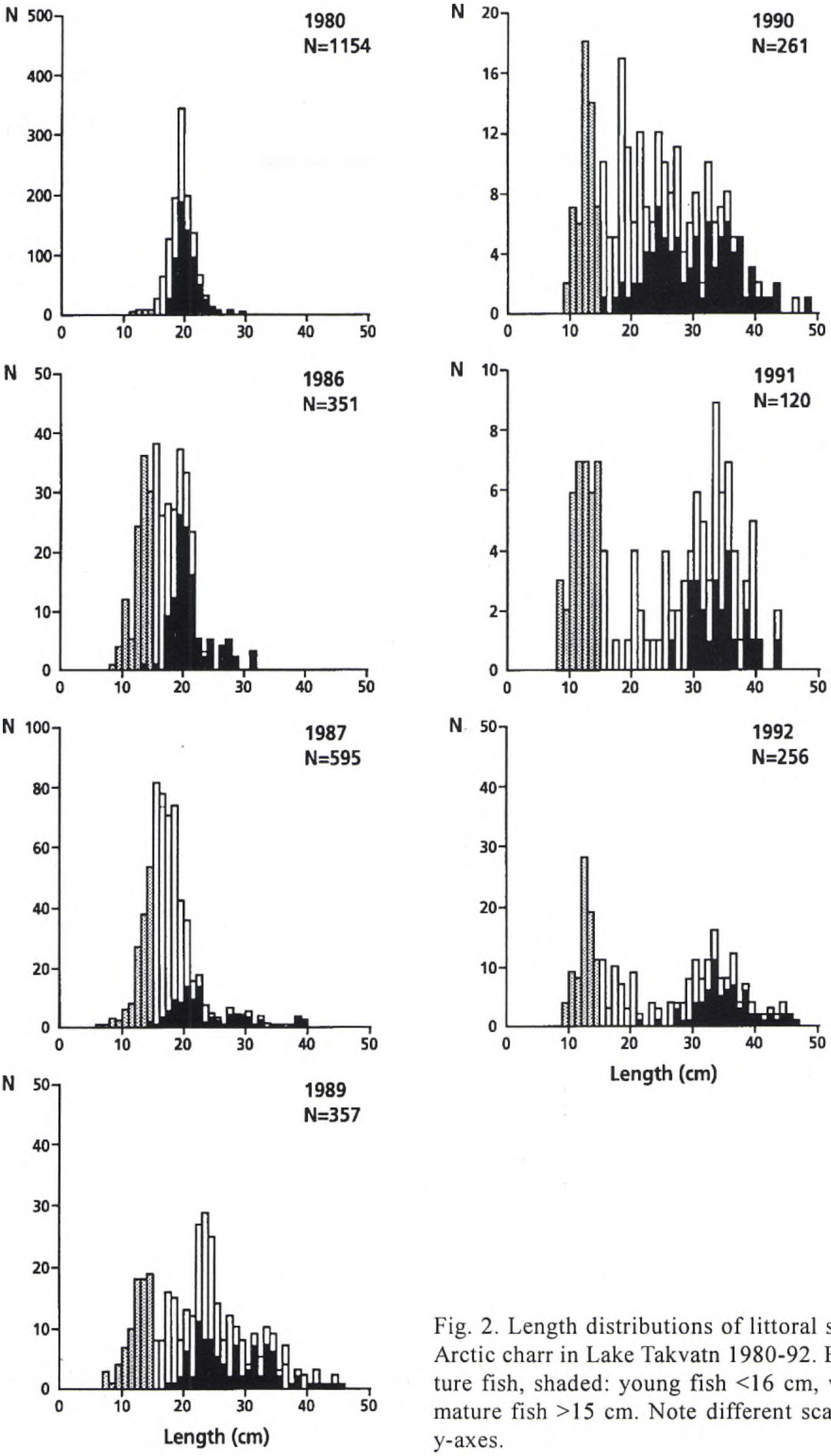

Fig. 2. Length distributions of littoral samples of Arctic charr in Lake Takvatn 1980-92. Black: mature fish, shaded: young fish <16 cm, white: immature fish >15 cm. Note different scales on the y-axes.

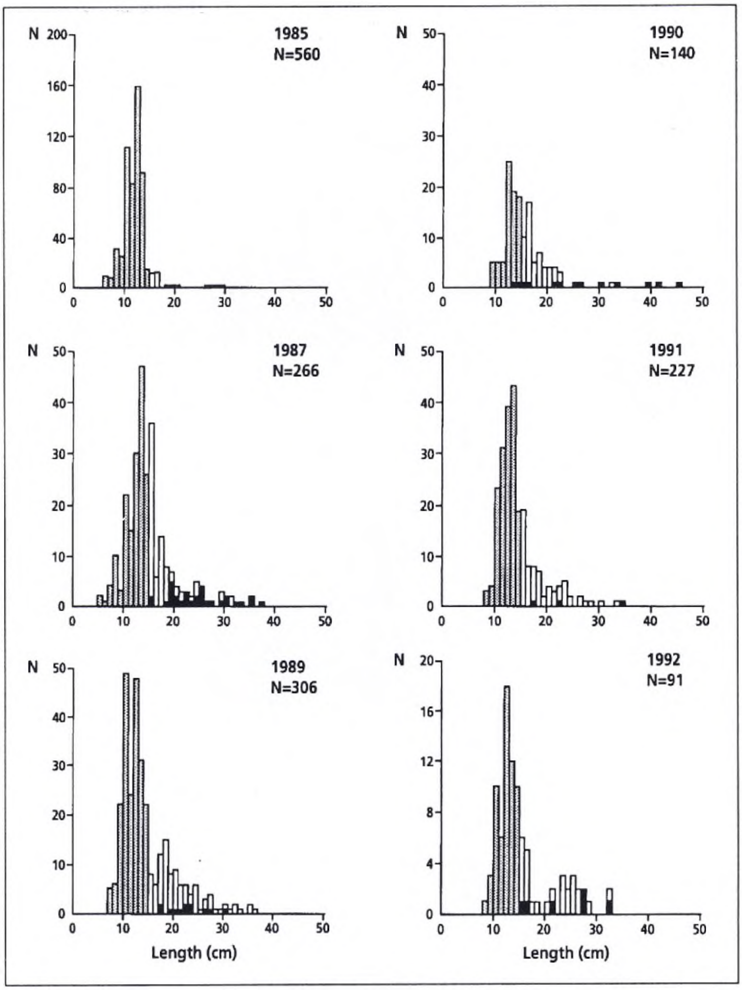

Fig. 3. Length distributions of profundal samples of Arctic charr in Lake Takvatn 1985-92. Shadings as in Fig. 2. Note different scales on the y-axes.

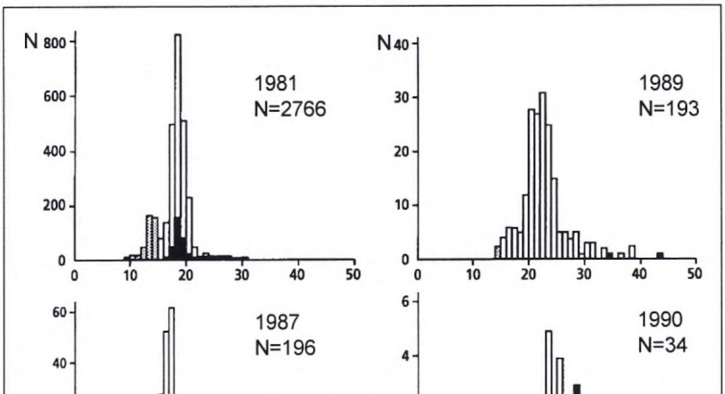

Fig. 4. Length distributions of pelagic samples of Arctic charr in Lake Takvatn 1981-90. Shadings as in Fig. 2. Note different scales on the y-axes.

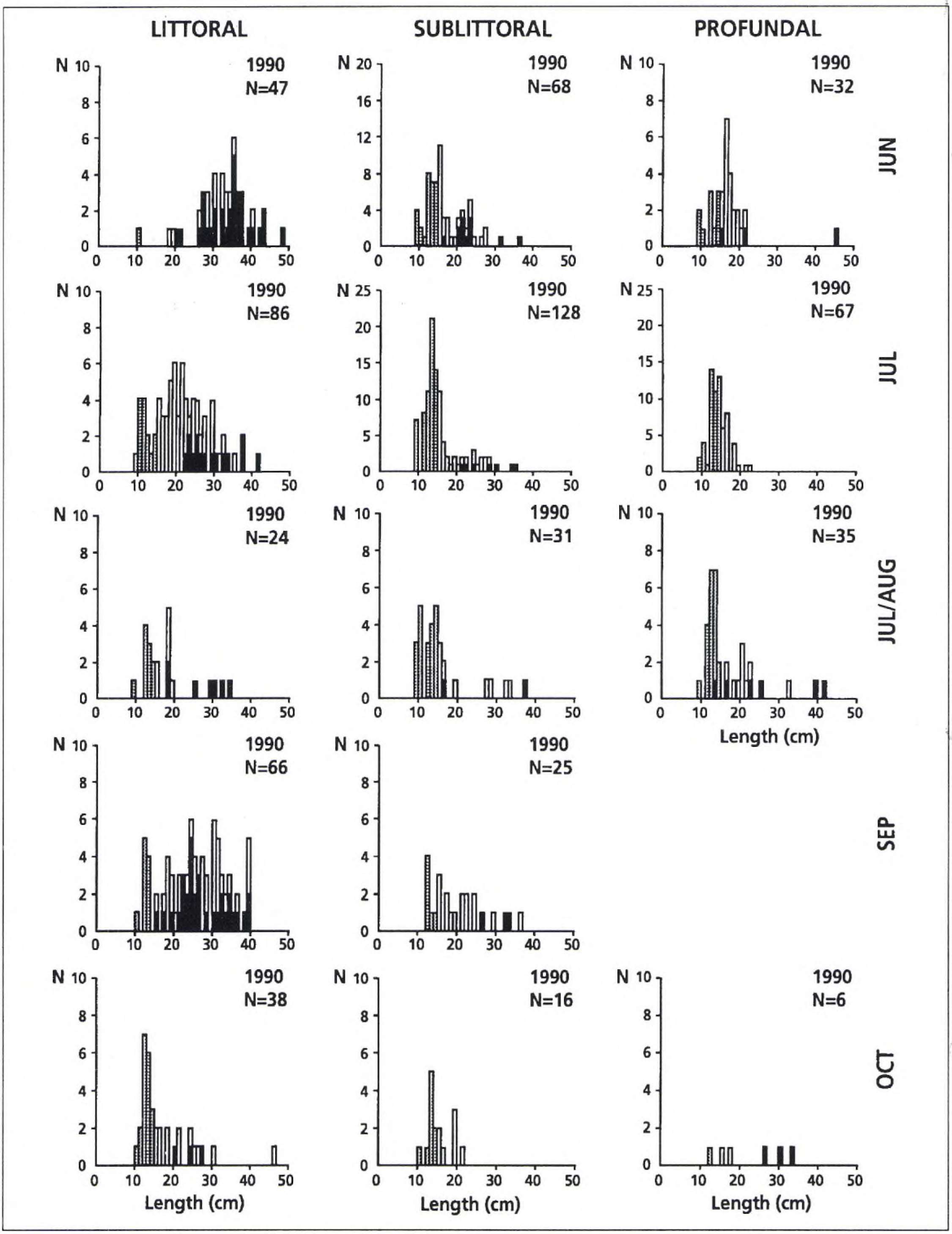

Fig. 5. Seasonal length distributions of littoral, sublittoral and profundal samples of Arctic charr in Lake Takvatn 1990. Shadings as in Fig. 2. Note different scales on the y-axes.

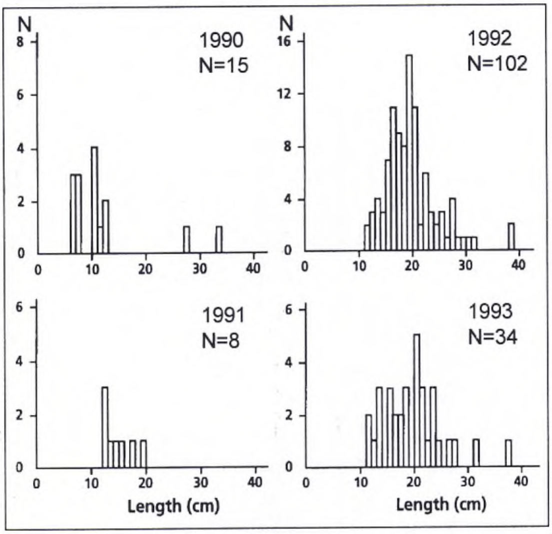

Fig. 6. Length distributions of littoral samples of brown trout in Lake Takvatn 1990-93. Note different scales on the y-axes.

tion of the charr density in the lake. Arctic charr is a fecund fish and a compensation for the increased mortality by increased survival and strong yearclasses could not a priori be ruled out. The CPUE results show that this did not happen. Before the programme, the littoral CPUE alone was about 17 charr per 100 m^2 net area and night (Fig. 1). In the third year of the programme (1986) the value was about 12 and by the end of the programme (1989-92) it had decreased to about 5. The pelagic CPUE decreased from about 5 to zero during the programme. In the period 1989-92, the CPUE of all habitats together was about 9. This is about one third of the total CPUE before the programme started (taken to be the sum of the 1980 value for littoral catches, the 1981 value for pelagic catches and the 1985 value for profundal catches, see Fig. 1). We conclude that the mass removal programme strongly reduced the charr density in the lake. The premise of a density reduction of charr was therefore satisfied.

The growth and size of the charr increased greatly during the intensive fishing (Amundsen et al. 1993). Before 1984, the average fish weight was below 70 g and we hardly caught fish above 150 g. By 1989, the average weight of the oldest fishes were close to 800 g and we recorded charr above 2 kg. Because the population had no large fish before the experiment, changes in their habitat use could not be studied. It is, however, interesting to note that the large charr also appeared in the profundal zone (Fig. 3) and, to some extent, in the pelagic zone (Fig. 4, and see also Dahl-Hansen et al. 1994). This may indicate that the adult charr, as a direct result of their increased sizes, have started to search all habitats for small prey fish. Before the experiment, cannibalism was not possible because of the gape limitations of the stunted adult charr. Cannibalism has increased in Takvatn and probably is a very important mortality factor for young charr in the lake (Amundsen et al. 1993, Amundsen 1994) and, as discussed by Svenning (1993) and Amundsen (1994), in general in Arctic charr lakes.

The mass removal experiment affected the young and small charr most explicitly. The disappearance of smolt type charr from the pelagic zone was the most striking effect. In 1991, we were not able to catch any offshore pelagic charr in spite of a heavy effort with floated nets. Before 1984, surfacing schools of charr could commonly be seen all over the lake on calm days. After the heavy fishing, surfacing charr schools are only seen close to the shores. Floated net samples from inshore bays confirmed the presence of smolt type charr. This indicates that the young immature fish which previously were found in offshore epipelagic waters still may form surface oriented feeding schools, but now over littoral waters.

Selective feeding by pelagic charr had shaped a crustacean plankton community dominated by small copepods and the small cladoceran *Bosmina longispina* in Takvatn (Dahl-Hansen et al. 1994). The plankton biomass was low. The feeding conditions were not attractive but the smolt type charr nevertheless were abundant, feeding on hatching chironomids and plankton, predominantly *B. longispina.* After the pelagic charr moved inshore we observed the notable effect that *B. longispina* was replaced by the even smaller *B. longirostris* in the pelagic zone (Dahl-

Hansen 1995). We have indications that sticklebacks went pelagic for one or two years (possibly because the predation threat from the charr was no longer present) and enforced an even harder selective predation on the plankton. *B. longirostris* are too small to be of any value for charr. The abandonment of the pelagic habitat, therefore, led to an even less attractive food situation for charr in that habitat.

The profundal CPUE time series did not show any decrease (Fig 1), and the parr had the same size range as before (Fig. 3). Even with the increased predation risk from large charr (Fig. 3), the results show that the profundal zone, as the only habitat, supported about the same density of young charr as before the intensive fishing programme.

The dominant prey of profundal parr were immature *Heterotrissocladius subpilosus* (Chironomidae), *B. longispina* and, from August, some littoral benthos, especially the semibenthic cladoceran *Eurycercus lamellatus* (Klemetsen et al. 1992). The profundal zone of Takvatn is a poor feeding habitat, especially after the annual emergence of *H. subpilosus*. The occurrence of littoral prey in the diet of profundal parr suggested that some fish undertook feeding migrations up along the bottom profile but that high adult fish density probably did not allow a permanent stay in shallow water. During the intensive fishing programme, small charr started to appear permanently in the littoral zone (Fig. 2). Seasonal sampling showed that they moved into this zone in late July/early August and stayed there for the rest of the season (Fig. 5). This coincides with the time when littoral prey were found in the profundal parr stomachs before the intensive fishing programme (Klemetsen et al. 1992).

The small fish which appeared in the littoral samples after the reduction of the littoral charr density were mixtures of parr types and smolt types of fish. We conclude that the reduced density of adult fish has reduced intraspecific competition and permitted the access of immature, small charr from both the pelagic and the profundal habitats to the feeding grounds in the littoral with attractive benthos prey like *E. lamellatus, Gammarus lacustris* (Amphipoda), *Lymnaea peregra* (Gastropoda) and large insects.

Brown trout is the original fish species of Takvatn. Before 1930, the lake was famous for its large and beautiful trout but it was overfished and Arctic charr was introduced in the 1930s (Svenning and Grotnes 1991). Threespined stickleback was introduced in the 1940s. Fingerling brown trout of the piscivorous Tunhovd stock from southern Norway were put out in Takvatn in the years 1976-81. Several thousands were stocked yearly. In the years before the intensive fishing programme they never grew larger than the stunted charr and the trout:charr ratio was usually below 1:100 in littoral net catches. Two years into the intensive fishing programme we started to catch a few large trout. Fin-clipping showed that these were stocked fish. Their sizes grew to more than 4 kg (1989). Autumn specimens were ready to spawn. From 1991 the trout CPUE started to increase (Fig. 1). These were small (Fig. 6) and young fish, and were most probably the progeny of the few remaining, and now large, stocked trout. Trout are only caught in the littoral habitat, and the trout:charr ratio has increased to about 1:4 in the latest years. We conclude that the return of the trout is a result of the intensive fishing programme. The significance for the development of the Takvatn fish community may turn out to be very important because brown trout have strong ecological interactions with other fish.

In a study of several lakes from central Norway, Langeland et al. (1991) found that allopatric charr were found in shallow benthic areas while charr living in sympatry with trout tended to live in deeper areas. They concluded that charr were excluded from the littoral areas by brown trout in the summer. This did not happen in Lake Takvatn with the return of the brown trout. The reason may be that the densities of the two species were still too low for strong interspecific interactions to develop. The CPUE values in Takvatn after the mass removal were, however, of the same magnitude as found by L'Abèe-Lund et al. (1993) in several of the central Norwegian lakes. A more likely explanation is the deterioration of the pelagic feeding conditions which came when the sticklebacks moved into the open waters (Dahl-Hansen 1995). We agree with L'Abèe-Lund et al. (1993) that the spatial segregation of sympatric charr and trout is always a trade-off between feeding possibilities and predation risk. There is little use in venturing the pelagic when there is little suitable crustacean plankton to find. This was the case in Takvatn the first years after the mass removal of charr.

In this contribution we find support for the hypothesis that the ontogenetic habitat shift pattern of the Takvatn charr was disrupted when the fish density was experimentally reduced. The prediction that the charr density should decrease in the less productive habitats was supported for the pelagic but not for the profundal habitat. As predicted, charr of all sizes and all ontogenetic stages were found in the littoral zone when the charr density decreased. With the abandonment of the offshore epipelagic habitat, the population became concentrated along the bottom profile and displayed a more obscure pattern of ontogentic habitat use than before. The results suggest that the ontogenetic habitat use in monomorphic, landlocked Arctic charr populations depends on charr density through the operation of intraspecific competition. This full-scale experiment demonstrates the extremely high life history flexibility of the Arctic charr.

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Relationships between Habitat, Prey Selection and Parasite Infection in Arctic Charr (*Salvelinus alpinus*)

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Abstract

The relationship between prey selection and infection of food transmitted parasites in individual Arctic charr (*Salvelinus alpinus*) caught in pelagic and near shore benthic habitats in Lake Fjellfrøsvatn, northern Norway, was followed throughout the year. The charr parasites *Cystidicola farionis* (Nematoda), *Cyathocephalus truncatus* (Cestoda) and *Crepidostomum* spp. (Digenea) are transmitted to fish mainly through benthic amphipods, while *Diphyllobothrium dendriticum*, *D. ditremum* and *Eubothrium salvelini* (Cestoda) are transmitted through copepods. An observed strong segregation of charr in limnetic and benthic foraging groups was closely associated with high infections of parasites transmitted by copepods and amphipods, respectively. Close associations between infection of a parasite species and the occurrence of the corresponding intermediate host in stomach content of individual charr was demonstrated, indicating an individual feeding specialisation. The specialisation toward specific prey items was maintained throughout all seasons, and over an appreciable period of time, using parasites of different longevity as indicators of past prey selection.

Keywords: Arctic charr, foraging behaviour, food transmitted parasites.

Introduction

Arctic charr (*Salvelinus alpinus*) are known to utilise lake habitats with marked differences in dietary preference (Nilsson 1955, Klemetsen et al. 1989, Langeland et al. 1991, Sandlund et al. 1992). The infection levels of different food transmitted parasites are supposed to be greatly dependent on the habitat and prey selection by the individual fish host (Halvorsen and Andersen 1984). Generally, salmonid populations often segregate in habitat choice with large differences in parasite infection (Vik 1954, Petersson 1971, Henricson and Nyman 1976, Konovalov and Buttorina 1985, Frandsen et al. 1989, Amundsen and Kristoffersen 1990), included allopatric Arctic charr populations (Skogsholm 1990). In a winter study, Knudsen (1991) found strong indications of individual feeding specialisation by using parasites as indicators of past prey selection.

In northern lakes, two main pathways of food transmitted parasites to fish are through benthic (mainly amphipods) and pelagic (mainly copepods) crustaceans (Curtis 1982). In Lake Fjellfrøsvatn, northern Norway, the Arctic charr are infected with nine species of food transmitted parasites, among them four species are transmitted to fish exclusively from copepods and four species mainly from amphipods. These intermediate hosts represent two fundamental feeding strategies for charr; one oriented towards "planktonic" prey (copepods) and the other towards benthic prey (amphipods).

The present study was set up to test the foraging behaviour and duration of habitat selection of the Arctic charr by using infection of food transmitted parasites as indicators of past prey selection. Charr caught in different lake habitats should exhibit different levels of infection with parasite species transmitted from copepods (pelagic habitat) and amphipods (benthic habitat). If individual charr specialise on certain prey, a strong correlation between parasite infection and the occurrence of the corresponding intermediate hosts in the stomach contents in individual fish should be expected.

Material and methods

Fjellfrøsvatn (69°05' N, 19°20' E, 125 m a.s.l.) is an oligotrophic lake situated in northern Norway with a surface area of 6.5 km² and a maximum depth of 88 m. The lake is surrounded by birch and pine. Fish species in the lake are Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*).

The periods of field work in 1992, together with water temperatures (°C in parenthesis) were: 1-5 June (3.4°), 6-10 July(10.2°), 10-14 August (11.6°), 8-12 September (8.8°), 5-9 October (6.6°), 2-6 November (2.8°), 29-2 November/ December (categorised as "December", 0.6°) and in 1993: 8-12 March (0.7°), 3-7 May (0.7°). Ice breakup was last week of May 1992 and freezeup about 10 November. Vertical plankton hauls (<30m, 90µ) were taken each month except in Sepember and December.

The Arctic charr (*N*=2,814) were sampled by multimesh gill nets (40 m) with mesh sizes (knot to knot) of 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm. The charr were caught in three different habitats: in the benthic littoral zone (<10 m, *N*=1,566 charr), the benthic profundal zone (>25m, *N*=978) and the pelagic zone (*N*=270). The fish were weighed, measured (fork length) and age determined by surface reading of otoliths placed in glycerol. Stomach contents were preserved in 70% alcohol. The prey items were identified and their relative contribution to the stomach fullness estimated according to Amundsen (1989). The encountered food items were divided into two groups based on their origin from limnetic or benthic habitats. Insect pupae and terrestrial insects were classified as limnetic prey according to Bérubé and Curtis (1986). When limnetic or benthic prey items contributed more than 50% of the stomach contents, the charr individuals were classified as limnetic or bentic feeders respectively. Charr with stomach fullness less than 10%, are excluded to reduce accidental stomach-parasite relations. The occurrence of potential intermediate hosts from the stomachs are expressed as frequency of occurrence (%) and percentage contribution to stomach content (% volume).

A sample of 1,114 charr from littoral and 234 charr from pelagic gill nets were examined for parasites. The swim-bladders were preserved in 70% ethanol. In the laboratory the bladders were opened, and the nematodes (*Cystidicola farionis*) were enumerated and classified into three groups according to Giæver et al. (1991): L3-larvae, preadults (L4) and adults. The intestine was opened, parasites removed, identified after Chubb et al. (1987) and enumerated. Both *Crepidostomum farionis* and *C. metoceus* are known to occur, but were not regularly identified as species and are termed as *Crepidostomum* spp. Presence or absence of *Phyllodistomum umblae*, a trematode in ureters, was noted. The stomach wall, visceral organs (except the swim bladder and intestine) and all cysts in the flesh were placed in digestive fluid (1 litre = 2 ml HCl, 5 gr pepsin, 9 gr NaCl, water). The excysted plerocercoids of *Diphyllobothrium* spp. were identified according to Andersen and Gibson (1989). The charr were divided into small (150-199 mm) and large (200-250 mm) fish to diminish the variance in the parasite material.

Copepods are the first intermediate host of *D. dendriticum*, *D. ditremum* (Vik 1964, Halvorsen 1966) and the only intermediate host of *E. salvelini* (Vik 1963, Boyce 1974) and *Proteocephalus* sp. (Sysoev et al. 1994). The amphipod *Gammarus lacustris*, acts as the only intermediate host of *C. truncatus* (Vik 1958) and *C. farionis* (Smith and Lankester 1979), while *Crepidostomum* spp., may also utilise mayfly larvae (Ephemeroptera) (Thomas 1958). These parasites are referred to as amphipod or benthic transmitted parasites. The charr were also infected with *Diplostomum spathaceum* (Trematoda) and *Salmincola edwardsii* (Copepoda).

The terms prevalence and relative density (= abundance) are used according to Margolis et al. (1982).

Results

Arctic charr were caught in the littoral zone throughout most of the year, except in June when all fish were caught below 15m. The size of littoral caught charr ranged from 91 mm (1+ year-class) to 358 mm (11+), and the size of fish in the pelagic samples ranged from 139 mm (3+) to 273 mm (8+). There were few fish older than eight years and these were pooled into one group (≥9+).

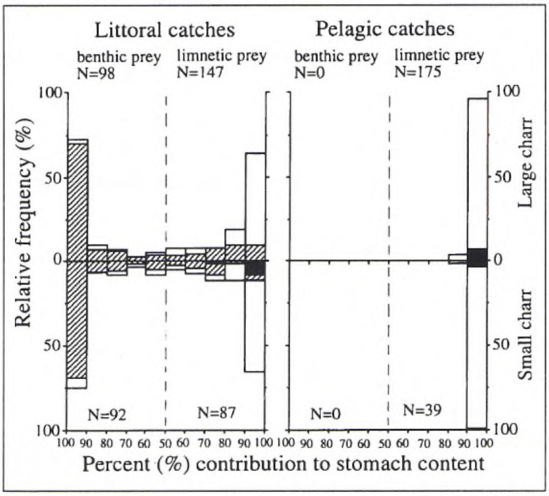

Fig. 1. The frequency distribution (%) of large (20-25 cm) and small (15-20 cm) Arctic charr feeding on benthic and limnetic prey items in littoral and pelagic habitats. The proportion of charr with amphipods (shadded area) and copepods (black area) present in stomach content are given. *N*=number of charr.

The benthic prey items were mainly insect larvae (mayflies, stoneflies, caddisflies, tipulids, chironomids), molluscs (gastropods, bivalves) and benthic crustaceans (amphipods, chydorids). The limnetic prey items were mainly terrestrial adult insects, insect pupae (chironomids, caddisflies) and pelagic crustaceans (copepods, cladocerans). No charr were found to be piscivorous. Charr caught in the pelagic zone were exclusively limnetic feeders (Fig 1.). The food choices of littoral charr were either dominated by benthic or limnetic prey items, and few fish had a mixed diet. Most of the benthic feeders in both length classes had eaten *Gammarus lacustris*. Amphipods were eaten throughout the whole year by littoral charr, but none of the pelagic charr had fed upon this prey. Few charr ate *G. lacustris* during the summer, but from August amphipods contributed significantly to the stomach content of littoral charr (Table 1). The zooplankton community was completely dominated by copepods, mainly the calanoid *Eudiaptomus gracilioides.*

Table 1. Frequency of occurence (*Fq*%) and percent contribution (*Pc*%) of amphipods and copepods to stomach content of Arctic charr (15-25 cm) caught in littoral and pelagic habitats throughout the year in Lake Fjellfrøsvatn. The relative frequency (%) of copepods denotes the proportion of *Eudiaptomus graciloides\Cyclops scutifer* (cop4+5 and adults) from the total count of zooplankton (copepods plus cladocerans) in vertical tows. *N*=number of charr.

	Gammarus lacustris					Copepods				
	Littoral			Pelagic		Littoral		Pelagic		Relative
	N	*Fq*%	*Pc*%	*N*	*Fq*%	*Fq*%	*Pc*%	*Fq*%	*Pc*%	frequency %
Jun	41	4.9	0.5	0	0	0	0	0	0	58\40
Jul	47	12.8	3.8	30	0	2.1	0.1	3.3	<0.1	63\16
Aug	60	41.0	19.3	77	0	0	0	0	0	80\6
Sep	59	32.8	15.6	75	0	11.3	0.8	2.7	0.1	-
Oct	55	63.0	34.3	45	0	16.4	5.0	22.2	4.6	81\11
Nov	66	60.6	36.0	-	-	30.3	14.2	-	-	89\8
Dec	56	60.8	40.3	-	-	3.6	0.1	-	-	-
Mar	36	59.3	29.3	-	-	8.3	1.7	-	-	95\5
May	72	52.2	27.4	-	-	1.4	2.4	-	-	80\7

Table 2. Prevalence (prev.), relative density ($\overline{x}$) and variance to mean ratio ($s^2/\overline{x}$) of eight species of food transmitted parasite species in different age groups of Arctic charr in littoral (Lit.) and pelagic (Pel.) habitats in Lake Fjellfrøsvatn. *N*= number of charr. Charr length ±95% confidence interval (C.I.).

Age	1+yr	2+yrs	3+yrs		4+yrs		5+yrs		6+yrs		7+yrs		8+yrs		≥9+yrs
Habitat	Lit.	Lit.	Lit.	Pel.	Lit.	Pel.	Lit.	Pel.	Lit.	Pel.	Lit.	Pel.	Lit.	Pel.	Lit.
Charr length (mm)	99.9	122.1	145.2	177.1	179.1	197.7	218.6	218.7	233.7	229.1	258.2	237.4	274.6	241.7	297.9
±95% C.I.	±2.8	±2.4	±1.8	±12.0	±3.8	±4.4	±3.4	±2.8	±4.4	±3.0	±3.8	±8.0	±12.2	±20.0	±24.0
N	23	112	158	8	176	44	169	107	109	59	52	10	29	5	11
Phyllodostmum spp.															
prev.	0	11.0	34.0	100.0	74.2	100.0	94.1	100.0	92.7	100.0	98.1	100.0	93.1	100.0	100.0
Crepidostomum spp.															
prev.	52.2	68.8	85.4	75.0	89.8	97.6	96.5	97.2	97.3	98.3	94.2	100.0	100.0	80.0	100.0
$\overline{x}$	1.2	4.5	17.0	32.9	48.0	25.4	97.2	24.9	83.3	49.9	159.7	46.6	199.4	13.0	167.6
$s^2/\overline{x}$	1.8	11.6	54.6	106.7	201.5	63.5	190.0	50.6	160.6	173.1	281.5	55.7	618.4	16.8	156.7
C. truncatus															
prev.	21.7	37.5	50.6	0	51.2	2.4	50.2	1.9	50.5	5.1	69.2	0	72.4	0	45.5
$\overline{x}$	0.4	1.2	2.6	0	6.2	<0.1	11.8	<0.1	11.9	0.6	18.8	0	13.5	0	19.5
$s^2/\overline{x}$	1.5	4.3	16.4	0	23.1	1.0	75.6	1.6	69.5	24.3	68.6	0	53.7	0	63.7
C. farionis															
prev.	4.8	37.5	63.7	37.5	80.6	56.8	89.9	65.1	91.7	84.8	96.7	50.0	100.0	80.0	100.0
$\overline{x}$	0.3	0.9	3.3	8.6	12.7	3.7	24.8	7.5	38.8	9.6	96.9	6.3	165.0	10.0	320.6
$s^2/\overline{x}$	5.7	3.8	10.1	64.7	30.0	15.2	43.5	39.2	77.5	22.1	126.0	24.7	119.4	14.2	247.3
Protocephalus sp.															
prev.	4.4	8.3	6.5	0	3.0	2.4	4.7	12.2	2.8	10.2	0	0	0	20.0	9.1
E. salvelini															
prev.	4.4	23.0	60.8	87.5	75.6	90.5	85.2	90.7	83.5	84.8	80.8	100.0	75.9	100.0	72.7
$\overline{x}$	0.1	0.4	1.3	2.7	2.3	2.6	3.9	3.6	4.0	3.7	3.1	4.6	3.2	6.6	1.7
$s^2/\overline{x}$	1.0	2.0	1.9	1.3	2.8	1.7	16.0	2.6	5.4	2.9	3.8	5.5	4.3	1.0	1.2
D. ditremum															
prev	4.4	47.3	71.1	100.0	93.8	100.0	97.6	100.0	99.1	100.0	100.0	100.0	100.0	100.0	100.0
$\overline{x}$	0.2	1.2	2.6	16.4	8.7	12.5	20.1	25.7	31.4	34.8	36.1	72.4	31.0	50.5	46.7
$s^2/\overline{x}$	3.5	3.0	5.3	56.8	13.7	10.2	15.5	11.4	31.7	20.1	22.3	30.6	15.6	27.3	24.8
D. dendriticum															
prev	4.4	1.8	16.4	75.0	34.1	72.7	62.7	60.8	65.1	76.3	76.9	80.0	72.4	60.0	72.7
$\overline{x}$	0.1	0.1	0.3	4.4	1.2	2.0	1.9	1.7	2.2	2.6	2.4	3.1	2.3	1.5	1.6
$s^2/\overline{x}$	1.0	1.0	4.7	6.6	6.5	2.8	3.1	2.8	5.3	6.4	2.5	2.5	3.6	2.5	2.5

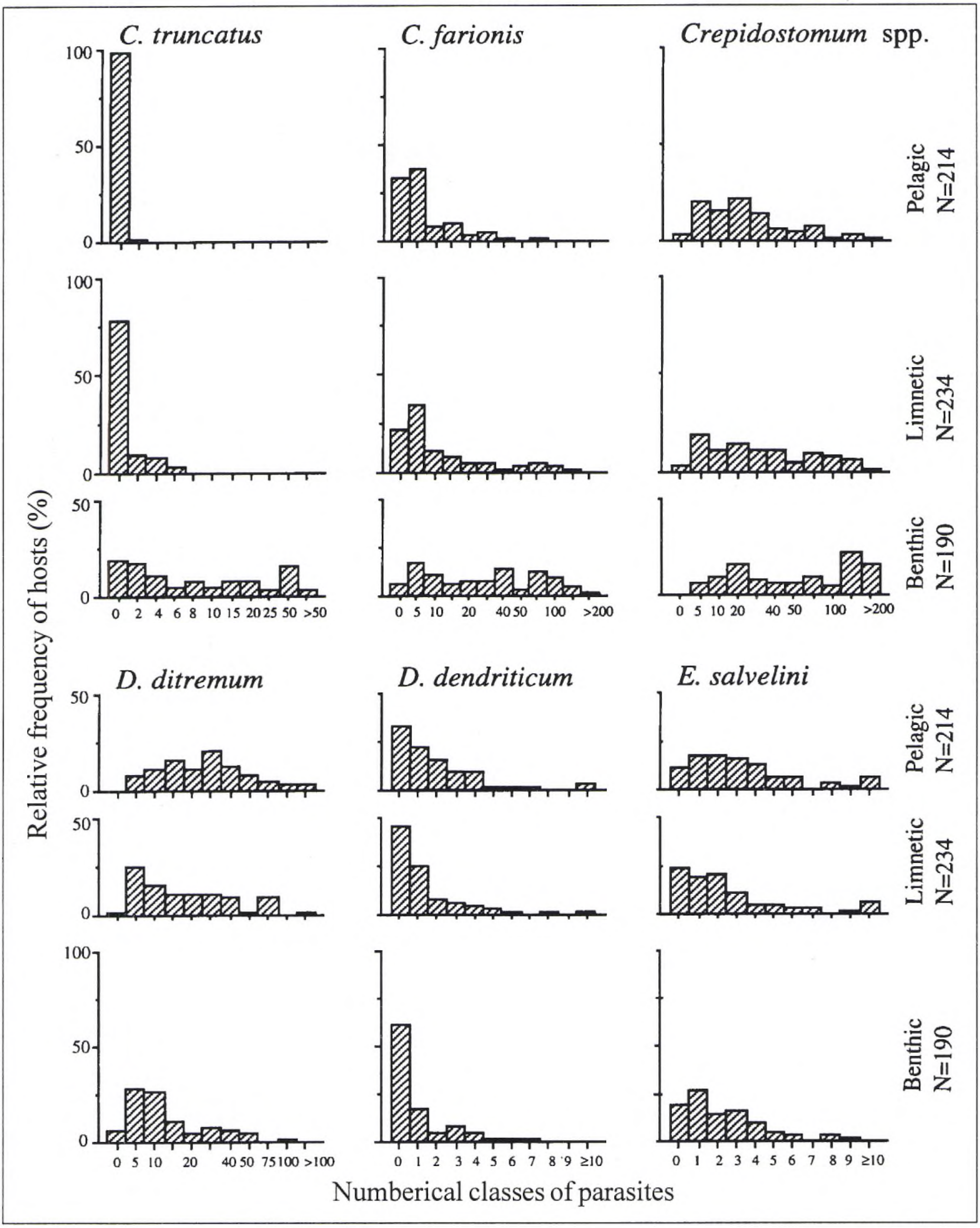

Fig. 2. Frequency distribution (%) for amphipod and copepod transmitted parasite species in Arctic charr (15-25 cm) from the pelagic zone and from benthic and limnetic feeders in the littoral zone. Note different scaling on x-axes. *N*=number of charr.

However, copepods were eaten only occasionally during the summer (June-August) and under ice cover (December, March, May) of both littoral and pelagic charr. The most frequent feeding on copepods occurred from September to November mainly by limnetic feeders (Table 1, Fig. 1). *E. gracilioides* contributed 97% and 81% of the stomach content of copepods in pelagic and littoral charr, respectively. The remaining percentage was made up of *Cyclops scutifer* (ice-free season), *Achanthocyclops gigas* (ice bound period) and *Heterocope appendiculata*.

In littoral charr, the prevalence and relative density of *C. truncatus*, *C. farionis* and *Crepidostomum* spp. increased with increasing age of charr, but were much lower and nearly unchanged in pelagic charr (Table 2). The density of *D. dendriticum*, *D. ditremum* and *E. salvelini* increased to fish age 5+ or 6+ and remained more or less unaltered in older age classes. The pelagic charr were slightly more infected with these parasite species than the littoral charr.

High infection levels of different species of amphipod transmitted parasites were closely associated with littoral charr exhibiting a benthic prey selectivity (Fig. 2). Limnetic feeders from the littoral and pelagic habitats, were almost identically infected by the same parasite species. These charr had slightly higher infection levels of copepod transmitted parasites compared to benthic feeders.

Charr of age 5+ and 6+ were numerous and similar in size. These fish were therefore pooled to follow the infection level in different feeding groups throughout the year. The samples from March and May were pooled because of relatively small catches. In general, the amphipod feeders had significantly more *C. truncatus*, *C. farionis* and *Crepidostomum* spp. than limnetic feeders from littoral and pelagic habitats throughout the whole year (Fig. 3). Results of Mann-Whitney *U*-tests of parasite infection between the feeding groups are given in Table 3. From August onward, the amphipod feeders had lower infec-

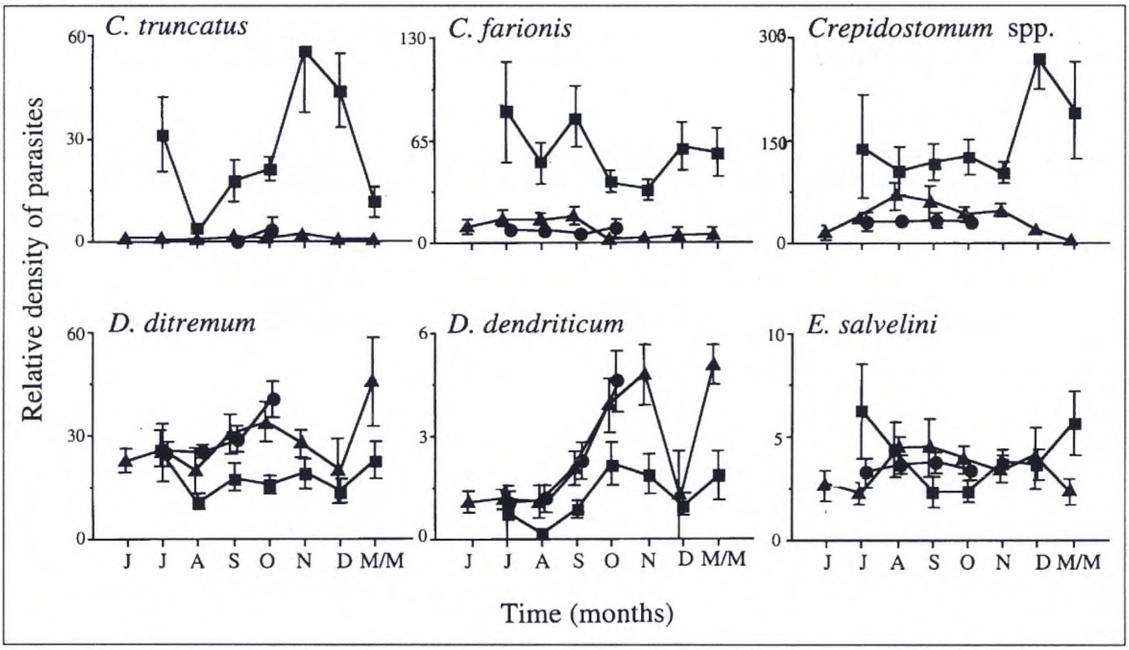

Fig. 3. Relative density of different amphipod and copepod transmitted parasite species in Arctic charr (5+ and 6+ years) from the pelagic zone (circle) and from amphipod (square) and limnetic (triangle) feeders in littoral zone throughout the year. Vertical bars represent standard error (±1SE). For numbers of charr see Table 3.

Table 3. Results from Mann-Whitney *U*-tests of the distribution of six species of food transmitted parasites between different foraging groups (amphipod feeders, limnetic littoral feeders and pelagic feeders) of Arctic charr (5+ and 6+ years) throughout the year in Lake Fjellfrøsvatn. *N*=number of charr. Significance: **$P \leq 0.001$, * $P \leq 0.05$, NS=$P > 0.05$

Feeding groups	Limnetic littoral vs Amphipod						
	Jul	Aug.	Sep	Oct	Nov	Dec	Mar/May
N	39	25	26	26	39	23	20
C. truncatus	**	**	**	**	**	**	*
C. farionis	*	*	**	**	**	*	*
Crepidostomum spp.	*	NS	*	**	*	*	*
D. ditremum	NS	NS	NS	*	NS	NS	NS
D. dendriticum	NS	NS	NS	NS	*	NS	**
E. salvelini	NS	NS	NS	NS	NS	NS	NS

Feeding groups	Limnetic littoral vs Pelagic				Amphipod vs Pelagic			
	Jul	Aug	Sep	Oct	Jul	Aug	Sep	Oct
N	60	78	60	60	31	75	55	36
C. truncatus	NS	*	*	*	**	**	**	**
C. farionis	*	*	NS	NS	**	**	**	**
Crepidostomum spp.	*	*	NS	NS	*	**	**	**
D. ditremum	NS	*	NS	NS	NS	**	NS	**
D. dendriticum	NS	NS	NS	NS	NS	*	*	*
E. salvelini	NS	NS	NS	NS	NS	NS	NS	NS

tion of *D. dendriticum* and *D. ditremum* compared to limnetic feeders from pelagic and littoral habitats (Fig. 3). When samples from two months were pooled (e.g. July/August, September/October, November/December) the differences were significant (except for *D. dendriticum* in July/August) in all periods ($P \leq 0.05$). The infection level of *E. salvelini* was not significantly different among the three different feeding groups.

Both copepods and amphipods were heavily preyed upon in the autumn (e.g. littoral: September-November, pelagic: September-October, see Table 3). In this period, charr were divided into pelagic feeders, limnetic littoral feeders and benthic feeders. In addition, each of these groups were further divided into specific feeding groups for potential intermediate hosts. These are named amphipod feeders (when *G. lacustris* contributes to >75% of stomach content), littoral copepod feeders and pelagic copepod feeders (copepods present in the stomach content of littoral and pelagic charr respectively). In general, the amphipod feeders had significantly higher infection of amphipod transmitted parasites compared to all other feeding groups (Fig. 4.). The patterns of infection for copepod transmitted parasites were otherwise. The amphipod feeders were always least infected of all the copepod parasites. Copepod feeders had significantly higher infections of *D. ditremum* and *D. dendriticum*, compared to most other feeding groups. The relative densities of amphipod transmitted parasites were very low in the limnetic and copepod feeders. The infection levels of *E. salvelini*, were similar between these latter two feeding groups. Infection patterns were equal between the two size classes of charr. The results of Mann-Whitney *U*-tests between the different feeding groups are presented in Table 4.

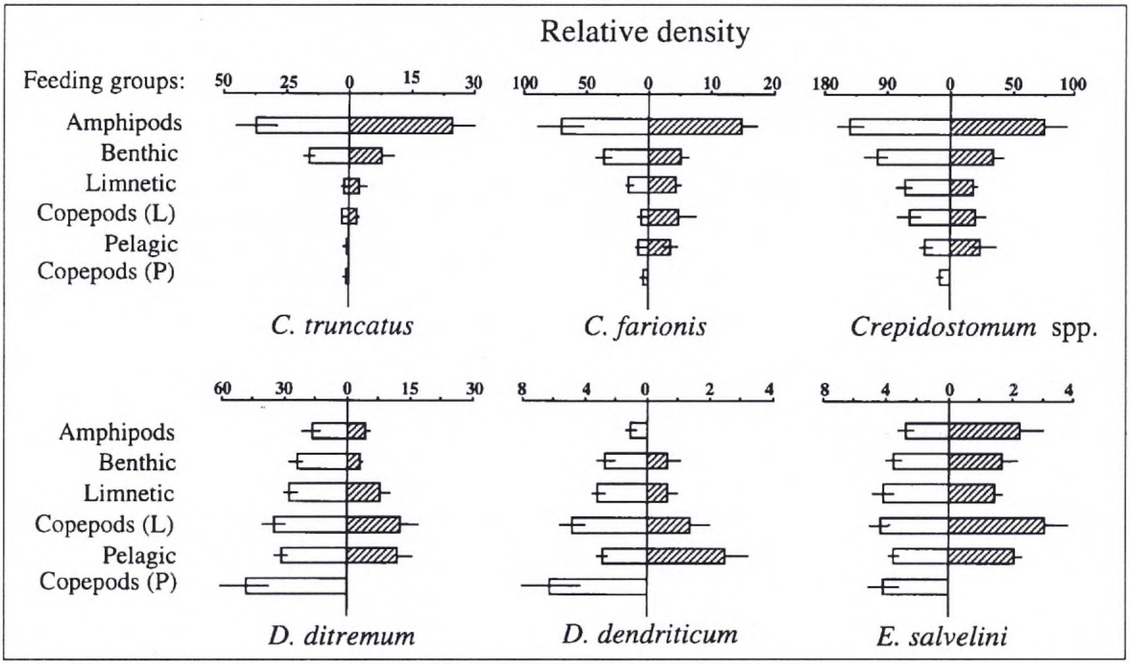

Fig. 4. Relative density of different amphipod and copepod transmitted parasite species in large (open bars) and small (shadded bars) Arctic charr having different prey selection in littoral (L) and pelagic (P) zone from September to November. Horizontal line represent standard error (±1SE). For numbers of charr in each group see Table 4.

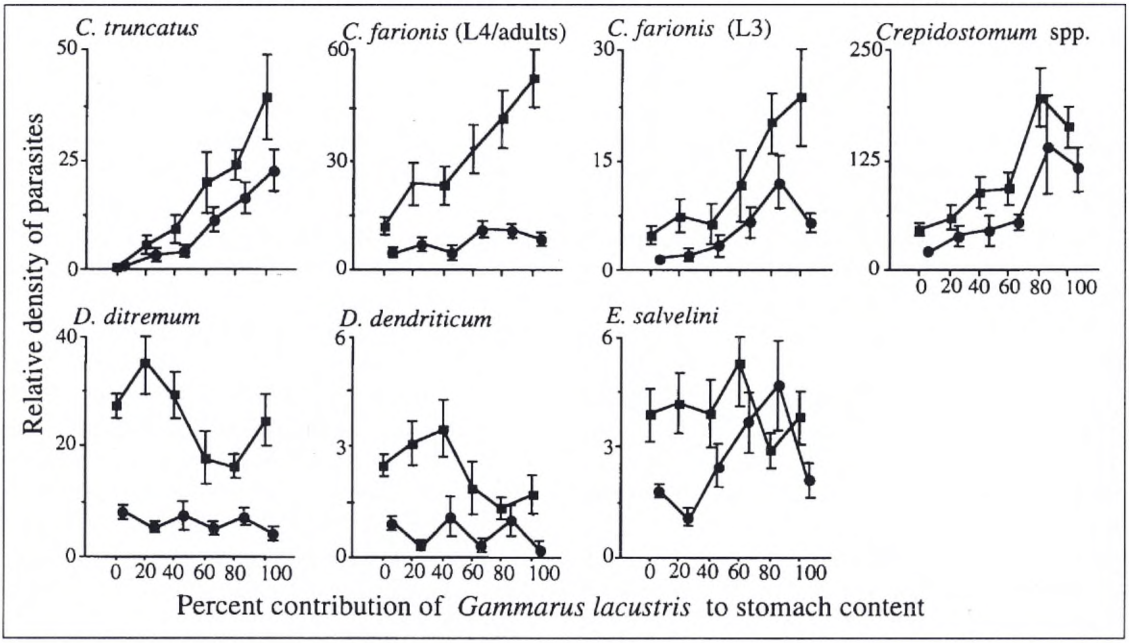

Fig. 5. Relative density of different amphipod and copepod transmitted parasite species in small (circle) and large (square) Arctic charr with increasing percent contribution of *Gammarus lacustris* to stomach content.

Table 4. Results of Mann-Whitney *U*-tests in infection of six species of food transmitted parasites of large (lower half) and small (upper half) Arctic charr having different food selection in littoral (September-November) and pelagic (September-October) habitats in Lake Fjellfrøsvatn. *N*=number large (20-25 cm) \ small (15-20 cm) charr in each feeding-group. Significance: ** $P \leq 0.001$, * $P \leq 0.05$, NS=$P > 0.05$

		Cyathocephalus truncatus					***Cystidicola farionis***					***Crepidostomum* spp.**				
Feeding groups	*N*	AM	BE	LL	CL	PE	AM	BE	LL	CL	PE	AM	BE	LL	CL	PE
Amphipods (AM)	**21\12**	----	**	**	**	**	----	**	**	**	**	----	*	**	*	**
Benthic (BE)	**24\17**	**	----	**	**	**	**	----	NS	NS	NS	**NS**	----	NS	NS	NS
Limnetic littoral (LL)	**46\26**	**	**	----	NS	**	**	**	----	NS	**	**	**	----	NS	**
Copepods littoral (CL)	**23\13**	**	**	**NS**	----	**	**	**	*	----	NS	**	**	**NS**	----	NS
Pelagic (PE)	**81\27**	**	**	**NS**	**NS**	----	**	**	**NS**	**	----	**	**	**NS**	**NS**	----
Copepods pelagic (CP)	**11\-**	**	**	**NS**	*	**NS**	**	**	*	**NS**	**NS**	**	**	**	**	*

		Diphyllobothrium ditremum					***Diphyllobothrium dendriticum***					***Eubothrium salvelini***				
Feeding groups	*N*	AM	BE	LL	CL	PE	AM	BE	LL	CL	PE	AM	BE	LL	CL	PE
Amphipods (AM)	**21\12**	----	NS	NS	NS	**	----	NS	**	**	**	----	NS	NS	NS	NS
Benthic (BE)	**24\17**	*	----	NS	NS	**	**NS**	----	NS	NS	**	**NS**	----	NS	NS	NS
Limnetic littoral (LL)	**46\26**	**	**NS**	----	NS	**	**	**NS**	----	NS	**	**	**NS**	----	NS	NS
Copepods littoral (CL)	**23\13**	**	**NS**	**NS**	----	NS	**	**	**NS**	----	NS	*	**NS**	**NS**	----	NS
Pelagic (PE)	**81\27**	**	**	**	**NS**	----	**	*	**NS**	**NS**	----	**	**	**NS**	*	----
Copepods pelagic (CP)	**11\-**	**	**	*	**NS**	*	**	**	*	**NS**	*	**	**NS**	**NS**	**NS**	**NS**

The amphipod *G. lacustris* was heavily preyed upon by the two size classes of charr (Table 1.). Infection involving all of the amphipod transmitted parasites was strongly associated with occurrence of *G. lacustris* in the stomach contents (Fig. 5.). This relationship was not found for copepod transmitted parasite species.

Discussion

The present results demonstrate a strong relationship between the occurrence of intermediate hosts in the stomach contents when the fish were caught, and the abundance of the corresponding parasite species. The most striking difference between littoral and pelagic Arctic charr was the consistently higher prevalence and relative density of *C. farionis*, *C. truncatus* and *Crepidostomum* spp. in the littoral charr. This difference was apparently maintained throughout the host's lifespan. The benthic feeders have much higher infection levels of all the amphipod transmitted parasites compared to limnetic feeders. The infection levels for *D. dendriticum*, *D. ditremum* and *E. salvelini*, were similar among limnetic and benthic feeders, although the latter group was less infected. Consistent differences in parasite infection between feeding groups, indicate a maintainance of a specialised diet over a long period. The overall infection levels of pelagic and limnetic littoral feeders were almost identical, which suggests that limnetic feeders could alternate between littoral and pelagic habitats, or that the littoral charr segregate into benthic and limnetic feeders.

The strong relationship between parasite infection and occurrence of the corresponding intermediate hosts in the diet of individual charr implies feeding specialisation. The indications of feeding specialisation on copepods have similarities to other studies of Arctic charr (Curtis 1985, Bérubé and Curtis 1986, Knudsen 1991). The copepod feeders had a decidedly lower infection of amphipod transmitted parasites. No charr were observed to be piscivorous, and copepods seemed to be the main source of *Diphyllobothrium* spp. in charr (<250 mm) from Lake Fjellfrøsvatn. *E. salvelini* was the only parasite displaying a weak association with the diet of charr. This parasite utilises both benthic and pelagic copepods as intermediate hosts (Boyce 1974, Poulin et al. 1992) while in contrast, planktonic copepods seem to be the most suitable intermediate hosts of *Diphyllobothrium* spp. (Vik 1964, Halvorsen 1966). Charr mainly fed on planktonic *E. graciloides* during the ice-free season, which may explain the close relation between copepod feeders and infection of *Diphyllobothrium* spp. in the autumn. The recruitment of *E. salvelini* may also take place during winter when the charr feeds more on benthic copepods, and may explain its different infection pattern.

Relative density of all the amphipod transmitted parasites remained continuously high throughout the year in amphipod feeders compared to limnetic feeders. This indicates a year round specialisation on amphipods. Knudsen (1991) found strong indications of individual specialisation on both amphipods and copepods in a winter study in Lake Takvatn. These results indicate that specialisation on copepods may take place during all seasons, although the present results indicate that specialisation occurs only during the autumn. Relative density of the long-lived parasite *C. farionis* (Giæver et al. 1991) decreased from summer to autumn, indicating that less infected charr start to feed on *Gammarus* in the autumn. This suggests that the most infected individuals specialise on amphipods during all seasons. In August, all caught charr had low abundances of the shortlived species *C. truncatus*. This may be explained by the observed low feeding on amphipods in June and July with a corresponding reduction in recruitment input. The similarity in the infection pattern of different amphipod transmitted parasites, implies that amphipods are more important than mayfly nymphs in transmission of *Crepidostomum* spp. to charr.

Evidence for feeding specialisation on the large prey *G. lacustris* is stronger than for copepods. Copepods are regarded as less profitable prey, but some charr seem to specialise on copepods (or planktonic crustaceans generally) as indicated in the present and other studies (Curtis 1985, Bérubé and Curtis 1986, Knudsen 1991). Piscivorous charr seems capable to specialise under experimental (Amundsen et al. 1995) and natural conditions (Bérubé and Curtis 1986, Knudsen 1991, Amundsen 1994). From stomach analyses Amundsen (1995) shows that individual charr may spesialise on most food categories.

The stability of feeding specialisation is exceedingly difficult to demonstrate in natural populations. Duration over a period of some months is indicated by some studies (Bryan and Larkin 1972, Curtis 1985, Knudsen 1991). The amphipod transmitted parasites *C. truncatus*, L3-larvae and preadults/adults of *C. farionis* and *Crepidostomum* spp, have different longevity or are in different ontogenetic stages in the fish host. The combination of parasite infection and the degree of *Gammarus* feeding in individual hosts, may represent past selection on amphipods. The life expectancy of the cestode *C. truncatus* is 1-2 months (Vik 1958) and *Crepidostomum* spp. approximately one year (Thomas 1958) in fish hosts. The L3-larval stage of *C. farionis* may last for several months, and the development from L3-larvae to adults takes up to two years in charr (Black and Lankester 1980). The charr individuals feeding most heavily on *G. lacustris* at the time of catch, are observed to have highest infection of both short-lived parasite species (or ontogenetic stages) and preadults/adults of *C. farionis*. This implies a high persistence of the dietary specialisation in some individual fish from days (stomach content) to weeks, month (short-lived parasites) and years in the past.

The observed indications of prey specialisation over longer time will give large variance in parasite exposure to individual hosts. Thus, large individual differences in foraging behaviour between hosts may contribute significantly to the commonly observed pattern of overdispersed parasite distribution within host populations. In other words, the relatively few specialists are located in the high infection classes, while non-specialists make up the major proportion of low infection classes.

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Nordic J. Freshw. Res. (1995) 71: 345-351

Seasonal Dynamics of Helminth Parasites in Arctic Charr, *Salvelinus alpinus* (L.), from a Lake Resident Population in Northern Quebec, Canada

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Abstract

Intestinal parasites of Arctic charr were studied at a lake in northern Quebec where past investigations indicated that the fish were heavily infected with cestodes. Our present study seeks to examine changes in the parasite fauna of 3+ to 5+ charr sampled just prior to freeze-up and briefly after ice breakup. Of the eight helminth species, *Eubothrium salvelini* and *Echinorhynchus lateralis* were the most prevalent (>60%) and abundant in both the fall and spring. *Diphllobothrium ditremum*, *D. dendriticum*, *Proteocephalus* sp., *Crepidostomum farionis*, *Phyllodistomum umblae* and *Philonema agubernaculum* were present but much less prevalent. Increased numbers of juveniles in spring samples for both *E. salvelini* and *E. lateralis* indicate parasite acquisition under the ice. This resulted in consistently higher overall infection levels in spring than in fall. Numbers of maturating *E. salvelini* remained relatively constant over the same time interval while gravid worms decreased in abundance but increased in size. Total biomass for both *E. salvelini* and *E. lateralis* was augmented over the winter.

Keywords: *Salvelinus alpinus*, intestinal parasites, seasonal dynamics.

Introduction

Despite numerous studies on the parasite fauna of Arctic charr, there is comparatively little information on seasonal changes in parasite populations (Henricson 1977, Kennedy 1978, Halvorsen and Andersen 1984, Curtis 1984), especially during the overwintering period. However, there are relevant investigations on a number of charr parasites which also occur in other fish species (Chubb 1967, Awachie 1965, Brown 1989, Valtonen and Crompton 1990). In the present study we attempt to elucidate the overwintering distribution patterns of gut helminths in a lake resident Arctic charr population. This may be of particular interest because Arctic charr appear to feed little if at all during winter (Boivin and Power 1990), and it is conceivable that parasites may affect host survival (Henricson 1977, Bérubé and Curtis 1986).

Materials and methods

The study site was a 9 hectare lake in northern Quebec, Lac Kitturiak: 57°49'N, 69°28'W, located about 70 km southwest of Kuujjuaq. A detailed description of Kitturiak is given by Bérubé and Curtis (1986).

The charr population was sampled at the time of ice formation in Fall 1992 (19-29 September) and again in the late Spring of 1993 (26 June-6 July) just after the ice breakup. The fish were captured with sinking gill nets of 25, 32, and 38 mm stretched mesh. In total, 170 Arctic charr were captured in the fall and 163 in the spring. The fish were measured for fork length and total body weight, individually labelled and frozen at -25 C° in a portable freezer, and later deep frozen (-70°C). Postmortem fish examination included sex and age determination. Ageing was based on sagitta otolith readings according to

Grainger (1953) and Barber and McFarlane (1987). Only age classes 3+ to 5+ were included for analyses. The viscera of defrosted fish were necropsied in a cold room at 4°C. Parasites were transferred into a preweighed vial along with stomach and intestinal contents, and a cold 5% formalin saline solution added. The vials were stored at 4°C. *Eubothrium salvelini* Schrank, 1790 and *Echinorhynchus lateralis* Leidy, 1851 were analysed for total wet weight (after blotting on filter paper) and dry weight (after freeze-drying in -50°C for 48 hrs). In addition to the biomass assessment, total body length (mm) of *Echinorhynchus lateralis* was measured, and width of the largest proglottid of *Eubothrium salvelini* was evaluated (in ocular units, 1 unit=41.7µm) under 12x10 magnification of a dissecting microscope. During the measurements of *E. salvelini*, the worms were categorized in one of three groups: juveniles with up to 10 segments, mid-size maturing worms and gravid worms with ripe proglottids and fully developed eggs. Statistical analyses were carried out with Statistical Analysis System software (SAS Institute Inc. 1988) and Systat 5.03 (Systat, Inc. 1993). The terms prevalence, abundance and mean intensity of parasites are used following Margolis et al. (1982).

Results

General results

Fish samples taken in both seasons were similar with respect to the charr age-length relationship (Fig. 1). The 3+ to 5+ charr subsample taken for parasite analysis contained fish ranging in length from about 120-180 mm. The most prevalent species in the intestinal lumen of the charr were *E. lateralis* and *E. salvelini* (Table 1). Among helminths occupying sites in the abdominal cavity of the fish, *Philonema agubernaculum* Simon and Simon, 1936, and *Diphyllobothrium ditremum* Creplin, 1825 prevailed. These four species are considered in the following analyses, with special emphasis on *E. lateralis* and *E. salvelini*.

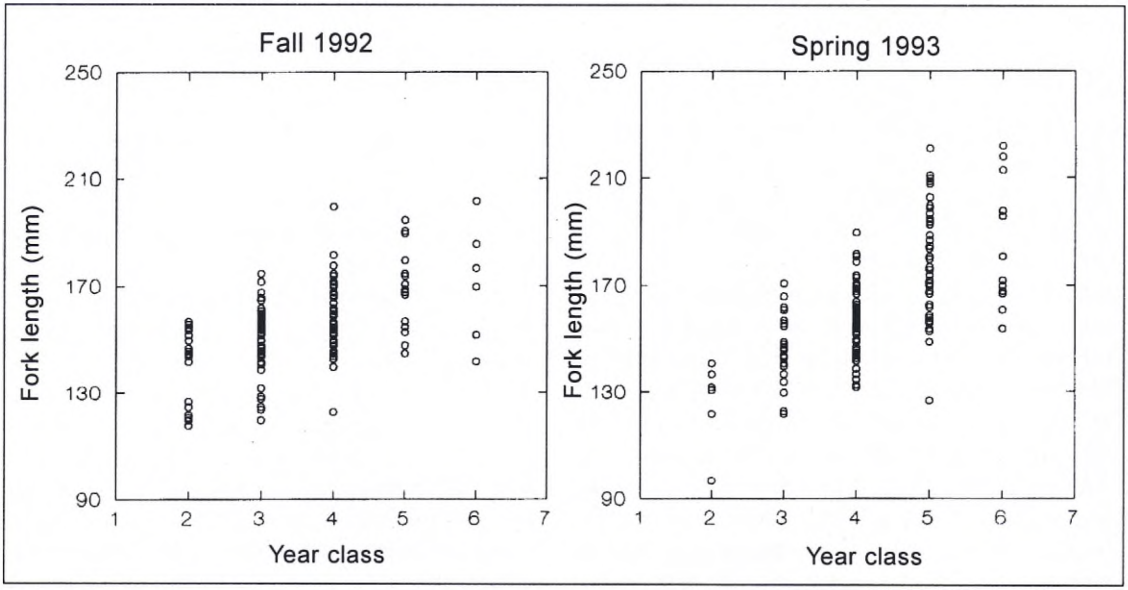

Fig. 1. Length-age scatter plots for the sampled Arctic charr in September 1992 and June 1993.

Table 1. Seasonal data on the prevalence, abundance, mean intensity and maximum number of helminths in Arctic charr samples from fall (F) and spring (S).

Species	Season	*N*	Prevalence (%)	Abundance	Mean intensity	Maximum
Eubothrium	F	132	63.64	3.48	5.48	29
salvelini	S	124	62.10	8.01	12.90	266
Diphyllobothrium	F	132	19.70	0.34	1.73	8
ditremum	S	124	8.87	0.35	4.00	21
Diphyllobothrium	F	132	2.27	0.02	1.00	1
dendriticum	S	124	2.42	0.05	2.00	4
Proteocephalus	F	132	0	0	0	0
sp.	S	124	4.03	0.04	1.00	1
Echinorhynchus	F	132	60.61	6.07	10.01	44
lateralis	S	124	68.55	15.73	22.94	117
Crepidostomum	F	132	16.67	0.25	1.50	6
farionis	S	124	40.32	3.74	9.28	208
Phyllodistomum	F	132	55.30	0.55	1.00	1
umblae	S	124	55.65	2.32	4.17	12
Philonema	F	132	25.76	0.33	1.29	3
agubernaculum	S	124	29.35	0.25	1.29	3

Eubothrium salvelini

Over 60% of all Arctic charr were infected by the cestode *E. salvelini* in both fall and spring. Although there was no significant overwintering difference in the prevalence and abundance of this parasite for all charr age classes combined (Mann-Whitney U-test), the mean intensity of infection significantly increased over this same time period. For 3+ charr prevalence declined, but mean intensity and abundance remained stable from fall to spring (Table 2). Prevalence in the 4+ age class also declined over the winter but was accompanied by an augmentation of mean intensity and abundance. Prevalence, abundance and mean intensity for 5+ charr were all higher in spring compared to fall. The mean intensity of infection ranged between 5 and 20 worms per infected fish for 3+ to 5+ charr. Over winter it was observed that intermediate levels of infection, from 7 to 18 worms per fish, disappeared. Frequency distributions of *E. salvelini* widths (Fig. 2) revealed three developmental groups: juveniles, mid-size maturing worms and gravid worms. There was an increase in numbers of both juveniles and maturing stages from the fall to the spring in age classes 4+ and 5+. In the 5+ age class the numbers of gravid worms also increased. Only in age class 3+ did all three stages decrease in numbers over the fall to spring period. There was an augmentation of total *E. salvelini* biomass from fall to spring (Table 3) mainly owing to large gravid worms which survived overwintering.

Echinorhynchus lateralis

From fall to spring this acanthocephalan exhibited increases in prevalence, abundance and mean intensity of infection (Tables 1 and 2). This pattern occurred in all age classes, except 4+ where those parameters remained relatively constant over the winter. The parasite length frequency distribution (Fig. 3), revealed increased

Table 2. Age specific seasonal data on selected helminth species from Arctic charr in Lac Kitturiak.

Season	Age class	*N*	Prevalence (%)	Abundance	Mean intensity	Maximum
			Eubothrium salvelini			
Fall	3+	62	67.74	3.77	5.57	29
	4+	54	59.26	3.22	5.44	29
	5+	16	62.50	3.25	5.20	15
Spring	3+	24	62.50	3.67	5.87	24
	4+	56	53.57	10.75	20.07	266
	5+	44	72.73	6.89	9.47	110
			Echinorhynchus lateralis			
Fall	3+	62	54.84	4.23	7.71	35
	4+	54	62.96	5.31	8.44	37
	5+	16	75.00	15.75	21.00	44
Spring	3+	24	66.67	17.79	26.69	108
	4+	56	62.50	11.36	18.17	111
	5+	44	77.27	20.16	26.09	117
			Diphyllobothrium ditremum			
Fall	3+	62	20.97	0.27	1.31	3
	4+	54	16.67	0.39	2.33	8
	5+	16	25.00	0.44	1.75	3
Spring	3+	24	4.17	0.04	1.00	1
	4+	56	8.93	0.13	1.40	3
	5+	44	11.36	0.82	7.20	21

acquisition of juveniles from fall to spring in all charr age classes, with the most marked increase in 5+. The biomass of *E. lateralis* also increased from fall to spring (Table 3).

Diphyllobothrium ditremum

The prevalence of infection of the cestode *D. ditremum* declined from 19.7% in the fall to 8.9% in the spring (Table 1). Abundance remained unchanged at about 0.3 parasites per host over this same time interval, while mean intensity of infection increased from 1.7 to 4.0. Age specific analysis of these three variables revealed overwinter diminution of the parasite prevalence in all age classes of the charr and an increase in intensity of infection in the charr age class 5+.

Philonema agubernaculum

This nematode had prevalences of 25.8% and 29.4% in Kitturiak charr for fall and spring, respectively (Table 1). The mean intensity of infection did not significantly differ with the season and among the age classes sampled.

Table 3. Total biomass (mg dry weight) of the two dominant parasites of Arctic charr in fall and spring.

Parasite	Season	*N*	Mean	SE
Eubothrium salvelini	Fall	76	3.8	0.5
	Spring	72	10.2	1.5
Echinorhynchus lateralis	Fall	76	14.3	1.9
	Spring	78	21.9	3.3

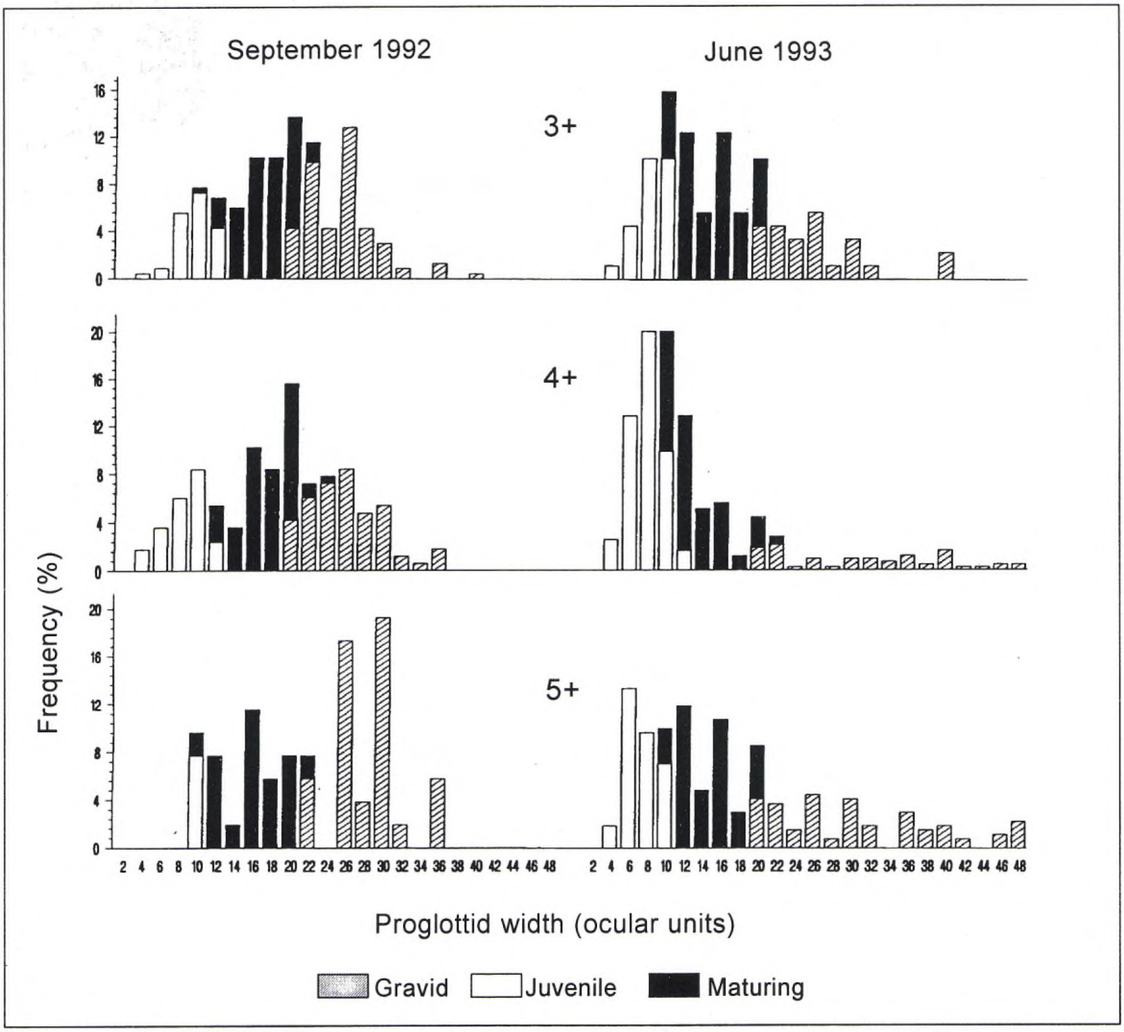

Fig. 2. Seasonal changes in the proglottid width frequency distributions of *E. salvelini* in 3+ to 5+ Arctic charr from Lac Kitturiak. (1 unit=41.7 μm).

Discussion

The two most prevalent helminth species in Lac Kitturiak, *E. salvelini* and *E. lateralis*, were transmitted to Arctic charr during the period the lake was ice covered. This was demonstrated by the comparatively high abundance in late spring of small plerocerciform (Kennedy 1978) *E. salvelini* and juveniles of *E. lateralis*. Considering that the time required for *E. salvelini* development from the oncosphere in the egg to the juvenile in the fish host is at least 4-6 weeks (Boyce 1974) and that the time of our spring sampling was late June, it appears that infections of the copepod intermediate host took place in April or May under ice cover. Increased spring abundance of juvenile *E. lateralis* also implies an under ice recruitment pattern for this acanthocephalan species. However, it is difficult to precisely estimate the timing of the process, because the life cycle has been barely investigated.

Based on our data there was no evidence for overwintering recruitment of *D. ditremum* and

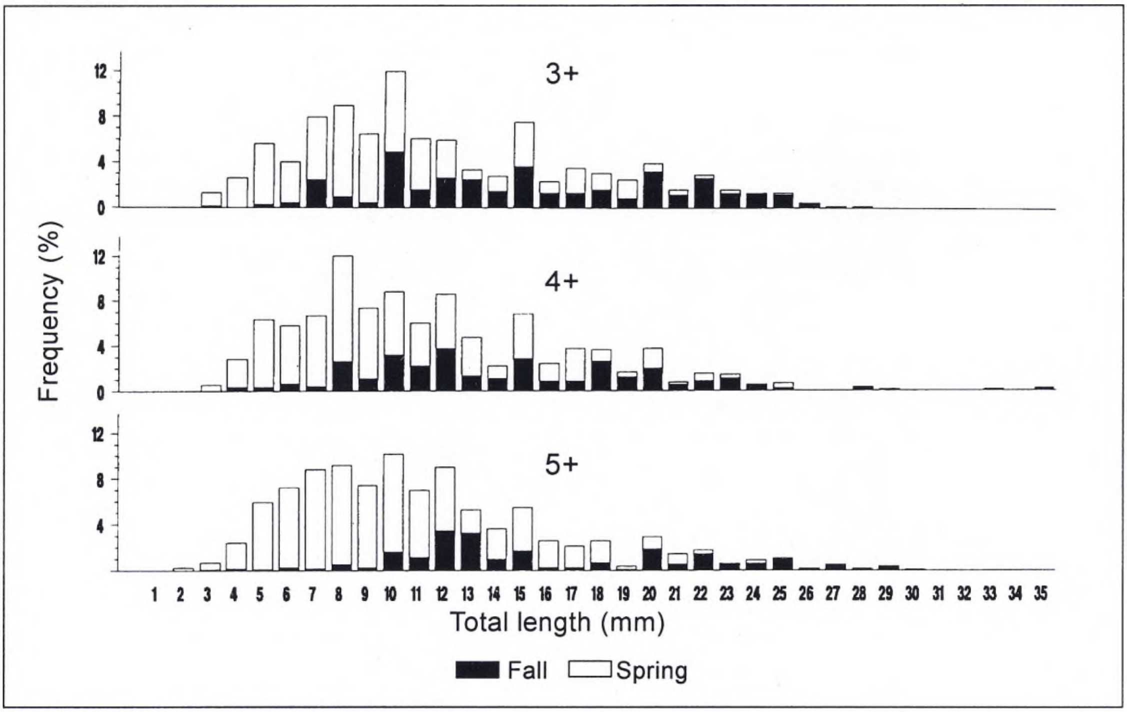

Fig. 3. Seasonal changes in length frequency distributions of *E. lateralis* in 3+ to 5+ Arctic charr from Lac Kitturiak.

P. agubernaculum. The prevalence and abundance of these species were low in both seasons.

The augmentation of total biomass for both *E. salvelini* and *E. lateralis* may lead to increasing morbidity for the overwintering Arctic charr. The biomass gain of *E. salvelini* results primarily from growth of gravid worms than spring increases in numbers of newly acquired juveniles.

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The Status of *Salvelinus* in France

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Abstract

France is a new land for brook charr (*Salvelinus fontinalis*) and for lake charr (*S. namaycush*). Eggs of the former received in 1878 gave a good number of fish and this species has been introduced into waters in many parts of France since then. Lake charr eggs were first received in 1883 and this fish was also reared between 1913 and 1922, but no further information is available on these stocks. The widespread introduction of lake charr began in 1953 and the fish has been established since then. Arctic charr (*S. alpinus*) is indigenous to France. It was a rare species in 1800, confined to only three lakes but its geographical distribution has become enlarged by man since at least 1860. There are now 138 Arctic charr lakes in France, and in 136 of them Arctic charr is an exotic species. The time has come to think carefully about nature protection before introducing fishes, including these *Salvelinus* species, into natural waters.

Keywords: Geographical distribution, Introduction, *Salvelinus* spp., France.

Introduction and methods

Since the 19th century, several foreign fishes have been introduced into France and many of them have become established here (Vivier 1951a,b, 1955, Hubault 1955, Allardi 1984, Keith et al. 1992). Although it was believed desirable to introduce them at the beginning, some fishes have now become pests, e.g. black bullhead (*Ictalurus melas*). *Salvelinus* species have a good image, therefore these fishes were also introduced into several new waters. The world distribution of brook charr (*Salvelinus fontinalis*) is now well known (MacCrimmon and Campbell 1969, MacCrimmon et al. 1971). The French distribution of Arctic charr (*S. alpinus*) is also now known in detail (Machino 1991a) updated by the additional inquiry carried out until June 1993 whose detailed results will be published elsewhere. It is now possible to review Arctic charr introductions and the first introductions of brook charr and lake charr (*Salvelinus namaycush*) into France using bibliographical analyses, the results from the 1991-93 questionary and the information from some other countries.

Results and discussion

Brook charr

The first attempt to introduce this species into France was probably the importation of eggs of brook charr and of two other salmonid species, sent by Seth Green who had a trout farm at Caledonia (New York, USA). These eggs arrived in bad condition in 1874 in Paris (for Société d'Acclimatation). About a hundred brook charr fry were obtained in April 1875, but no further information on the fry is available (Raveret-Wattel 1875a,b). At the second attempt, eggs of brook charr and lake whitefish (*Coregonus clupeaformis*) were received in Paris in 1876, but no fry were obtained from them (Raveret-Wattel 1876). In February 1878, Société d'Acclimatation received 12,000 eggs of brook charr from Seth Green, in good condition this time, and these were re-distributed throughout France (Raveret-Wattel 1878a,b). In the same winter 1877/1878 there may have been another batch of brook charr sent to France, but no details are available (i.e. Raveret-Wattel 1878c). In the spring of 1878 some brook charr fry were released into the Grand Morin River, a tributary of the Marne River (the Seine Basin), by Braun who reared several fishes at Guérard (Seine-et-Marne 77) (Grisard 1878). General brook charr introductions and rearing throughout France began in February 1878 by Société d'Acclimatation and the introductions have continued since then.

Beside the introduction efforts made by Société d'Acclimatation of Paris, there were also trials made via England. Every winter from 1875/1876 to 1878/1879, William MacAllister, living in La Mauvaisiniére at Bouzille (Loire-Atlantique 44), received eggs of brook charr from Cumberland (England) and fry were introduced into a pond in his garden (Raveret-Wattel 1876, 1879, 1904).

It should be noted that by 1873, Troutdale Fishery (owned by J.J. Armistead and J. Parnaby) at Keswick, Cumberland was a European distribution centre for Brook charr, with prices of £25.00 per thousand eggs and £30.00 per thousand fry (Raveret-Wattel 1873).

Lake charr

The first importation on this species into France, was probably made by Société Nationale d'Acclimatation de France in Paris which received eggs in January 1883, sent by Spencer F. Baird of Washington D.C. (USA), and these eggs were re-distributed throughout France. However, most aquaculture centres which received the eggs seem to have failed to rear them, only Pisciculture de Bouzey at Sanchey (Vosges 88) had these fish by the end of 1884 (Raveret-Wattel 1883, 1885). No further information on this importation is available.

According to Laurent (1972), some lake charr were introduced into Lac Léman (Lake Geneva) in 1886 but without success. Around 1913, hybrids of lake charr and Arctic charr were introduced into Lac du Bourget (Savoie 73) and recaptures were made (Ginésy 1914). Lake charr were reared in an aquaculture centre at Thonon-les-Bains (Haute-Savoie 74) from at least 1913 to 1922 (Kreitmann 1922).

Since the first arrival of lake charr in 1883, no serious introduction efforts had been made and the fish was not a very attractive species in France until 1952. An aquaculture centre at Cauterets (Hautes-Pyrénées 65) received eggs of lake charr from Canada in 1953 and this species has been introduced into lakes in the French Pyrenees where it has since become established (Chimits 1955, 1960). Introduction efforts in other parts of France also have been made since the 1960s. Lac Léman received lake charr in 1966 but the introduction failed (Laurent 1972).

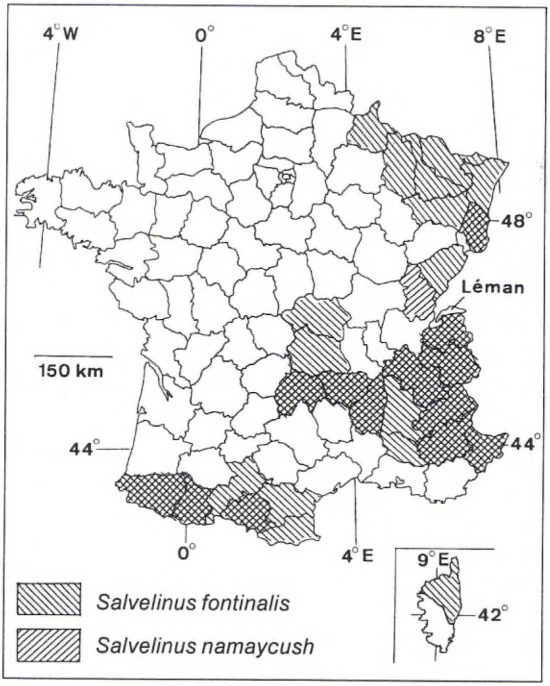

Fig. 1. The geographical distribution of brook charr (*Salvelinus fontinalis*) and lake charr (*S. namaycush*) in France (information given by Duquet 1992 included).

Here must be noted that eggs of lake charr (sic, truite du lac Huron, or Lake Huron trout) may have been received by C. Millet in Paris in the winter 1854/1855 (Calemard de la Fayette 1859).

Fig. 1 shows a simplified view of the present geographical distribution of brook charr and lake charr in France, but this map is not complete, because the exact distributions are not known yet. Compared with rainbow trout (*Oncorhynchus mykiss*) which is found now throughout France (Duquet 1992), these two *Salvelinus* species have a limited distribution. Natural reproduction of brook charr occurs in only some waters in France (Vivier 1955), e.g., in the upper part of the Drugeon River (tributary of the Doubs, the Rhône Basin; Doubs 25) (Verneaux 1971); in Lac de Bastani (Haute-Corse 2B) (Rivier and Dumont 1987).

Some information for other countries may be of interest. Piscifactoria del Monasterio de Piedra (Province of Zaragoza, Spain) reared Brook charr in 1888 and also in 1929 (Sauvage 1889, Pellegrin 1930). An aquaculture centre at Azrou (Morocco) hatched eggs of brook charr in 1942 (Prudhomme 1943). However, the Moroccan government seemed not to be interested in this species, because few fry survived and became adults in natural waters and no spawning was observed (Anonymous 1960).

Switzerland received 50,000 eggs of lake charr from the USA in 1886 (Clark 1886, Smiley 1886), and 39,038 lake charr were released into Swiss waters in the same year (Belloc 1898), e.g., Sägisthal Lake (canton of Bern) received 355 fry of lake charr where they established successfully (Delachaux 1901) and 7,638 lake charr were released into the Rhône River at Geneva (Fatio 1890). In 1896, 86,300 fish of the same species were released into Swiss waters (Belloc 1898). In 1922 Switzerland again received lake charr eggs from the USA, and 845 fingerlings were introduced into Lac de Fully in 1922 (canton of Valais) where they became established (Vouga 1926, 1931). At least once, Morocco tried to acclimatize lake charr: this species was present in 1960 in Sidi-Ali Lake (Itzer Region; Moyen-Atlas) (Anonymous 1960), but recent information is not available.

Arctic charr

This fish is indigenous to France, but to two lakes, Lac Léman and Lac du Bourget. It was also known from Lac de Paladru (Isère 38) since at least the 16th century (Fig. 2), but because of lake eutrophication, the last specimen of Arctic charr from this lake was seen in 1956 (Machino 1991a). A recent introduction (1987) of Arctic charr into this lake ended unsuccessfully (Machino, unpubl.). CEMAGREF (1986) reports Arctic charr from Lac d'Allos (Alpes-de-Haute-Provence 04) whose origin is unknown. Recent bibliographical studies suggest that Arctic charr would have been introduced into this lake by man in the 1920s (Machino, unpubl. data).

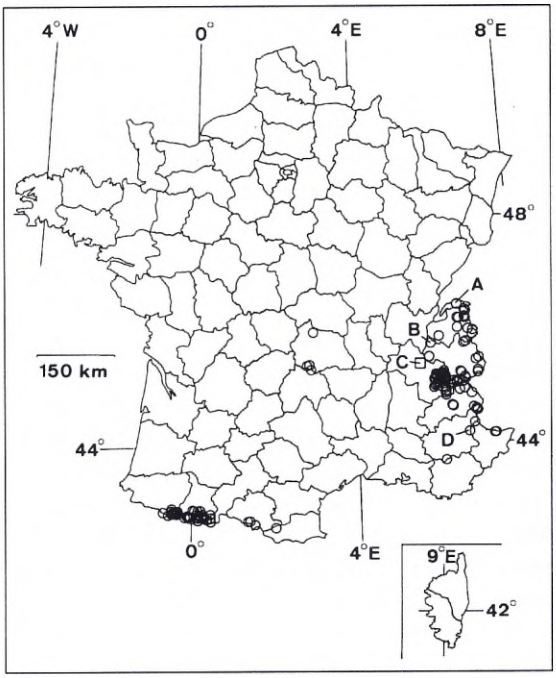

Fig. 2. French Arctic charr lakes in 1800 (*N*=3 lakes; A, B, C) and today (*N*=138 lakes; white circles, see Table 1). A: Lac Léman, B: Lac du Bourget, C: Lac de Paladru. D is Lac d'Allos (see text for detail).

Table 1. Number of lakes with and without Arctic charr in different regions of France. Based on inquiries from October 1986 to June 1993, which gave ichthyological data for 659 lakes *.

Name of region	Lake category **					Total
	A	B	C	D	E	
Vosges	24			2	6	32
French Jura	36			1	3	40
French Alps	184	82	9	14	12	301
Massif Central	47	4	4		6	61
French Pyrenees	140	52	9	4	10	215
Corsica	9					9
Other regions	1					1
Total	441	138	22	21	37	659

* This table does not include Lac des Fougères (49°25'S, 69°40'E, Kerguelen Islands) which is in category E since 1991.

** Lake categories

Category A: Lakes which we know have never contained Arctic charr.

Category B: Arctic charr lakes, with supposed selfsustaining populations.

Category C: Lakes which have contained selfsustaining populations, but where it is now extinct.

Category D: Lakes into which Arctic charr were introduced but where acclimatization failed.

Category E: Lakes into which Arctic charr have been introduced recently, but where the result of the acclimatization is not yet known.

With aquaculture techniques developed since the 1850s, Arctic charr have been reared and introduced into natural waters everywhere (Machino 1991a,b, unpubl.), e.g. into ponds in Paris in the 1850s. The first success in France with a known date was from Lac Pavin in the Massif Central (Puy-de-Dôme 63) into which Arctic charr were introduced in 1860 and where they have become established (Rico 1876). Successes have also been reported from lakes in the French Alps since 1890 (Lac d'Annecy; Haute-Savoie 74) (Brocchi 1893) and in the French Pyrenees since 1928 (Estany d'Esparver; Pyrénées-Orientales 66) (Gay and Toubert 1955). Today, spawning populations of Arctic charr are found in 138 lakes spread across the French Alps, Massif Central and French Pyrenees (Table 1, Fig. 2). This species is still being introduced into lakes with no Arctic charr. Altogether, 37 lakes are recently reported as containing Arctic charr but their spawning is not yet verified; these lakes are spread out in the following mountain ranges: Vosges, French Jura, French Alps, Massif Central, French Pyrenees (Table 1, Fig. 3). Corsica does not yet have Arctic charr.

Thus the number of Arctic charr lakes in France is increasing slowly but surely (Fig. 4). At the beginning (1800), there were three Arctic charr lakes in France (Lac Léman, Lac du Bourget, Lac de Paladru). Now there are 138, and in future there will be more. It must be noted here that one lake in the Kerguelen Islands (French territory) in the Southern Hemisphere recently received Arctic charr, Lac des Fougères (49°25'S, 69°40'E), in 1991 (P. Davaine, pers. comm.)

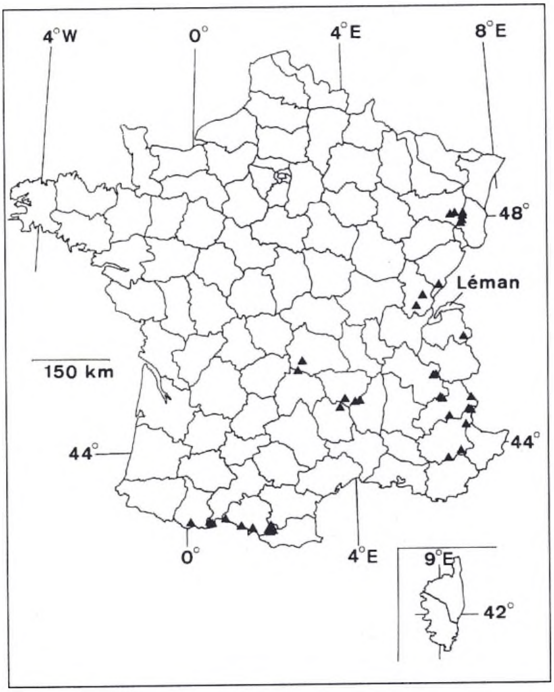

Fig. 3. French lakes with recent introductions of Arctic charr (N=37 lakes; black triangles, see Table 1).

It is interesting to note that at least once an African water received Arctic charr: they were introduced into Tislit Lake (Imilchil Region, Moyen-Atlas, Morocco) in 1948 but without success (Anonymous 1960).

Arctic charr and some other fishes are believed to be declining species and protection measures have been proposed in Europe and in France (Lelek 1987, Premier Ministre 1988, Allardi and Keith 1991). The Secrétariat de la Faune et de la Flore of Muséum National d'Histoire Naturelle in Paris has assigned a status or degree of threat to certain freshwater fishes. At the national level, Arctic charr is a "Vulnerable" species in France. At the local level, this species is "Vulnerable" in the Garonne-Adour Basin, "Endangered" in the Rhône-Mediterranean-Corsica Basin, and "Indeterminate" in the Rhine-Meuse Basin where Arctic charr was introduced and is present without natural spawning ever having occured (Machino 1991a,b, unpubl., Keith et al. 1992).

The present study shows that Arctic charr is extending its area of distribution in France (Figs. 2, 3 and 4). Among the 138 existing Arctic charr lakes, it is exotic to 136, and the official "declining status" gives rise to the possiblity of introducing it into natural waters everywhere. Such an argument may be welcome by sport fishermen and by political ecologists. Since the 18th century, fish introductions into mountain lakes have been carried out in France, and they intensified in the 20th century. France probably does not now have any fishless lakes which are habitable for fish. All mountain lakes habitable for fish have received fishes introduced by man, particularly brown trout (*Salmo trutta*), rainbow trout, lake charr, brook charr, Arctic charr, and

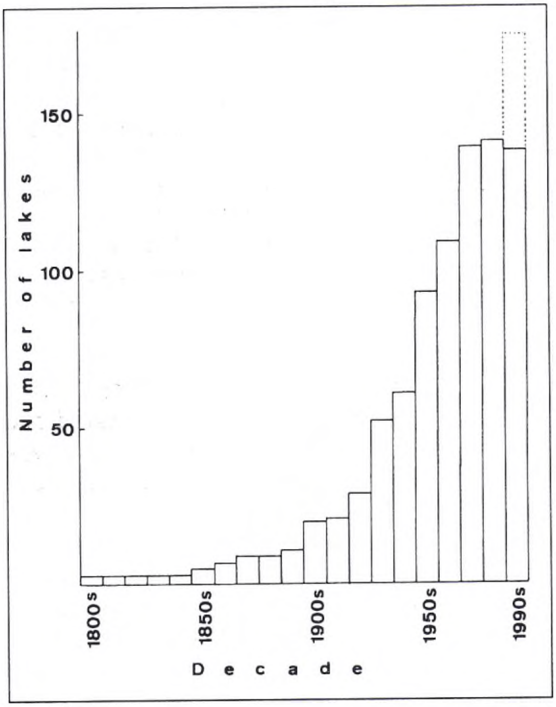

Fig. 4. Evolution of the number of Arctic charr lakes in France since the 1800s. All lakes containing or having once contained a supposed self-sustaining population of Arctic charr were taken into account (N=165 lakes). The broken part of the column for the 1990s represents recent introductions (N=37 lakes, see also Table 1).

European minnow (*Phoxinus phoxinus*). Recently, even Splake (hybrid of lake charr and brook charr) was proposed for French lakes (Venable 1989). Introduction into one lake may not be a problem, but introduction into all lakes is a disaster. The time has come to think about the protection also of aquatic organisms other than fish by forbidding fish introductions to some waters. France also has known several dubious fish introductions, e.g., carp (*Cyprinus carpio*), nase (*Chondrostoma nasus*), pikeperch (*Stizostedion lucioperca*), pumpkinseed (*Lepomis gibbosus*) and black bullhead. Now, Arctic charr may be added to this list too. Finally, the author is not against Arctic charr nor fighting for its destruction. In France, this fish is exploited by 83 professional fishermen (Castelnaud and Babin 1990) and several thousand sport fishermen. Therefore, Arctic charr must be protected in order to be exploited by man. At the same time, introductions into new lakes should be restricted.

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Effects of Introduced *Mysis relicta* on Habitat Utilisation and Feeding of Arctic Charr

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Abstract

The purpose of this paper is to study food, growth and habitat utilisation of 0+ and older Arctic charr to detect harmful effects of introduced *Mysis relicta*. Arctic charr had a first year growth of 20.5 mm at an instantaneous yearly growth rate of 0.59. Second year growth was better, being 107 mm at an instantaneous growth rate of 0.84. After this yearly growth decreased. Age-0 class of Arctic charr were only caught in the benthic habitat, from the littoral zone and down to approximately 30 m. Overall, *M. relicta* was the most important food item for 0+ fish, being almost the exclusive prey item for newly hatched fry in the spring and juveniles in the autumn. Older benthic fish were evenly distributed down to 50 m during spring and summer. During autumn, however, most benthic fish stayed in the 10-30 m zone. In the pelagic habitat most Arctic charr stayed in the upper 20 m zone. *M. relicta* constituted a larger part of the food of benthic than pelagic charr.

Keywords: Juvenile Arctic charr, *Mysis relicta,* feeding, growth, competition.

Introduction

Arctic charr (*Salvelinus alpinus)* is one of the most important fish species in many Sub-Arctic and northern temperate lakes where it often inhabits both benthic and pelagic habitats (Johnson 1980). In several lakes, populations of Arctic charr have been reduced drastically due to man-made activities e.g. hydroelectric power plants and introductions of exotic invertebrates and fish species. In the mid-1960s and 1970s the opossum shrimp *Mysis relicta* was introduced to lakes and reservoirs throughout Scandinavia, Canada and Western United States. The main object of these introductions was to supplement the forage base of salmonid fish populations (Nesler and Bergersen 1991). The adverse consequences of these introductions came several years after establishing populations of *M. relicta*. The first negative impact became apparent in the zoolankton community where species of *Daphnia* disappeared and other species of cladocerans declined significantly (e.g. Richards et al. 1975, Morgan et al. 1978, Nero and Sprules 1986, Langeland 1988). In some lakes reductions in copepod species have also been recorded (Koksvik et al. 1991). Through the 1970's and 1980's an increasing number of papers reporting hazards to fish popoulations, notably Arctic charr and kokanee (*Oncorhynchus nerka*) were published (e.g. Northcote 1973, Richards et al. 1975, Morgan et al. 1978, Fürst et al. 1984, Lasenby et al. 1986).

It is generally accepted that one of the main reasons for these reductions in fish populations was predation by *M. relicta* upon the zoolankton, reducing the pelagic forage base of fish (c.f. Nesler and Bergersen 1991, Northcote 1991). The migratory behavior of pelagic *M. relicta*, descending into dark waters during daylight reduces the ability of pelagic fish to exploit them as substitute prey. Næsje et al. (1991) showed that in Lake Jonsvatn, Norway, both *M. relicta* and Arctic charr performed diel vertical migrations. The daytime descent of Arctic charr, however, ended at depths above the highest densities of pelagic *M. relicta*. Thus habitat overlap during daytime was minor. However, nighttime habitat overlap between zooplankton, pelagic *M. relicta* and Arctic charr was great, allowing *M. relicta* to feed on zooplankton without being eaten by the visually hunting Arctic charr (Næsje et al. 1991).

M. relicta lives in both benthic and pelagic habitats (Northcote 1991) and has a remarkably flexible feeding strategy. It is an opportunistic omnivor capable of filter-feeding or raptorial feeding (Grossnickle 1982). It eats phytoplankton, zooplankton, benthos and detritus (cf. Lasenby 1991). Densities of pelagic *M. relicta* vary from 35 m^{-2} to 1980 m^{-2}, the density being higher for introduced populations (Lasenby 1991). The methods of sampling benthic mysis (benthic sledge or trawl) are not well suited for quantitative estimates, but the size of the bottom dwelling part of the population might be in the same order of magnitude or greater than the pelagic part. Little is known, however, about the impact of *M. relica* on the benthic fauna, and it is possible that *M. relicta*s predation upon benthic invertebrates has resulted in the decline of benthic fish species (Lasenby 1991).

First year survival is often considered to be one of the most critical periods during the lifespan of fish (Wootton 1990). However, the niche breadth of Arctic charr with respect to feeding ecology is wide (Johnson 1980). Juveniles might feed on both benthos (e.g. chironomids, *Gammarus* spp.) and zooplankton (e.g. cladocerans) (c.f. Johnson 1980, Sandlund et al. 1992a), but both these groups of invertbrates might be reduced after introductions of *M. relicta*. Therefore, if age-0 Arctic charr do not feed on *M. relicta* as substitute food, introduction of this exotic species might increase the mortality of Arctic charr juveniles through increased inter- and intraspecific competition.

The objectives of this paper are twofold: (1) to study the food and growth of 0+ Arctic charr to detect harmful effects of introduced *M. relicta,* (2) to study the habitat utilisation and food of older Arctic charr after introductions of *M. relicta.*

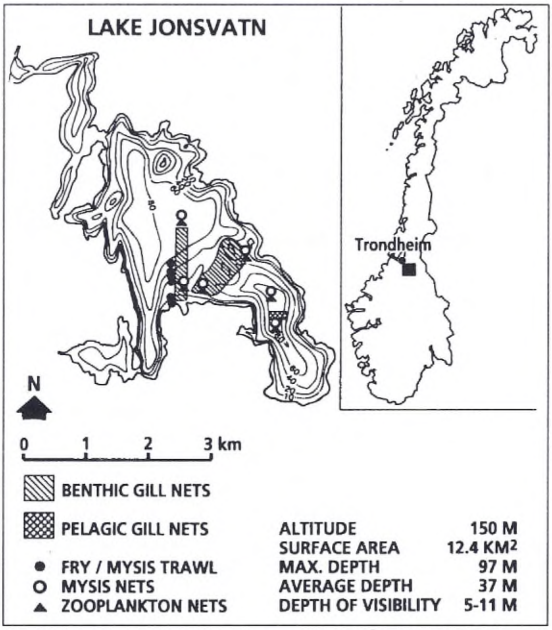

Fig. 1. Lake Jonsvatn with morphometric data and sampling stations, September 1986-December 1990.

Study area

The oligotrophic Lake Jonsvatn (63°22' N, 10° 37' E) is used as a water reservoir for the city of Trondheim, Norway (Fig. 1). In 1978 *M. relicta* were introduced to the lake, and in 1981 densities of 2-3 mysids m^{-2} surface area were recorded in the pelagic zone (0-80 m depth).

During the sampling period the crustacean zooplankton was dominated by the cladocerans *Bosmina longispina, Holopedium gibberum* and *Daphnia galeata*, and by the copepods *Cylops scutifer*, *Diaptomus* (*Arctodiaptomus*) *laticeps* and *Heterocope appendiculata*. The fish fauna consisted of Arctic charr, brown trout *Salmo trutta*, pike *Esox lucius* and threespine stickleback *Gasterosteus aculeatus*. Arctic charr segregate into benthic and pelagic populations during certain times of the year, but individuals occupying the two habitats are conspecifics and might even belong to the same spawning population (Hindar et al. 1986). Brown trout, pike, and threespine stickleback occur in the littoral zone (T.F. Næsje, unpublished).

Mysis relicta in Lake Jonsvatn

The food and habitat utilisation of *M. relicta* in Lake Jonsvatn has been studied by Næsje et al. 1991, and T. Næsje, R. Saksgård and A. Jensen (unpublished). Ninety percent of the *M. relicta* population have a one-year life cycle. Young *M. relicta* are released from the female's marsupium from February until July, with a peak in May. The size of newly released *M. relicta* are approximately 3 mm; males grow to 16 mm and females to 20 mm, respectively. Juvenile *M. relicta* are released in both benthic and pelagic habitats and live in littoral, profundal and pelagic waters.

The distribution of *M. relicta* varied throughout the year. Juveniles and adults lived only partly in the same areas. From May until July immature individuals remained higher in the water column than mature ones. The most pronounced vertical migrations were performed by pelagic adults in the autumn when they stayed deeper than 50 m during daylight and above 20 m during dark. In the benthic habitat the vertical migrations along the bottom were much smaller than the corresponding movements in the pelagic zone. From May until July juveniles stayed in shallow water (<20 m) both during day and night. During autumn the tendency to undergo vertical migrations increased and in August immature individuals were found at great depths (>50 m). Furthermore, larger individuals stayed in shallow benthic waters during spring and only performed diel vertical migrations down to greater depths in autumn.

There were only minor differences in the food of juvenile and adult pelagic *M. relicta.* The diet of pelagic individuals mainly consisted of rotifers and the copepods *Cyclops scutifer* and *Diaptomus laticeps* during winter, spring and early summer. Later in the summer and in the autumn the cladocerans *Holopedium gibberum*, *Daphnia galeata* and *Bosmina longispina* were most important. The food of benthic *M. relicta* in Lake Jonsvatn is more uncertain as more than 80% (volume) of the stomach content was impossible to visually classify into prey categories.

Materials and Methods

Age-0 Arctic charr were sampled with a benthic beam trawl in the main basin of Lake Jonsvatn (Fig. 1). The trawl had a frame opening of 1 m • 0.2 m and with a mesh size of 1 mm along the sides and 200 µm in the bag (Fürst 1965). Depths between 1 and 60 m were sampled horizontally from 19:00 and 05:00 hours (Norwegian Standard Time) from September until December in 1986 and from May until December in 1990. The trawl was pulled at a speed of 0.4-0.6 m s^{-1}, and most individuals were caught from the littoral zone down to 30 m depths. Fortyeight and 221 age-0 Arctic charr were caught in 1986 and 1990, respectively.

Sampling sites for Arctic charr captured with survey nets were located in both basins of Lake Jonsvatn (Fig. 1). Gill nets were set during seven periods from February to November 1987 at three sampling sites. The nets consisted of series of 12 panels with different bar-mesh sizes (8-52 mm). The pelagic nets (panel size: 6 m • 25 m) were placed at the following depths: 0-10, 10-20, 25-35 and 40-50 m. The benthic nets (2 m • 25 m) were set from the shoreline down to the deepest part of the sampling area (80 m). The exact depth of each net was recorded by an echo sounder (Simrad EY-M). A total of 1455 Arctic charr were caught in the survey nets. Catch per unit effort (CPUE) was calculated as the number of fish per 100 m^2 of net area for 24 hours. Arctic charr were aged by burning and breaking the sacculus otoliths (Christensen 1964). Total fish length was measured to 1 mm with the tail spread in a natural position.

Food items eaten were identified and counted under a stereoscopic microscope. Calculations of body length of *M. relicta* were done using the length of the antennal scale, measured by stereoscopic microscope. This length is linearly related to total body length of *M. relicta* (Grossnickle and Beeton 1979).

Water temperature and oxygen were measured with a YSI-meter concurrently with the vertical net hauls and benthic trawl samples of *M. relicta.* Oxygen varied between 7.4 mg l^{-1} (56.5% satu-

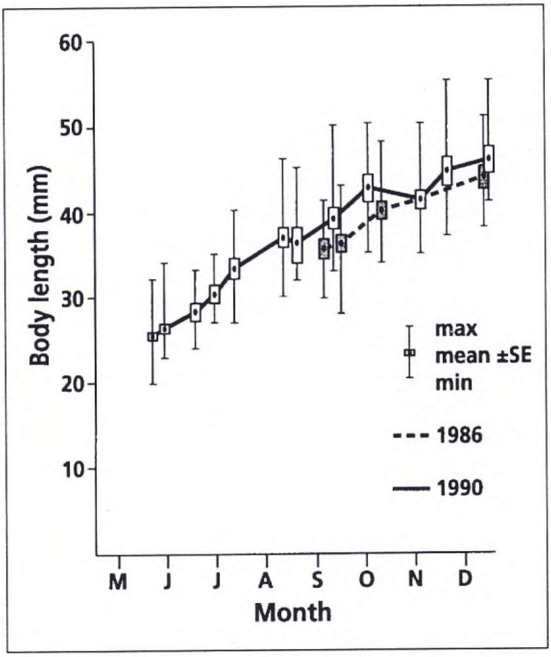

Fig. 2. Empiric growth of age-0 Arctic charr in Lake Jonsvatn sampled with benthic trawl from September to December 1986 and from May to December 1990. Mean total length, SE, and maximum and minimum lengths are given.

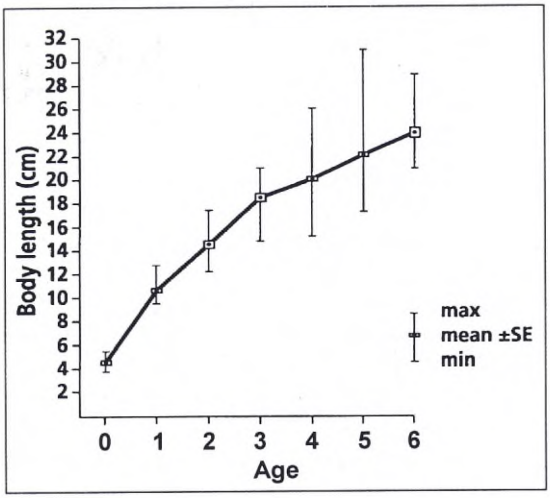

Fig. 3. Empiric growth of Arctic charr in Lake Jonsvatn based on fish sampled with benthic and pelagic gillnets in November 1987. Length of age-0 fish is from November 1990. Mean total length, SE, and maximum and minimum lengths are given.

ration) and 12.2 mg l^{-1} (104.2% saturation), and was always higher than critical values for *M. relicta* (Sherman et al. 1987). *M. relicta* can survive at water temperatures ranging from near 0°C to approximately 22°C (Juday and Birge 1927, Ricker 1959). Pennak (1953) however, suggested that the highest temperature tolerated by *M. relicta* for extended periods of time is 14°C. At depths greater than 3 m in Lake Jonsvatn, water temperature was lower than 14°C in all sampling periods. Therefore, during our study the water temperature should not put any significant limit to the habitat use of *M. relicta.*

Results

Growth and sexual maturation

In 1990 age-0 Arctic charr grew from 25.5 mm just after absorbtion of the yolk sack in May to 46.0 mm in December, an increase of merely 20.5 mm or an instantaneous yearly growth rate of 0.59 (Fig. 2). The mean length of age-0 charr in 1986 (September-December) was not significantly different from 1990 (*t*-test, $P>0.05$). After the first year of life there was a remarkable increase in growth rate with its highest growth rate during the second growing season reaching a mean of 107 mm (Fig. 3), at an instantaneous yearly growth rate of 0.84. After this, yearly growth decreased to a mean length of 241 mm after the 7th growing season (age-6). The instantaneaous growth rate between 3rd and 7th growth seasons were 0.31, 0.24, 0.11, 0.08 and 0.07 respectively. The oldest fish caught in the survey gillnets were four individuals of age-8 (mean size 285 mm). When the empiric lengths were fitted to von Bertalanffy's growth equation (Bertalanffy 1957), the asymptotic length and Brody's coefficient were 301 mm and 0.18 respectively.

Fifty percent sexual maturation was reached at age 5 for both male and females. Males, however, seemed to mature somewhat earlier than females as 49% of the males and only 29% of the females were sexually mature at age 4.

Habitat utilisation of Arctic charr

Arctic charr were caught in the benthic habitat of Lake Jonsvatn at all depths down to 80 m with exception of February when only one individual was caught deeper than 30 m (Fig. 4). In May and July, fish were evenly distributed down to 50 m depth. During autumn, however, most fish stayed in the 10-30 m zone. Age-0 Arctic charr were only caught in the benthic trawl from 5 m down to 30 m depth. This distribution of juveniles was confirmed by the benthic survey fishing where very few fish (3 individuals) smaller than 10 cm were caught deeper than 30 m, and no fish smaller than 10 cm were caught in the 0-10 m depth zone (Fig. 5). In May and July, more fish larger than 18 cm lived in the upper bethic zone (0-30 m depth) than deeper than 30 m.

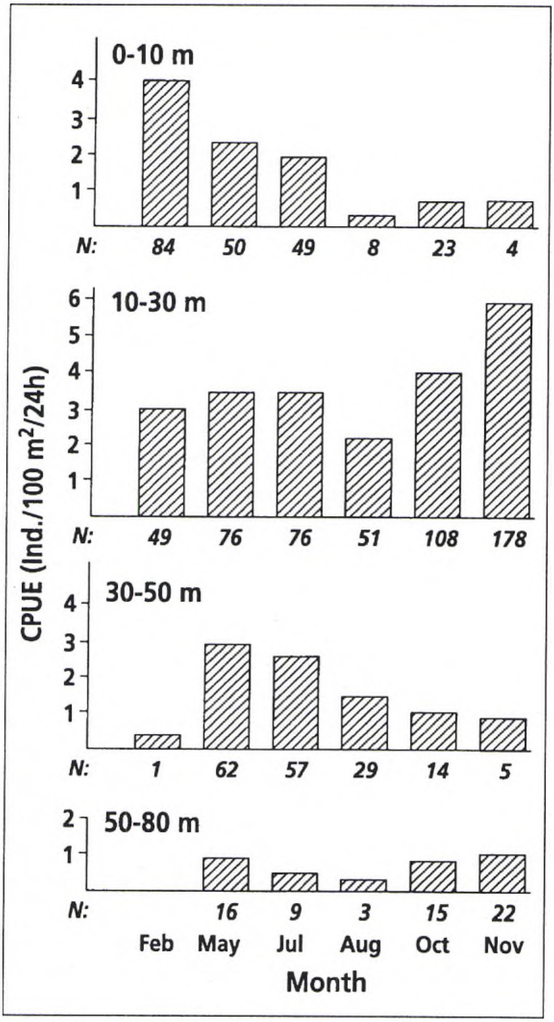

Fig. 4. Numbers of benthic Arctic charr caught per 100 m^2 net area for 24 hours fishing (CPUE) in Lake Jonsvatn, February-November 1987. Sample sizes for each month are below bars. (Revised from Næsje et al. 1991).

In the pelagic habitat most fish stayed in the upper 20 m zone and catch per unit effort was largest in August and October (Fig. 6). There were no differences in the depth distribution of the different size groups. The length and age distribution of pelagic fish were different from the benthic fish as most pelagic individuals were between 18 and 25 cm (68-97%) and no fish younger than 3 years were caught in the pelagic habitat (Figs. 7 and 8). However, the relative age distribution of fish older than 3 years was similar in the two habitats and most fish were 4 years of age.

Diet

The food of 0+ Arctic charr varied throughout the year, but overall *M. relicta* seemed to be the most important food resource as it was eaten by a large number of individuals in all sampling periods from May until December (Fig. 9 and Table 1). In the spring most individuals ate this prey almost exclusively. However, the mean weight percent of M. *relicta* in the stomach contents and the frequency of individuals that had eaten this food item decreased from late July to a minimum in September/October before increasing again during late autumn. Other important food items were chironomid larvae and pupae in July, and both zooplankton and chironomids were as important as *M. relicta* in August, September and October. The most common zooplankton species to be eaten were the copepods *Cyclops* spp. and *Heterocope appendiculata* and the cladoceran *Bosmina longispina.*

During spring and summer the mean size of *M. relicta* eaten by age-0 Arctic charr was close to the size of the young-of-the-year individuals (Fig. 10). When *M. relicta* has a body length of approximately 3 mm they are released from the

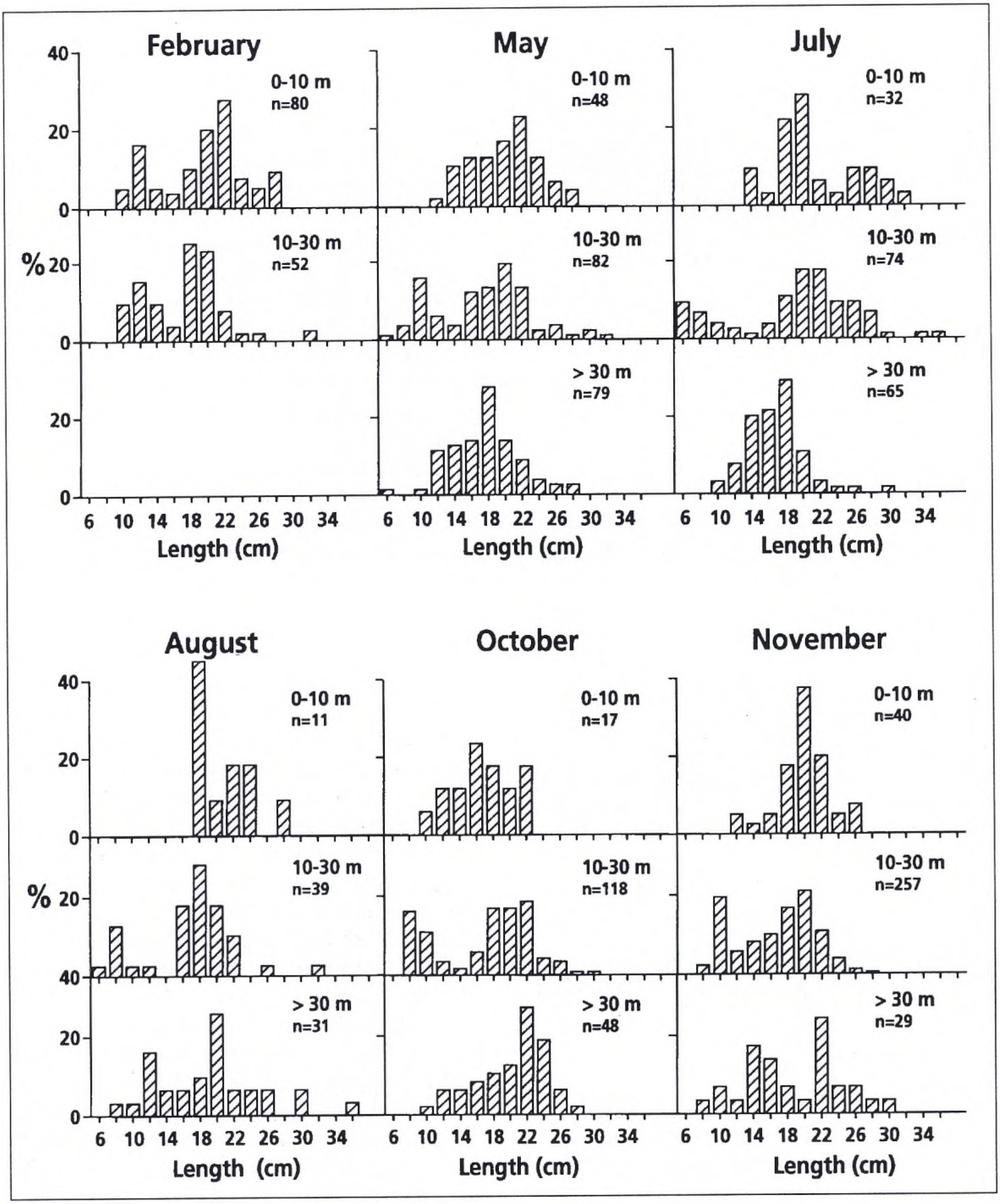

Fig. 5. Length distribution (total bodylength) of benthic Arctic charr caught in gillnets in the 0-10 m, 10-30 m and >30 m depth zones in Lake Jonsvatn, February-November 1987. n=total number of charr caught in the depth zone in the sampling period.

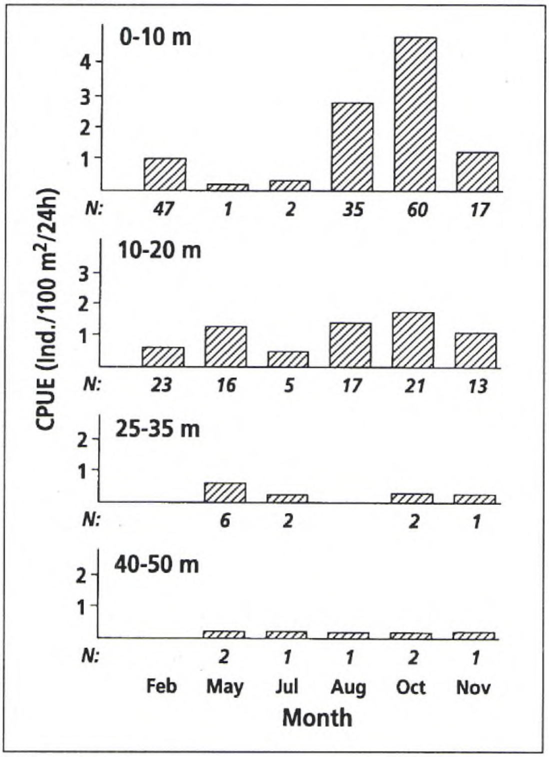

Fig. 6. Numbers of pelagic Arctic charr caught per 100 m^2 net area for 24 hours fishing (CPUE) in Lake Jonsvatn, February-November 1987. Sample sizes for each month are below bars. (Revised from Næsje et al. 1991).

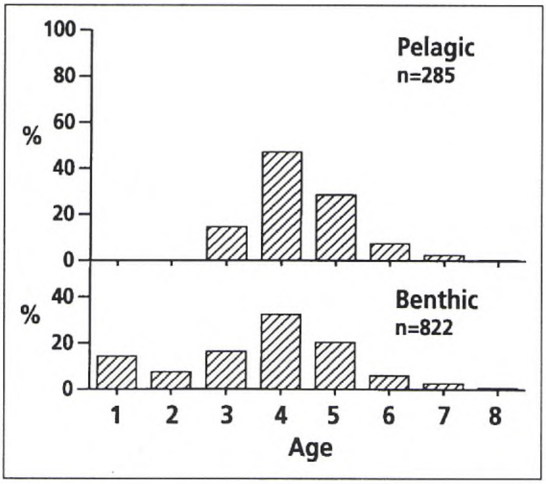

Fig. 8. Age distribution (%) of pelagic and benthic Arctic charr caught in gillnets in Lake Jonsvatn, February-November 1987.

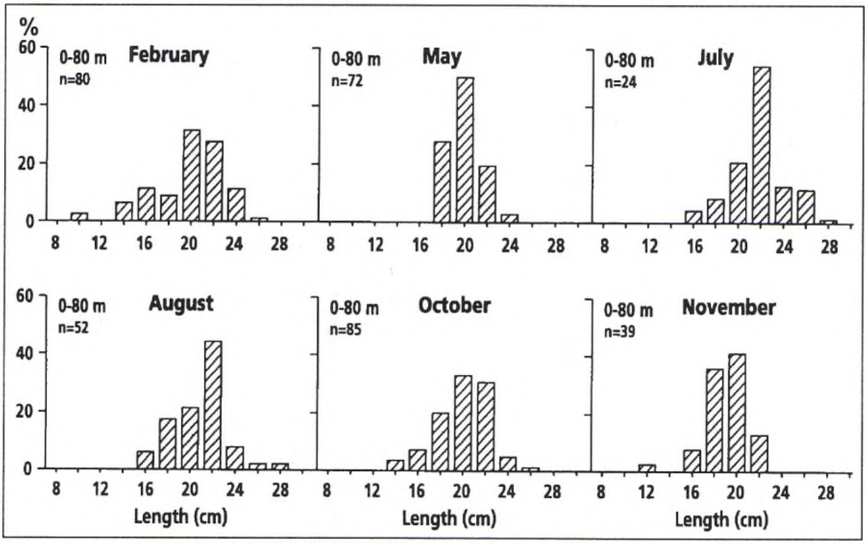

Fig. 7. Length distribution (total body-length) of pelagic Arctic charr caught in gillnets in Lake Jonsvatn, February-November 1987. n=total number of charr caught in the sampling period.

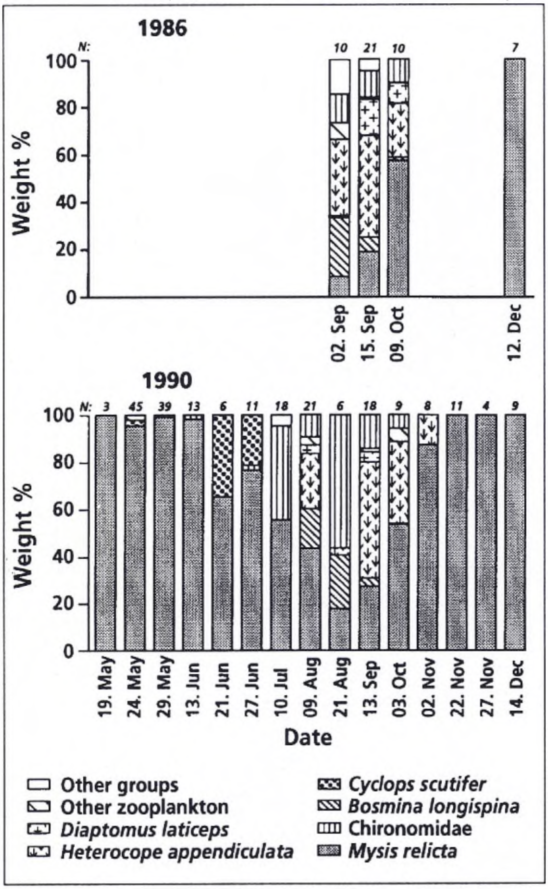

Fig. 9. Seasonal variation in percentage composition by weight of prey items in the stomachs of age-0 Arctic charr sampled from September to December 1986 and from May to December 1990 in Lake Jonsvatn. Sample sizes for each period are above bars.

female's marsupium, mainly in April and May. In this period the food of newly hatched Arctic charr almost exclusively consisted of this prey. Later in the season there was more variation in the size of *M. relicta* eaten, which corresponded to the total variation in the size of *M. relicta* in the lake.

M. relicta was also important food of older (≥age-1) benthic Arctic charr, and similar to the age-0 class, the importance of this food item decreased towards August-October (Fig. 11). This was due to reduced consumption of *M. relicta* by fish caught in the 0-10 m and 10-30 m zones. During August, October and November *Daphnia galeata* and *Pisidium* spp. were the most important food items in this depth zone.

The food of pelagic Arctic charr also changed throughout the year (Fig. 12). In this habitat *M. relicta* was the only food item eaten in February. The importance of *M. relicta* as food, however, decreased after February and from July very

Table 1. Number of stomachs analyzed (Total *N*), number and per cent empty stomachs (Empty), and number and frequency of occurrence of various groups of food items eaten by the age-0 class of Arctic charr in Jonsvatnet in 1990. Fish with empty stomachs are excluded in the estimates of occurrence of food items (per cent and frequencies in brackets).

	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Total *N*	101	37	19	30	23	9	26	10
Empty	15 (15)	5 (14)	1 (5)	1 (3)	0	0	1 (4)	0
M. relicta	85 (99)	26 (81)	18 (100)	13 (45)	7 (30)	5 (56)	22 (88)	9 (90)
Copepods	1 (1)	9 (28)	0	19 (66)	17 (74)	5 (56)	2 (8)	0
Daphnia	0	0	0	0	6 (26)	4 (44)	1 (4)	0
Bosmina	0	0	0	18 (62)	12 (52)	0	0	0
Holopedium	0	0	0	4 (14)	0	0	0	0
Chydoridae	0	0	0	1 (3)	1 (4)	0	0	0
Molluscs	2 (2)	0	0	0	0	0	0	0
Chironomids	0	2 (6)	9 (50)	8 (28)	5 (22)	2 (22)	0	0
Ostracoda	4 (5)	2 (6)	0	1 (3)	0	0	0	0
Other	0	2 (6)	0	0	1 (4)	0	1 (4)	1 (10)

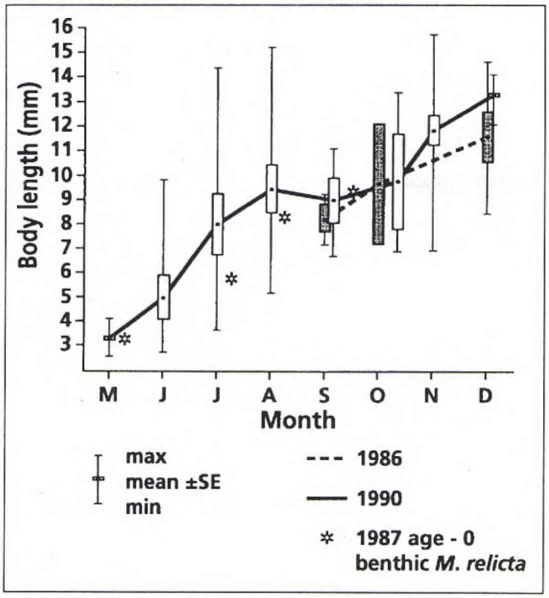

Fig. 10. Mean size (SE, maximum and minimum) of *M. relicta* eaten by age-0 Arctic charr in Lake Jonsvatn, September-December 1986 and May-December 1990. Stars indicate the mean size of juvenile *M. relicta* in the benthic zone in 1987.

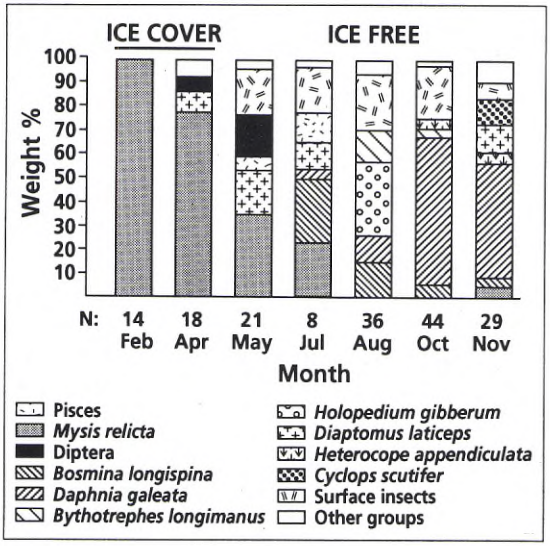

Fig. 12. Seasonal variation in percentage composition by weight of prey items in the stomachs of pelagic Arctic charr in Lake Jonsvatn. Sample sizes for each period are below bars. (Revised from Næsje et al. 1991).

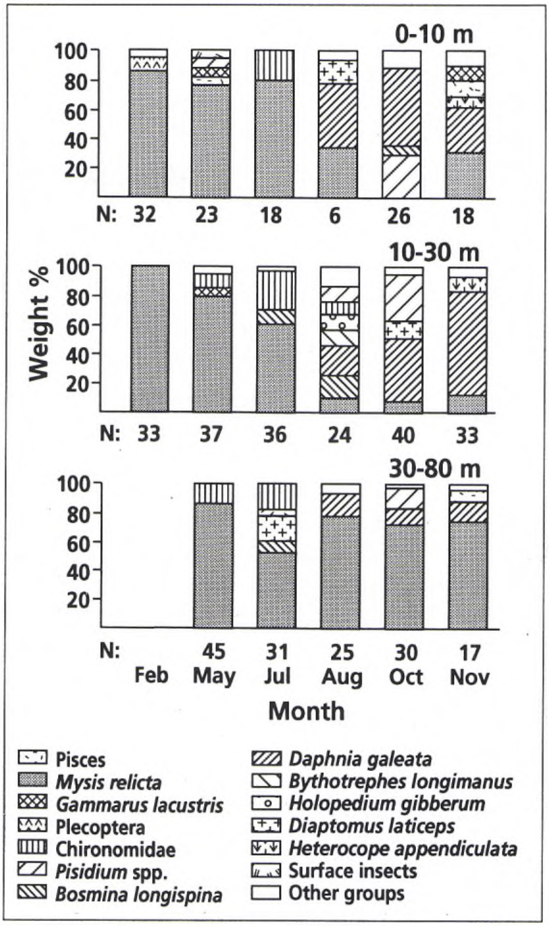

Fig. 11. Seasonal variation in percentage composition by weight of prey items in the stomachs of benthic Arctic charr in 0-10 m, 10-20 m and 30-80 m depth zones in Lake Jonsvatn. Sample sizes for each period are below bars. (Revised from Næsje et al. 1991).

few fish ate this food item. During spring, summer and fall (May-October), surface insects were important food by weight. From July until November, however, cladocerans were the most important food items (July: *B. longispina*, August: *Holopedium gibberum*, October and November: *Daphnia galeata*).

Discussion

Habitat selection among different sized groups of fish is based on trade-offs between benfits and costs in different habitats (Stephens and Krebs 1986). Major factors in this trade-off are foraging profitability (Werner and Hall 1976, Werner et al. 1983a, Holbrook and Schmitt 1988), risk of predation and/or the presence of competitors (Pitcher et al. 1982, Werner et al. 1983b, Mittelbach 1984, Holbrook and Schmitt 1988). *M. relicta* has been introduced to many lakes with the purpose of increasing the foraging profitability for fish in the pelagic habitat (Nesler and Bergersen 1991). However, introductions have led to disappearence of zooplankton species (e.g. *Daphnia*) whereas other cladocerans have declined significantly in abundance (Zyblut 1970, Richards et al. 1975, Kinsten and Olsén 1981, Nero and Sprules 1986, Langeland 1988). At the time of this study, approximately 10 years after the introductions of *M. relicta* to Lake Jonsvatn, Næsje et al. (1991) found the density of pelagic *M. relicta* to be more than 100 mysids/m^2 in the pelagic zone (December 1986) indicating that the *M. relicta* population was well established in the lake. The zooplankton community, however, had not changed significantly in number of species or in biomass from the situation before the introductions (Koksvik et al. 1991). This might be due to a refuge for zooplankton in the upper 0-5 m of the pelagial zone during summer and autumn as this zone was not exploited by zooplanktivorous *M. relicta* (Koksvik et al. 1991, Næsje et al. 1991). Hence, the Arctic charr in Lake Jonsvatn still performed both phenological and ontogenetic niche shifts into the pelagic habitat at the time of this study.

The CPUE data indicate that most pelagic fish migrate into the pelagic habitat in August and back to the benthic habitat in November. This result was confirmed by echo survey of the pelagic waters of Lake Jonsvatn (Næsje unpublished). The length distribution of pelagic fish indicate that there is a minimum size for fish moving into this habitat. The pelagic Arctic charr consisted mainly of fish between 18 and 25 cm being 3 to 5 years old. This threshold size of approximately 18 cm of fish performing a habitat shift into the pelagic zone is confirmed by L'Abbée-Lund et al. (1993) who studied niche shifts of Arctic charr in five Norwegian lakes. In lakes with piscivorous fish species such as brown trout, the unstructured pelagic habitat is often considered to be a more risky habitat for small fish than the more structured benthic habitat (Werner 1986, McIvor and Odum 1988, Ehlinger 1990, Sandlund et. al. 1992b, L'Abée-Lund et al. 1993). In addition, zooplankton abundance peaked during autumn (August) in Lake Jonsvatn (Næsje et al. 1991) making this habitat a more nutrient rich habitat where large Arctic charr with low risk of predation fed. This study therefore supports the hypothesis that young Arctic charr that are vulnerable to predation inhabit the low-risk benthic habitat, while older and larger fish inhabit both this low-risk habitat and the high-risk pelagic habitat.

The benthic part of the Arctic charr population in Lake Jonsvatn consisted of all size groups. In May and July the CPUE data indicates that Arctic charr were distributed down to approximately 50 m, but during the rest of the year most fish stayed in more shallow waters (<30 m). However, the length distribution varied in the different depth zones. Juveniles mainly lived at 10-30 m depth throughout the year, while larger fish were also caught in more shallow waters. The littoral and shallow benthic waters are more productive than the profundal zone, and in Lake Jonsvatn predatory brown trout and pike inhabit these areas making them a high risk area with respect to predation. In addition, brown trout and Arctic charr might be potential food competitors as they have the same preferred prey (Nilsson 1963, 1965). However, due to differences in the utilization of food resources Langeland et al. (1991) ascribe the niche shifts of Arctic charr in sympatry with brown trout to be caused by interference competition and not exploitative competition. The presence of piscivorous fish and territorial brown trout in littoral and shallow benthic waters might therefore be the reason for juveniles not inhabiting these otherwise profitable habitats.

The introduction of *M. relicta* has caused drastic changes in the feeding ecology of Arctic charr in Lake Jonsvatn, and *M. relicta* have become an important food item for all size/age groups of benthic fish. During spring and summer the population of *M. relicta* consisted of two size groups, namely juveniles (3-5 mm) and large adults (10-15 mm) (T. Næsje, R. Saksgård and A. Jensen (unpublished). Juvenile *M. relicta* are released from the females marsupium during spring (mainly in April-May). The start of exogenous feeding of Arctic charr and the main release of 0+ *M. relicta* therefore coincided, and nearly 100% (weight) of the initial food of Arctic charr consisted of these 3 mm long shrimps (approximately 0.08 mg dry weight). The increase in the mean size of *M. relicta* eaten during spring corresponded to the increase in the size of 0+ *M. relicta.* However, the range in the size of *M. relicta* eaten increased and in late autumn reflected the total length distribution of *M. relicta* in the lake. This study shows that fry of Arctic charr are able to feed on *M. relicta* from the start of exogenous feeding, but their growth rate indicates that *M. relicta* is poor food for Arctic charr in their first year of life. Studies of the instantaneous yearly growth rate of Arctic charr in the nearby Lake Høysjøen has been performed by Forseth et al. (1994). Lake Høysjøen contains both brown trout and Arctic charr and is similar to Lake Jonsvatn in morphometry and nutrient content, but *M. relicta* has not been introduced to this lake. The mean adult size (e.g. 6+) of Arctic charr in Lake Høysjøen is smaller than in Lake Jonsvatn, approximately 19 vs 24 cm respectively (Forseth et al. 1991), and age at sexual maturation occurred one/two years earlier in Lake Høysjøen than in Lake Jonsvatn. Therfore it should be expected that the juvenile growth rate is lower in Lake Høysjøen than in Lake Jonsvatn. The opposite, however, seems to be the case for age-0 fish, as the instantaneous growth rate during the first growing season was approximately 2.5 higher in Lake Høysjøen than in Lake Jonsvatn (1.29-1.38 vs 0.59, respectively) (Forseth et al. 1994). During the next two years, however, growth rate in Lake Jonsvatn tended to be better than in Lake Høysjøen (2. year: 0.88 vs. 0.57-0.59; and 3. year 0.31 vs. 0.22-0.26). Therefore, based on the growth rate, charr fry in Lake Jonsvatn seemed to have poor growing conditions both compared with those in Lake Høysjøen and the larger juveniles in Lake Jonsvatn. There were no major differences in the food of age-0 and larger fish with the exception that larger fish in shallow benthic habitat ate more zooplankton in late autumn. *M. relicta*, however, seemed to be an important food item for all sizegroups of benthic Arctic charr. The difference in growth might therefore be due to differences in the total energy intake and the energetic costs when feeding on *M. relicta*. The relationship between the cost of prey capture, prey size and predator size has been shown first to decrease with an increase in prey size, then to increase sharply with a further increase in prey size (Werner 1974, Kislalioglu and Gibson 1976). This is explained initially by a slow increase in the handling costs as prey size increase, and later by a rapid increase in the handling costs as the prey get close to the maximum handling size possible for the predator. Compared with other food items e.g. zooplankton and chironomids, *M. relicta* is a large and/or mobile prey. Age-0 fish might therefore now spend more energy on pursuing and handling *M. relicta* than they did on food items eaten before its introduction. Age-1 and age-2 fish, however, are larger than age-0 fish and therefore may spend less energy handling *M. relicta* and hence, gain a larger net energy intake to spend on growth.

In general *M. relicta* constituted a larger part of the food of benthic than pelagic Arctic charr in Lake Jonsvatn. Fish caught in the 0-30 m benthic zone, however, fed more on *Daphnia galeata* and *Pisidium* spp. during August to November than fish caught in greater depths. This might be due to a greater vertical migration of benthic *M. relicta* in this period where most individuals stayed deeper than 30 m during the day (Næsje et al. 1991). Arctic charr are considered to be a visually dependent predator (Nilsson 1963, Ali and Wagner 1980). The lack of habitat overlap during daylight between Arctic charr and *M. relicta* might therefore be the reason why few fish in shallow water ate this prey. In addition this was the period with most alternative prey such as zooplankton as their abundance peaked at this time of the year (Næsje et al. 1991).

The pelagic Arctic charr fed to a lesser extent on *M. relicta* than benthic conspecifics, as *M. relicta* only constituted the major part of the stomach content of pelagic charr during spring. Pelagic *M. relicta* performed large diel vertical migrations during late summer and autumn descending to depths greater than 40-50 m during daylight. Næsje et al. (1991) has shown that the amount of *M. relicta* eaten was positively correlated with the daytime habitat overlap between *M. relicta* and Arctic charr. Corresponding to the feeding of fish in the upper 0-30 m in the benthic habitat, the success of Arctic charr feeding on *M. relicta* seemed to be dependant on a visual detection of this prey during daylight, and hence the low utilisation of *M. relicta* as prey.

This study supplements information from earlier studies of interaction between introduced *M. relicta* and Arctic charr. In releasing *M. relicta* man has introduced a competitor to Arctic charr. Most documented cases of competition can be classified as interference competition, i.e. competition based on direct antagonistic interactions between individuals (c.f. Begon and Mortimer 1986). The reduction in abundance of pelagic Arctic charr which often occurs after introduction of *M. relicta* is one of few good documented examples of exploitative competition, i.e. individuals compete for a limited resource, e.g. food, without overt agression. This study indicates that interactions between *M. relicta* and age-0 Arctic charr is based on both exploitative and interference competition. The competition is exploitative in the sense that *M. relicta* reduce the forage base of age-0 Arctic charr to such an extent that the growth of fry has been reduced and it is interference competition in that age-0 charr feed heavily on *M. relicta*. The reduced growth rate of fry, however, indicates that exploitative competition seems to be most important in the interactions between age-0 Arctic charr and *M. relicta*.

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Random Amplified Polymorphic DNA (RAPD) in Arctic Char

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Abstract

We evaluated RAPD-PCR as a method to obtain genetic markers in Arctic char. The method is based on PCR-amplification using short, randomly selected oligonucleotid primers. The PCR products were separated on an agarose-gel and variation was detected as absence or presence of amplified DNA-fragments. We tested 20 different 10-mer primers and were able to amplify approximately 140 DNA-fragments. Most bands were identical in all individuals studied. Of the band variation observed, some could not be reliably scored because of weak staining and in a few cases because of inconsistencies between repeated amplifications. However, four polymorphic fragments were considered useful as genetic markers and significant population differences in the presence of these fragments were observed. The study included two suggested subspecies which are thought to have colonized Scandinavia after the last glacial period. The variation we observed could not discriminate between these suggested subspecies and geographic distance between populations may better predict genetic differentiation.

Keywords: Arctic char, RAPD-PCR, subspecies, populations, genetic similarity.

Introduction

Studies of population genetic structure of Scandinavian Arctic char (*Salvelinus alpinus* L.) have been hampered by the lack of polymorphic genetic markers. In Swedish lakes Andersson et al. (1983) observed useful variation in two out of 37 studied protein loci. In a survey of Norwegian lakes Hindar et al. (1986) found extensive variation in two out of 42 studied enzyme loci. Mitochondrial DNA analysis (Hartley et al. 1992) has revealed a variant that could discriminate between pelagic and benthic Arctic char in Loch Rannoch, Scotland. However, mt-DNA variation appears not to be extensive in Arctic char. Thus, alternative methods to reveal genetic variation in Arctic char are required.

Nyman (1972) and Nyman et al. (1981) suggested colonization of Scandinavia by three different allopatric subspecies after the last glacial period. An opposing view of Scandinavian Arctic char systematics has been put forward by Andersson et al. (1983) and Hindar et al. (1986) who suggested that a single line invaded Scandinavia. The present diversity is then a consequence of subsequent differentiation from this single lineage. Finding more polymorphic markers would increase the possibilities to evaluate the genetic relationship between different Arctic char forms and truly test these alternative scenarios. Also, the monitoring of genetic changes in hatchery strains would be improved when a larger number of genetic markers are used than is possible today. Advances in DNA technology now offer a number of opportunities to study variation in nuclear DNA.

In this study, we aimed to evaluate Random Amplified Polymorphic DNA (RAPD) (Williams et al. 1991) as a tool for population genetic studies of Arctic char. With this method, PCR amplification of random DNA fragments is achieved by the use of a single short randomly constructed primer. In a number of organisms where protein variation has been low, the RAPD method has revealed DNA-polymorphism (e.g. Black et al. 1992). The RAPD-PCR method is now being used extensively to generate genetic markers for a variety of purposes including paternity testing (Hadrys et al. 1993) and population studies (Dawson et al. 1993; Elo and Vuorinen, 1993). Postlethwait et al. (1994) used RAPD markers to construct a recombination map for the zebrafish (*Danio rerio*) and to obtain genetic markers for lethal and visible mutations.

Material and methods

Populations studied

Samples were taken from three hatchery populations of Arctic char originally derived from three different Swedish lakes: Lake Hornavan, Lake Rensjö and Lake Ottsjö. All Arctic chars were reared at the Fisheries Board Research Station in Kälarne, Sweden. Samples were taken from newly hatched fry or from one-year-old fish. The Lake Hornavan fish were the second generation in the hatchery. Lakes Rensjö and Ottsjö fish were the third generation in cultivation.

Lakes Rensjö and Ottsjö are situated in the county of Jämtland and both lakes drain into the River Indalsälven. Lake Hornavan, in the county of Norrbotten, is approximately 400 km to the north of the other lakes and is part of the river Skellefteälven drainage system. According to the classification of Arctic char suggested by Nyman et al. (1981), Lake Hornavan and Lake Ottsjö Arctic chars represent the N-char (*Salvelinus salvelinus*) whereas Lake Rensjö char is a F-char (*Salvelinus alpinus*). In Sweden the N-char is claimed to dominate in large lakes at lower altitudes and to be characterised by an intermediate frequency of the most anodal allele at the EST-2 locus. The F-char is claimed to be typical of alpine headwater lakes in the Swedish mountain range bordering Norway and to show a high frequency of the most anodal EST-2 allele.

DNA extraction

We extracted DNA using phenol extraction according to Taggart et al. (1992) from small pieces of muscle tissue (100-200 mg) or from whole newly hatched fry. As an alternative we tried a simplified protocol without phenol extraction (Laird et al. 1991). The methods gave DNA that worked equally well and resulted in identical amplification products.

PCR amplifications

Primers: A total of 20 10-mer primers were used. All primers were purchased from Operon Technologies (Alameda, Cal., USA) and were designated OPA1-OPA20.

Amplification reactions were performed in volumes of 25 µl containing 10 mM Tris-Hcl,pH 8.3, 50 mM KCl, 2.3 mM $MgCl_2$, 0.001% (w/v) gelatin, 200 µM each of dATP,dCTP,dGTP,dTTP (Perkin Elmer Cetus), 0.3 µM primer, 5-25 ng of template DNA, and 0.625 units of Taq DNA Polymerase (Perkin Elmer Cetus). When using the primer OPA-10, 1.9 mM $MgCl_2$ was used in the amplification reaction. The reactions were overlaid with oil. Amplifications were performed in a Coy Tempcycler using the following temperature profile: 4 min at 80°C, 1 min at 94°C, followed by 45 cycles of 1 min at 94°C, 1 min at 36°C, 1 min at 72°C, and ended with 10 min at 72°C. Taq DNA Polymerase was added when the temperature cycler had reached 80°C. Amplification products were analysed by electrophoresis in 1.4% agarose gels and stained with ethidium bromide. As a DNA molecular-weight marker, we used Eco RI and Hind III digested lambda-DNA (Boehringer).

The twenty primers were initially used to amplify DNA from samples of fish from Lake Rensjö and Lake Hornavan strains. This initial screening included 5-10 fish from each of the two strains. Samples from Lake Ottsjö strain were only used for comparison of variation observed in the other strains.

Band sharing similarity was estimated as

$$2\, n_{xy} / n_x + n_y$$

where n_{xy} is the number of shared fragments and n_x and n_y are the number of fragments in individuals x and y, respectively. Between population similarity was estimated according to Lynch (1990) and was obtained as

$$1 + S_{ij} - (S_i + S_j) / 2$$

where S_{ij} is the average similarity between pairs of individuals across populations i and j and S_i is the average similarity of individuals within population i.

Results

All primers gave amplification products. The number of fragments observed per primer varied between one and 13. Variation in banding intensity made it difficult to give an exact number of observed fragments. However, we estimated that approximately an average of seven DNA-fragments were observed per primer. Three primers (OPA-9,OPA-10,OPA-16) showed easily scorable and consistent variation in four DNA-fragments. Variation was observed also in a number of other fragments but because of variation in banding intensity or inconsistencies between repeated amplifications, some of the variation could not be reliably scored.

The OPA-9 primer was polymorphic for an 830 bp fragment as revealed by the presence or absence of this fragment among specimens (Fig. 1). Both Rensjö and Hornavan Arctic char showed this polymorphism, and the frequencies of the band phenotypes are given in Table 1. A chi-square test indicated this fragment to be significantly more common in the Rensjö strain ($\chi^2=9.1$, $P<0.01$).

Two fragments, amplified using the OPA-10 primer, were variable (Fig. 2). An approximately 550 bp fragment was found to be present in most specimens from the Hornavan strain but was less commonly observed in the Rensjö strain (Table 1). A significant difference in the frequency of this fragment was obtained between the Hornavan and Rensjö strains ($\chi^2=14.7$, $P<0.001$).

A shorter fragment, 520 bp, also amplified by the OPA-10 primer, was polymorphic in the Rensjö and Hornavan strains. This fragment was significantly more often observed with Rensjö char compared to Hornavan char ($\chi^2=17.0$, $P<0.001$), (Table 1).

Since the Rensjö and Hornavan strains were markedly different with respect to two fragments,

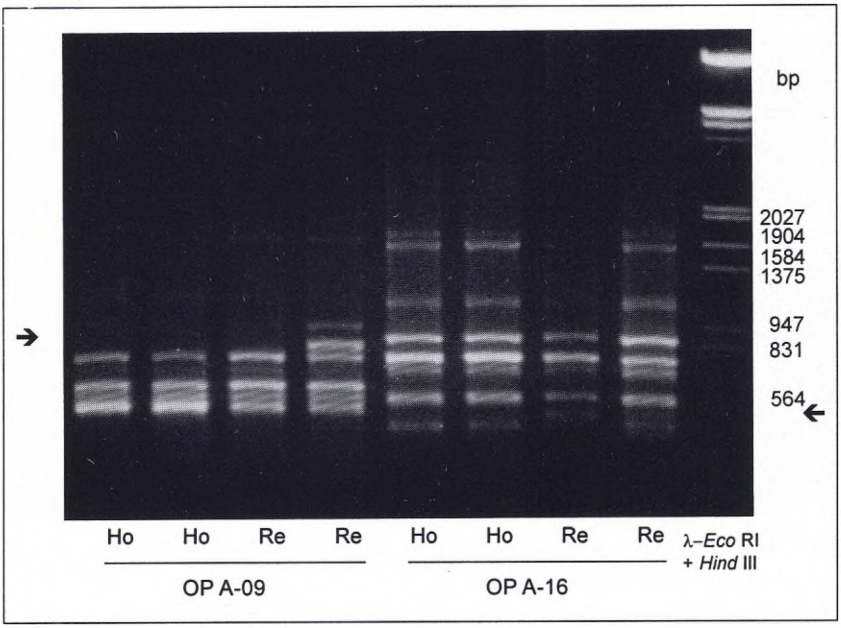

Fig. 1. Amplification products from two Arctic char strains (Ho = L. Hornavan, Re = L. Rensjön) obtained by RAPD primers OPA-9 (5'GGGTAACGCC) and OPA-16 (5'GACCGCTTGT). Arrows indicate polymorphic fragments.

Table I. Number of individuals that show presence (+) or absence (-) of four different RAPD fragments in three strains of Arctic char. The frequency of the null phenotype is given in parentheses.

Strain		DNA marker-base pair size OPA9-830	OPA10-550	OPA10-520	OPA16-510
L. Hornavan	+	12	18	7	23
	-	13 (0.52)	2 (0.10)	13 (0.65)	2 (0.08)
L. Rensjö	+	19	7	21	8
	-	3 (0.14)	15 (0.68)	1 (0.05)	16 (0.67)
L. Ottsjö	+	-	7	22	0
	-	-	18 (0.72)	3 (0.12)	24 (1.0)

Table 2. Band sharing similarity indices within (diagonal) and between (below diagonal) three Arctic char strains. Re = L. Rensjön, Ot = L. Ottsjön, Ho = L. Hornavan.

	Re	Ot	Ho
Re	0.76		
Ot	0.99	0.71	
Ho	0.60	0.54	0.84

we tested samples from a third strain (Lake Ottsjö strain). As can be seen from Table 1, the Ottsjö strain strongly resembled the Rensjö strain in the frequencies of the two OPA-10 fragments but was significantly different from the Hornavan strain for the 550 bp fragment ($\chi^2=17.3$, $P<0.001$) and the 510 bp fragment ($\chi^2=13.7$, $P<0.001$).

The OPA-16 primer showed polymorphism for a 510 bp fragment. Both Rensjö and Hornavan

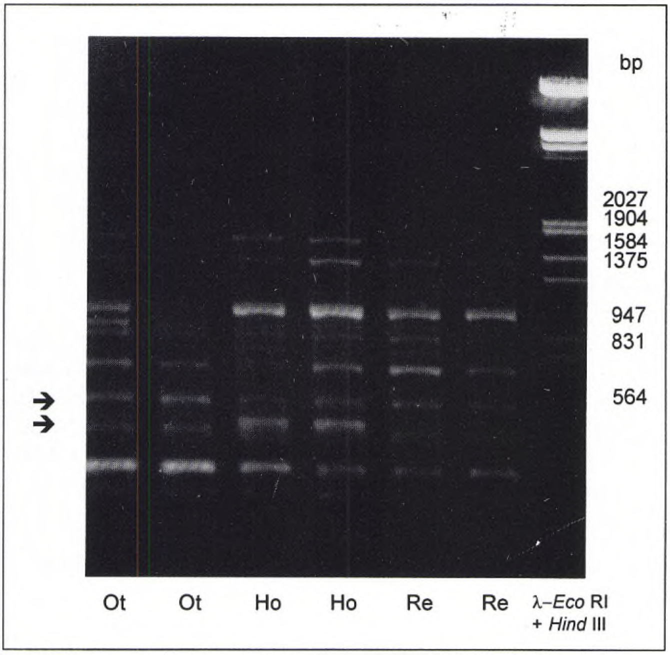

Fig 2: Amplification products of three Arctic char strains (Ot = L. Ottsjön, Ho = L. Hornavan, Re = L. Rensjön) obtained by RAPD primer OPA-10 (5'GTGATCGCAG). Arrows indicate polymorphic fragments.

Arctic char were polymorphic. The 510 bp fragment was significantly more common in the Hornavan strain compared to the Rensjö strain (χ^2=18.2, P<0.001), (Table 1). The Ottsjö strain was not polymorphic for the OPA-16 510 bp fragment. This fragment was not present in any of the amplifications of Ottsjö strain specimens (Table 1).

Band sharing similarity indices based on variation generated by primers OPA-10 and OPA-16 are given in Table 2. These indices indicated a high degree of genetic similarity between the geographically close Lake Rensjö and Lake Ottsjö chars and a low similarity between Lake Hornavan char and any of the other two chars.

Discussion

DNA polymorphism in Arctic char as revealed here by RAPD-PCR technique substantially increases the possibility of genetic characterization of populations in this species. Out of twenty primers tested, we observed consistently scorable variation in four DNA-fragments. Significant differences in banding phenotype (presence or absence of a fragment) between Arctic char strains from different geographic origin were observed for all four variable fragments. Assuming that the present results are representative and considering that a very large number of RAPD primers (at least one thousand) is commercially available, the amount of DNA polymorphisms that can be detected in Arctic char with RAPD-PCR must be very high. It should also be pointed out that it is likely that more variation can be detected with the primers used here. We observed several fragments that appeared to be polymorphic but which could not be reliably scored, mainly due to variation in banding intensity. Experimenting with magnesium ion concentration or with other reaction components may be a way to increase the yield of amplifications and increase the number of scorable amplification products. Also, for detection of recessive markers at low frequency, a larger number of specimens than used here needs to be tested.

A disadvantage with RAPD-PCR is that most variable fragments segregate as dominant markers, heterozygotes are indistinguishable from dominant homozygotes. This makes it necessary to use larger sample sizes compared to studies of codominant loci. Lynch and Milligan (1994) discussed some problems related to the use of RAPD analysis in population genetic studies and presented formulae for estimates of conventional population genetic parameters with dominant markers. However, the drawbacks with RAPD markers should be considered in relation to the fact that Scandinavian Arctic char are polymorphic in very few allozyme loci and that the possibility to perform population genetic studies of this species has been limited. The most widespread and studied polymorphism occurs at the Est-2 locus which has been questioned by Andersson et al. (1983) as a useful genetic marker.

We suggest that RAPD-PCR markers can be useful for studies of population genetic structure of Arctic char. Also, they may be used for monitoring of hatchery strains. Loss of rare alleles caused by too small size of a population is a likely effect of hatchery propagation. Monitoring of such changes is not effective with the genetic marker systems (Est-2, MDH-4,5) which are in use at present. With RAPD-PCR it should be possible to survey a large number of polymorphisms and select markers at suitable frequencies.

We observed here that the geographically more remote Lake Hornavan strain deviated significantly from the other two strains in the frequency of the OPA-10 and OPA-16 DNA-fragments. Lake Ottsjö and Lake Rensjö Arctic chars were similar with respect to the OPA-10 fragment frequencies but the OPA-16 fragment variation observed with the Lake Rensjö strain was not present in the Lake Ottsjö strain. Nyman et al. (1981) classified Lake Ottsjö and Lake Hornavan Arctic chars as belonging to the same sibling species, *S. salvelinus,* whereas Lake Rensjö char were classified as *S. alpinus.* Data here are from relatively few individuals and from strains reared in the hatchery for two or three generations. Still, it appears as if geographic distance better predicts genetic differentiation than does the proposed taxonomical subdivision of Arctic char. Thus, the evidence presented here supports the repopulation of Scandinavia by a single lineage of Arctic char.

Our interpretation of the variation observed using the OPA-10 primer follows the usual interpretation of RAPD-PCR fragments as dominant markers. However, we cannot exclude that these two fragments which are not very different in size and are amplified by the same primer, could be alleles at the same loci. Crossings will be needed in order to verify the segregation of these fragments.

Acknowledgment

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Relationships Among Charrs Based on DNA Sequences

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Abstract

A phylogenetic analysis of the subspecies in the *Salvelinus alpinus-Salvelinus malma* complex found in North America was done using sequences from the internal transcribed spacer (ITS1) of the ribosomal DNA (rDNA) and a portion of the 5' external transcribed spacer (5'ETS) of the (rDNA) with *Salvelinus namaycush* as an outgroup. In addition sequence data from ND3 gene of the mitochondrial DNA (mtDNA) was used to examine relationships among *Salvelinus* species including those of the *S. alpinus-S. malma* complex. Results supported Behnke's hypothesis of three major subspecies of *S. alpinus*, but indicated a very close relationship between members of *S. alpinus* and *S. malma* complex in the North Pacific. The sequences from *S. malma malma* from the Noatak River in northern Alaska were more similar to those of *S. albus* from Russia and *S. alpinus taranetzi* from south central Alaska than to *S. malma lordi* of southeastern Alaska. Comparison of the mitochondrial and nuclear data suggested that *S. confluentus* has hybridized with *S. alpinus erythrinus* in the recent past.

Introduction

According to Behnke (1965,1980) there are three major subgroups of the genus *Salvelinus* in North America. These are *S. namaycush* (lake trout), confined to northern lakes in the east, *S. fontinalis* (brook trout) found throughout the east and south, and the Arctic char complex, named subgenus *Salvelinus* by Behnke (1980). This latter group includes *S. alpinus* (Arctic char) which has a continuous circumpolar distribution in the Arctic, *S. malma* (Dolly Varden char) which occurs sympatrically with *S. alpinus* in the north Pacific, and *S. confluentus* (bull trout) which is found in the Rocky mountains. In the far east another species, *S. leucomaenis* (Japanese spotted char or kundscha char), is considered to be more closely related to *S. namaycush* by Savvaitova (1980) and Viktorovsky (1975, 1978), but is placed in the subgenus *Salvelinus* by Behnke (1984). Behnke divides the subgenus *Salvelinus* into the *S. alpinus -S. malma* complex and a group comprising *S. confluentus, S. leucomaenis*, and *S. albus* (from Kamchatka, Russia). Recent data from allozymes (Crane 1991) and sequences of the nuclear ribosomal DNA (Pleyte et al. 1992 and Phillips et al. 1994) have supported a sister relationship between *S. leucomaenis* and *S. confluentus*.

Many questions remain concerning the relationships of the western *S. alpinus* and *S. malma* groups (reviewed in Behnke 1980, 1984, 1989, Cavender 1980, Johnson 1980, Savvaitova 1980, Glubokowsky and Chereshnev 1982) to each other and to the other Asian chars. In Europe and Asia a large number of species and subspecies have been named by different authors, while other authors (Savvaitova 1980) believe that *S. malma* and *S. alpinus* are synonyms for the same species.

In western North America, McPhail (1961) recognized a northern and a southern form of *S. malma* and a western and eastern Arctic form of *S. alpinus*. The western Arctic-Bering Sea form of *S. alpinus* was very similar to the northern form of *S. malma* in meristic characters (Morrow 1980, McCart 1980) and is considered to be the same species (*S. malma malma*) recognized by

Behnke (1980). However, McPhail and Lindsey (1970) and McCart (1980) considered it to be a form of *S. alpinus*. A recent survey of char from east and west of the MacKenzie river system in Canada (Reist, pers. comm.) in which meristic characters and enzyme loci were examined has confirmed that the riverine char from the continental north slope west of the Mackenzie River are *S. malma* whereas the lacustrine char from this area are relictual *S. alpinus*. Reference groups in this study for *S. malma* were from the Klutina River in south central Alaska, and for *S. alpinus* from Cambridge Bay, Northwest Territory. Behnke (1984) divides *S. alpinus* into five major groups including two associated with Europe (*S. a. alpinus*), one from eastern North America (*S. a. oquassa*), one originating in Siberia and extending across northern North America (*S. a. erythrinus*, (the "eastern Arctic" form of McPhail), and another found in the Arctic Ocean in the Chukotsk Sea-Bering Sea region ("taranetz char"). He recognizes three forms of *S. malma* including a southern North American form (*S. m. lordi*) which occurs south from the Alaska pennisula to Washington State, a southern Asian form (*S. m. krascheninnikovi*), which is found south of the Amur River mouth to Sakhalin and Hokkaido), and a northern form (*S. m. malma*), which is found north from the Alaska pennisula and east to the Mackenzie River in Canada and in Asia from the northern Okhutsk area, Kamchatka north around Chukotka. On the Asian side another taxa, *S. albus* has been recognized in Kamchatka by Glubokowsky and Cheresnev (1982) although some Russian biologists consider it a form of *S. malma*. Behnke has suggested it may be related to the North American *S. confluentus*.

We wish to examine the relationships among the four major subspecies of *S. alpinus* and *S. malma* in western North America proposed by Behnke: *S. a. erythrinus* from the high Arctic and *S. a. taranetzi* from the Bering-Chukokst Sea which is found in inland lakes in Alaska, *S. m. malma* in northern Alaska and *S. m. lordi* in southeastern and south central Alaska.

In previous work we have examined the relationships among six species of the genus *Salvelinus* using restriction maps (Phillips and Pleyte 1991, Phillips et al. 1992) and sequence variation in the internal transcribed spacers (ITS1 and ITS2) of the ribosomal DNA (Pleyte et al. 1992, Phillips et al. 1994) which comprise approximately 1000 bp in these species. Restriction map data of the ribosomal DNA suggested that the 5' external spacer might be informative for interspecies relationships. We have now cloned a 300 bp portion of the 5' external transcribed spacer (5' ETS) from *S. namaycush* (lake trout) and designed primers which work for amplification of this region from species in the *S. alpinus-S. malma* complex, but not for other charrs. In this paper we report the results of a phylogenetic analysis of the subspecies of the *S. alpinus-S. malma* complex which occur in northwestern North America with *S. namaycush* as an outgroup using sequence data from the ITS1, ITS2 and a 300 bp portion of the 5'ETS.

Relationships based on our data from the nuclear ribosomal DNA differed in some respects from data based on RFLPs (Grewe et al. 1990) of mitochondrial DNA, especially with respect to the placement of *S. confluentus* (bull trout) which placed within the *S. alpinus-S. malma* complex with mtDNA data, but as a sister to *S. leucomaenis* with the nuclear ribosomal DNA data. To further investigate this discrepancy, we have examined relationships among all of the charrs using the 351 bp sequence of the ND3 gene from mitochondrial DNA and report our analysis in this paper.

Materials and Methods

Tissue samples for DNA extraction were obtained from the following sources: *S. leucomaenis* and *Hucho perryi* from the Hokkaido Fish Hatchery, Hokkaido, Japan; *S. namaycush* Marquette stock from Iron River Fish Hatchery, Iron River, Wisconsin; *S. fontinalis* from Wisconsin Department of Natural Resources, St. Croix, Wisconsin; *S. confluentus* from Arrow Lake, British Columbia; *S. alpinus erythrinus* from Nauyuk Lake, Northwest Territories; *S. alpinus taranetzi* from Dolly Varden Lake, Kenai

Peninsula, Alaska; *S. alpinus alpinus* from Norway; *S. malma lordi* from Auke Creek near Juneau, Alaska; *S. malma malma* from the Noatak River in northern Alaska; and *S. albus* from the Kamchatka River in Russia.

For samples obtained prior to 1992, DNA was isolated from liver by phenol extraction of proteins (Sambrook et al. 1989) and for samples obtained after 1992 the salt extraction method of Stratagene was used. Both mitochondrial and nuclear genes from one individual of each species were amplified using the polymerase chain reaction (PCR) (Saiki et al. 1988) and sequenced.

Amplifications of DNA by PCR were done with reaction volumes of 100ul containing 2.5 units of Taq (Promega, Madison, WI), 10ul of 10X magnesium free buffer with 6ul of 25mM $MgCl_2$ supplied by the manufacturer, and 2ul each of 1mM dATP, dTTP, dGTP, dCTP. Primers and templates were used at the concentrations given below. Amplifications were carried out in a Coy Model 60 thermal cycler with the parameters given below. The double-stranded PCR products were sequenced using the dideoxy method (Sanger et al. 1977).

Amplfication and sequencing of the rDNA genes

The primer sequences and sequencing strategies for the ITS1 and ITS2 are summarized in Fig. 1. The ITS1 and ITS2 were sequenced using two methods of template preparation. Magnetic beads or asymmetrical PCR were used to generate single stranded template. The magnetic beads (Dynal Inc., Great Neck, N.Y.) were used to isolate single stranded DNA according to the manufacturer's instructions. The amplification used a biotinylated reverse 28S primer and the forward primer MD-1 (30 pm each primer, and 100 ng template). The parameters were 36 cycles of 94°C for 1 minute 30 seconds, 50°C for 2 minutes, 72°C for 3 minutes, with 72°C at 7 minutes for final extension). For the ITS1, the off strand was sequenced with the 5.8S primer and the bead strand with the KP 2 primer. For the ITS2, sequencing was done from 5' to 3' only with the 5.8S primer using the bead strand as template. Single stranded DNA was also generated using the method of asymmetric PCR (Sudman and Hafner, 1992) with two amplifications. Round one PCR reactions used MD-1 and

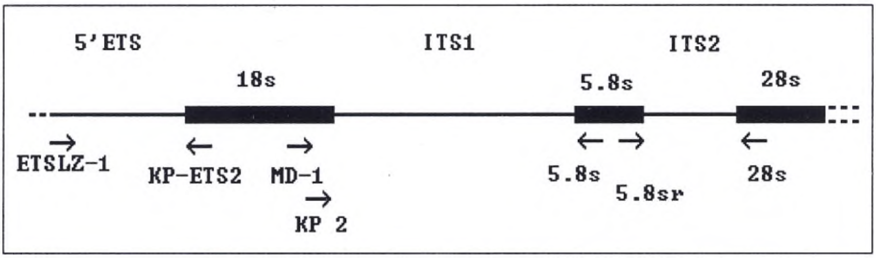

Fig. 1. Primer strategies for PCR and sequencing of the transcribed spacers of the rDNA. Primers were designed from published sequences as cited in the references below. Sequences for primers are as follows:

MD-1 5' CTT GAC TAT CTA GAG GAA GT 3' (Salim and Maden 1981)
KP-2 5' AAA AAG CTT CCG TAG GTG AAC CTG CG 3' (Salim and Maden 1981)
5.8S 5' AGC TTG CTG CGT TCT TCA TCG A 3' (Nazar and Roy 1978)
5.8Sr 5' CTA CGC CTG TCT GAG TGT C 3' (Nazar and Roy 1978)
28S 5' ATA TGC TTA AAT TCA GCG GG 3' (Ware et al. 1983)
KP- ETS2 5' GCA TAT GCT ACT GGC AGG 3' (Salim and Maden 1981)
ETS-LZ1 5' CAC GGT GGA TTA CAG TAC AG 3' (Zhuo et al. 1994)

28S primers (30pm of each primer, 100 ng template, 36 cycles of 94°C for 1 minute 30 seconds, 55°C for 2 minutes, 72°C for 3 minutes, with 72° for 7 minutes extension last cycle). Round two asymmetric PCR used 5 ul of the round one product as template (30 pm MD-1 or 30 pm 5.8s alone for the ITS1 and 30 pm 28s alone for the ITS2, cycled as above). The resulting products were washed 5 times in Millipore 30,000 NMWL filters 400ul capacity (Millipore, Burlington, MA) with 300 ul sterile distilled water, spun at 1200 x g after each addition, and reduced to <50 ul volume at the last spin. Each sequencing reaction used 7 ul of single stranded product. For ITS1, the strand produced with the MD-1 primer was sequenced with the 5.8s primer and the strand produced by the 28s or 5.8s primer was sequenced with the KP2 primer. For the ITS2 the strand produced by the 28s primer was sequenced with the 5.8sr primer.

The 300bp segment of the 5'ETS was amplified using primers designed for lake trout (Zhuo et al. 1994) and cloned into M13 for sequencing. Products obtained using the ETS-LZ1 and KP-ETS2 primers (30 pm each primer, 10 ng template, 94°C for 1 minute 30 seconds, 55°C for 2 minutes, 72°C for 3 minutes, 36 cycles with 72°C for 7 minutes extension last cycle) were electrophoresed in 3% low melt agarose (Fisher, Pittsburgh, PA) at 50 V, excised and purified using Magic PCR prep columns (Promega, Madison, WI) or Gene Clean (Bio 101, La Jolla, CA). Two different methods were used in cloning of PCR products: blunt end ligation into EcoRV cut Phagescript SK (Stratagene, La Jolla, CA) or TA ligation into T tailed modified M13 phage. Six to 12 clones were sequenced completely. Phagescript SK was sequenced with M13 universal primer (Stratagene, La Jolla, CA). The T tailed mp18 was sequenced with the -40 primer from U. S. Biochemical.

Amplification and sequencing of the ND3 gene

For the ND3 gene of the mitochondrial DNA, the primers used were:

(forward: 5'TTACAATCGCTGACGGCG 3')
(revers: 5'GGTGCGGTGAAACGCGAGTC 3').

The forward and reverse primers were designed from the cytochrome oxidase III gene and the ND4L gene respectively using published Pacific salmon sequences for these genes (Thomas and Beckenbach 1989). The 100ul reactions contained 10pmol of each primer and 1000ng genomic DNA. The parameters were 35 cycles of 94°C for 1 minute, 55°C for 2 minutes, 72°C for 3 minutes, with a final extension at 72°C for 7 minutes. The sequencing primer (5' AATAAAGGCTGAGGTAAAGC 3') was also designed from the ND4L gene sequence from Pacific salmon (Thomas and Beckenback 1989). A biotinylated forward primer was used in the amplification and magnetic beads (Dynal Inc., Great Neck, N.Y.) were used to separate the strands for sequencing according to the manufacturer's instructions.

Sequence analysis

The DNA sequences were aligned by eye to yield a minimal number of evolutionary changes, with gaps inserted to maintain the alignment. For the cladistic analysis, gaps were considered to be missing data if they occurred in runs of the same base pair (e.g. CCCC). Informative sites involving base changes were identified as those for which at least two different base pairs were present at a given site and each type of base occurred in at least two different species. Cladograms for the rDNA sequence data were constructed with *Salvelinus namaycush* as the outgroup for the *S. alpinus-S. malma* complex and cladograms for the ND3 data were constructed using *Hucho perryi* as an outgroup. The cladistic analyses were done using the maximum parsimony method with the branch and bound algorithm of the PAUP computer program (Swofford 1993). The data were bootstrapped 500 times retaining branches occurring at least 50% of the time.

Pairwise sequence divergences were calculated directly from the aligned sequences by dividing the number of differences by the total

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                                                                               60
S.namaycush      GGTTGCCAGC CGCCGGCATG GGGCTGTGCT CCGAAAACCA AACTCTGCTG TGGGTTGGGT
S.m.lordi        .......... .......... .......... .......... ..G....... ....G.....
S.m.malma        .......... .......... .......... .......... ..G....... ....G.....
S.albus          .......... .......... .......... .......... ..G....... ....G.....
S.a.taranetzi    .......... .......... .......... .......... ..G....... ....G.....
S.a.erythrinus   .......... .......... .......... .......... ..G....... ....G.....
S.a.alpinus      .......... .......... .......... .......... ..G....... ....G.....
                                                                              120
S.namaycush      TGGGTAGGGT ATGGGGGCTC ACGCCCCCCG CCTCGCCCAT CTCTCGGCGC AGGTGTCCTC
S.m.lordi        A.....---- -......... .......--. .......... .......... G.........
S.m.malma        A.....---- -......... .......... ......T... .......... G.........
S.albus          A.....---- -......... .......... ......T... .......... G.........
S.a.taranetzi    A.....---- -......... .......... .......... .......... G.........
S.a.erythrinus   A.....---- -......... .......--. .......... .......... G.........
S.a.alpinus      A.....---- -......... .......... .......... .......... G.........
                                                                              180
S.namaycush      GGTCTTAGCC CGGTTCCCTG CTATTCCTTT TGCCT--GGG TTGCGCCC-A CCGGCTCCAT
S.m.lordi        .......... ........C. .........A A....AA... ....A...G. ..........
S.m.malma        .......... ........C. .......... .....AA... ....A...G. ..........
S.albus          .......... ........C. .......... .....AA... ....A...G. ..........
S.a.taranetzi    .......... ........C. .......... .....AA... ....A...G. ..........
S.a.erythrinus   .......... ........C. .......... .....AA... ....A...G. ..........
S.a.alpinus      .......... ........C. .......... .....AA... ....A...G. ..........
                                                                              240
S.namaycush      CCCTTTTCCC CGTTAGCCAC GGCCACATGA CGCACCTATG GGCAGGTGAG TCGGCTGCTA
S.m.lordi        ...C...... .......... .........G .......... .......... .....C....
S.m.malma        .......... .......... .........G .......... .......... .....C....
S.albus          .......... .......... .........G .......... .......... .....C....
S.a.taranetzi    .......... .......... .........G .......... .......... .....C....
S.a.erythrinus   ...C...... .......... .........G .......... .......... .....C....
S.a.alpinus      .......... .......... .........G .......... .......... .....C....
                                                                              300
S.namaycush      CCGAAGGGGA CTGGGGGTGT CCGGTGAACC GGGACTTCCC GAAATGGTCT CCCATGTTTA
S.m.lordi        ........-. .......... .-........ .......... ....C.TAA. .....T.A..
S.m.malma        .......... .......... .......... .......... ......TAAA .....T.A..
S.albus          .......... .......... .......... .......... ......TAAA .....T.A..
S.a.taranetzi    .......... .......... .......... .......... ....C.TAA. .....T.A..
S.a.erythrinus   ........-. .......... .......... .......... ....C.TAA. .....T.A..
S.a.alpinus      .......... .......... .......... .......... ......TAA. .....T.A..
                                                                              360
S.namaycush      AGCGGCTTGA GTATCGCCCA GTATCCTCGC TCGGCACCGG GAACCCAGTC AACCGCTCTG
S.m.lordi        .......... .......... .......... .......... .......... ..........
S.m.malma        .......... .......... .......... .......... .......... ..........
S.albus          .......... .......... .......... .......... .......... ..........
S.a.taranetzi    .......... .......... .......... .......... .......... ..........
S.a.erythrinus   ..T....... .......... .......... .......... .......... ..........
S.a.alpinus      .......... .......... .......... .......... .......... ..........
                                                                              420
S.namaycush      CGCCGCGGCG CAGGCGGGGG TTTAATGTCT CCTC-AGCCC TCCCGGAGCT TCGGCGACGG
S.m.lordi        ....C....C G......... .......... ..C.C..... ..A...C... ..........
S.m.malma        ....C..... .......... .......... ..C.C..... ..A...C... ..........
S.albus          ....C..... .......... .......... ..C.C..... ..A...C... ..........
S.a.taranetzi    ....C..... .......... .......... ..C.C..... ..A...C... ..........
S.a.erythrinus   ....C....C G......... .......... ..C.C..... ..A...C... ..........
S.a.alpinus      ....C..... .......... .......... ..C.C..... ..A...C... ..........
                                                                              480
S.namaycush      CGGCGGCGGG TGAGCACCCG GAGGCCTCCAT CCTGAAACAA GACTTGTCTT TGAACTATGG
S.m.lordi        .......... .......... ......C...A .......... C......... -.........
S.m.malma        .......... .......... ......C...A .AAC..C... C......... -.........
S.albus          .......... .......... ......C...A .AAC..C... C......... -.........
S.a.taranetzi    .......... .......... ......C...A .......... C......... -.........
S.a.erythrinus   .......... .......... ......C...A .......... C......... -.........
S.a.alpinus      .......... .......... ......C...A .......... C......... -.........
                                                                              540
S.namaycush      GCCTCTCGCT CGGGCGAAGT GCGGGCGGGG GAAAGGAGGG CAACCT-CCC AACTCCGTCT
S.m.lordi        .......A.. .T........ .......... .-........ ......C... ..........
S.m.malma        .......A.. .T........ .......... .......... ......C... ..........
S.albus          .......A.. .T........ .......... .......... ......C... ..........
S.a.taranetzi    .......A.. .T........ .......... .......... ......C... ..........
S.a.erythrinus   .......A.. .T........ .......... .......... ......C... ..........
S.a.alpinus      .......A.. .T........ .......... .......... ......C... ..........
                                                    576
S.namaycush      AGCAACTAGC CTCTGTGT-G AAAAAA---- -GAGTA
S.m.lordi        .......... ........AC ..C...AAAA A.....
S.m.malma        .......... ........AC ......AA.. ......
S.albus          .......... ........AC ......AA.. ......
S.a.taranetzi    .......... ........AC ......AAA. ......
S.a.erythrinus   .......... ........AC ..C...AAA. ......
S.a.alpinus      .......... ........AC ......AAA. ......
```

Fig. 2. Aligned Sequences of the ITS1 from subspecies of Charrs. Dots (.) are same base, dashes (-) are gaps.

Table 1. Nucleotide substitutions per site among charrs based on ribosomal ITS1 sequences.

		1	2	3	4	5	6	7
1	*S. namaycush*	.000						
2	*S. m. malma*	.075	.000					
3	*S. m. lordi*	.087	.038	.000				
4	*S. a. alpinus*	.069	.012	.025	.000			
5	*S. a. taranetzi*	.066	.014	.023	.018	.000		
6	*S. a. erythrinus*	.083	.028	.088	.016	.014	.000	
7	*S. albus*	.078	.035	.040	.016	.018	.032	.000

number of sites. Genetic distances were calculated using MEGA by the Jukes Cantor method for rDNA because transition/transversion ratios were close to 1. For the ND3 data in which transitions greatly exceeded transversions, the Kimura two parameter method (1980) was used. Trees were constructed from the genetic distances with the neighbor joining method (Saitou and Nei 1987) of the MEGA (Kumar et al. 1993) computer program.

Results

Internal transcribed spacers

Sequences of the ITS1 and ITS2 from the same members of the *S. alpinus-S. malma* complex were sequenced directly and aligned with those of *S. namaycush* (see Fig. 2) and the distances between taxa based on the ITS1 are shown in Table 1. The aligned sequences of the ITS2 were identical except for a couple of 1 bp gaps, so we concluded there was no useful phylogenetic information in this region. The neighbor joining tree obtained using the ITS1 data (Fig. 3) clusters the taxa into 4 groups: the Alaskan *S. alpinus erythrinus* and *S. malma lordi*; Alaskan *S. taranetzi*; Norwegian *S. a. alpinus*; and *S. malma malma* and *S. albus*. There were 23 variable sites in the aligned ITS1 sequences of the *alpinus/malma* species including 8 gaps. When the gaps are excluded, there were 6 informative sites, and 5 of them were synapomorphies between *S. albus* and *S. m. malma* and the other one was a synapomorphy between *S. alpinus erythrinus* from the high Arctic and *S. malma lordi* from southern Alaska. The tree produced by PAUP counting gaps as missing data is shown in Fig. 4, and it is similar to the neighbor joining tree.

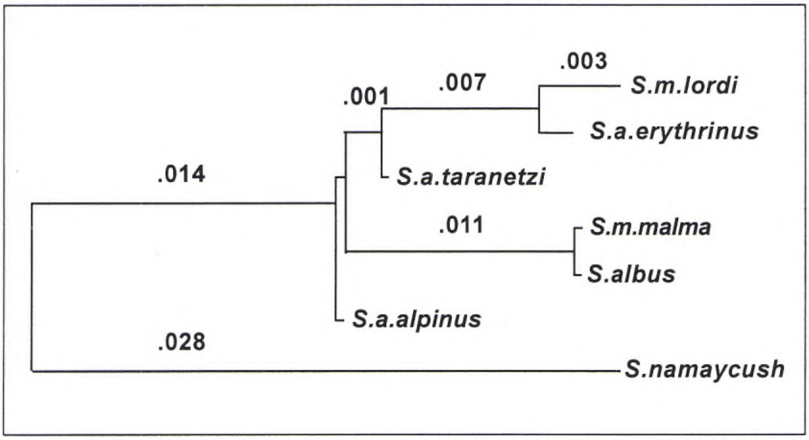

Fig. 3. Neighbor-joining tree based on the 575 bp of the ITS1 gene of the ribosomal DNA in charrs. Tree was produced using the MEGA (Nei,1993) program and the numbers are Jukes-Cantor genetic distances which are cumulative.

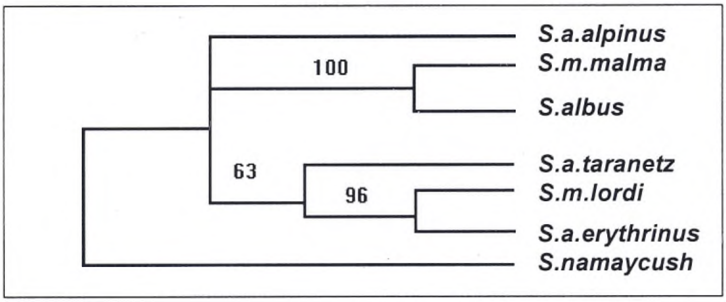

Fig. 4. Maximum parsimony consensus tree based on the 575 bp of the ITS1 gene of the ribosomal DNA in charrs. Tree was produced using branch and bound aligorithm of the PAUP (Swofford, 1993) program and the numbers are bootstrap values.

The 5' external transcribed spacer of the rDNA

A 300 bp portion of the 5'external transcribed spacer of the rDNA adjacent to the 18S coding region was amplified in one individual selected at random from five members of the *S. alpinus-S. malma* complex. The PCR products were cloned into M13 and 6-12 clones sequenced from each individual. These sequences were aligned with those of *S. namaycush*. The sequence of the high Arctic *S. alpinus erythrinus* aligned with *S. namaycush* is shown in Fig. 5. It can be seen that *S. namaycush* has a 198 bp insertion bounded by two 42bp direct repeats in the middle of the sequence. One repeat, but not the insertion, is present in the species of the *S. alpinus-S. malma* complex. In addition to this large insertion, there were 23 variable sites in the aligned sequence between *S. namaycush* and the other charrs. There was one fixed bp difference between the European *S. a. alpinus* and the other members of the *S. alpinus-S. malma* complex. Among the 23 nucleotide differences between *S. namaycush* and the other charrs, there were 6 sites which showed intraindividual variability in three of the charr species. All of the differences were TC transitions and there were a total of 7 haplotypes (see Table 2) including the haplotype found in *S. a. alpinus*. The frequency of these haplotypes found in 6-12 clones sequenced per individual is shown in Table 3. There was no intraindividual variation in the Norwegian *S. a. alpinus*, the southern *S. malma lordi* and variation was found in only 1 out of 6 clones in *S. a. erythrinus*. The individuals representing *S. albus*, *S. malma malma*, and *S. a. taranetzi* all share several haplotypes.

The ND3 gene of the mitochondrial DNA

The 351 bp mitochondrial ND3 gene was amplified and sequenced in nine species or subspecies of *Salvelinus* and the outgroup from the closely related genus, *Hucho perryi*. The sequences are shown in Fig. 6, and the observed nucleotide differences between the taxa are shown in Table 4. Almost all of the nucleotide differences within the *Salvelinus* species were transitions, but there were seven transversion mutations between *Hucho perryi* and the other species. Within *Salvelinus* the number of nucleotide differences ranged from 20 between the Norwegian *S. alpinus* and the North American *S. fontinalis*, to 0 between *S. alpinus taranetzi* and the northern *S. malma malma*, which are both from Alaska. There was only one nucleotide difference between each of these two species and the southern *S. malma lordi* which is also from Alaska. The neighbor joining tree (see Fig. 7) clusters these three members of the *S. alpinus-S. malma* complex from Alaska together, and this group is distinct from *S. alpinus erthyrinus* from Northwest Territories and *S. alpinus alpinus* from Norway. *S. confluentus* was a sister group to *S. alpinus erthyrinus*. Because of the small number of informative sites, the cladogram produced by PAUP produced 6 equally likely trees, with the 50% consensus tree shown in Fig. 8.

```
                                                       35 37           50
                   1                            *       ! !             !
S.a.erythrinus     CACGGTGGAT TACAGTACAG GG--CCCCCT C--TTGCTGA GG-TCAGG-T
S. namaycush       CACGGTGGAT TACAGTACAG GGCTCCCTCT CGCTCGCTGA GGATC-GGCA
                   51             65                      87          100
                   !              !                       !
S.a.erythrinus     CTCTGGACAA TCAATACGCT TGGCGCTCAG GTCCAATATC TAAGTTGATG
S. namaycush       TTCTGGACAA -CAATACGCT TGGCGCTCAG GTC-AACATC TAAGTTGATG
                                                                      150
S.a.erythrinus     GCATTCCGAA TAAGCCCTCC GGCTAGACGA GCG------- ----------
S. namaycush       GCATTCCGAA TAAGCCCTCC GGCCAGACGA GCGGCGACCT CGCGGATGCG
                                                                      200
S.a.erythrinus     ---------- ---------- ---------- ---------- ----------
S. namaycush       TGCATTTTCC AGAACCTAAA CCCATTCGAC CGTCAGGCCG TCTAGGGGGA
                                                                      250
S.a.erythrinus     ---------- ---------- ---------- ---------- ----------
S. namaycush       CCAGCTCTAG ATTAGCCCCG AATTAGATGC ACCTGGGAGG GCACTGGCGG
                                                                      300
S.a.erythrinus     ---------- ----------- --------- ---------- ----------
S. namaycush       CCGGCATACT GTCTGGTGTT CAGCCGGAAT GTTCCTCCCA CCCCGTGGCA
                                                                      350
S.a.erythrinus     ---------- ---------- ---------- ---------- ----------
S. namaycush       CTGACAACTA TCGGGAGAGC CCCCATGGTT CAGTTGATGG CCTTCCAATA
                                                                      400
S.a.erythrinus     ---------- ---------- ---------- ---------- -ACCTCTCGA
S. namaycush       AGCTCCGGCT AGACGAGCGC ATAGCTCCGG CTAGACAAGC GACCTCTCGA
                                                                      450
S.a.erythrinus     GCGGTGCCCC GG-ACCTGTG GCACATCCGG CCATGGGCAG TTCAGGGCGT
S. namaycush       GC--TGCCCC GGCACCTGTG GCACATCCGG CCATGGGCAG TTCAGGGCGT
                                                                      500
S.a.erythrinus     CCCGCTGGGC GCACGGTGGA TTGCACCAGG TCCTCCTCCC TGACGGGATA
S. namaycush       CCCGCTGGGC GCACGGTGGA TTGCACCAGG TCCTCCTCC- TGACGGGATA
                                                     *                550
S.a.erythrinus     GGACTGGTTC CTGGTCGTTC TTTGCTTAGT GCGCCCAGGT ACAACATCTA
S. namaycush       GGACTGGTTC CTGGTCGTTC TTTGCTTAGT GTGCCCAGGT ACAACATCTA
                   *              565
S.a.erythrinus     AGTTGTTGAG TGGCT
S. namaycush       CGTTGT-GAG TGGCT
```

* base pair differences in Arctic charr and lake trout excluding gaps

! differences which vary intraindividually in some Arctic charr species

Fig. 5. 5' ETS of *Salvelinus alpinus erythrinus* from Northwest Territories aligned with *S. namaycush* from Wisconsin, USA. A 198 bp insertion bordered by long terminal repeats (underlined bases) results in an additional 258 bp in *S. namaycush.*

Table 2. Bases present at the variable sites in the haplotypes found in the 5' ETS of the ribosomal DNA of charrs. Sites numbered as indicated in Fig. 8.

Haplo-type number	Site number 35	37	50	51	65	87
1	C	C	C	T	C	T
2	T	C	C	T	C	T
3	C	C	C	T	C	C
4	T	C	T	C	T	T
5	T	C	T	C	C	T
6	T	C	C	C	T	T
7	T	-	T	C	T	T

Discussion

Systematic Relationships

Behnke suggested that two major subspecies of *S. alpinus* and two subspecies of *S. malma* occur in western North America on the basis of morphological data: *S. a. erythrinus* (called *S. a. stagnalis* by Grewe et al. 1990) from the high Arctic and *S. a. taranetzi* from the Bering-Chukokst Sea which is found in inland lakes in Alaska, *S. m. malma* in northern Alaska and *S. m. lordi* in southern Alaska. Savviatova (1980) on the other hand, has suggested that the split

Table 3. Frequency of Haplotypes in the 5' ETS of Charrs. Numbers in parethesis are the number of clones examined for each individual.

	Haplotype 1	2	3	4	5	6	7
S. a. alpinus (6)							1.0
S. a. erythrinus (6)				.83		.17	
S. a. taranetzi (12)		.17	.08	.67	.08		
S. albus (11)	.55	.36	.09				
S. m. malma (10)	.20	.10	.40		.30		
S. m. lordi (12)		1.0					

Table 4. Nucleotide substitutions per site (above the diagonal) and transition/transversion ratios (below the diagnonal) among the mitochondrial ND3 gene of ten salmonid species.

		1	2	3	4	5	6	7	8	9	10
1	*H. perryi*	__	.111	.094	.123	.117	.105	.108	.108	.111	.108
2	*S. namaycush*	31/8	__	.031	.06	.031	.037	.034	.023	.026	.023
3	*S. fontinalis*	25/8	19/2	__	.057	.048	.057	.054	.048	.051	.048
4	*S. leucomaenis*	36/7	20/1	19/1	__	.046	.046	.043	.043	.046	.043
5	*S. confluentus*	33/8	9/2	16/1	15/1	__	.02	.014	.02	.023	.02
6	*S. a. alpinus*	30/7	12/1	19/1	16/0	6/1	__	.014	.014	.017	.014
7	*S. a. erythrinus*	31/7	11/1	18/1	15/0	4/1	5/0	__	.017	.02	.017
8	*S. a. taranetzi*	31/7	7/1	16/1	15/0	6/1	5/0	6/0	__	.003	.00
9	*S. m. lordi*	32/7	8/1	17/1	16/0	7/1	6/0	7/0	1/0	__	.003
10	*S. m. malma*	31/7	7/1	16/1	15/0	6/1	5/0	6/0	0/0	1/0	__

```
                                                                                 48
S.m.malma          ATG AAC TTG ATT ACA ACA ATC CTT GCT ATT ACC ATC ACA TTG TCC GCA
S.m.lordi          ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.alpinus        ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.leucomaenis      ... ... ... ... ... ... ... ... ... ... ... G.. ... ... ... ...
S.fontinalis       ... ... ... ... ... ... ... ... ... ... ..T ..T ... ... ... ...
S.namaycush        ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
H.perryi           ... ... ..A ... ... ... ... ... ... ... ... ..T ... ... ... ...
                                                                                 96
S.m.malma          GTA CTA GCC ACT ATT TCT TTC TGA TTA CCA CAA ATT TCC CCC GAC GCA
S.m.lordi          ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.alpinus        ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ... ... ... ... ... ... ... ... ..G ... ... ... ... ... ... ...
S.leucomaenis      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.fontinalis       ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.namaycush        ... ... ... ... ... ... ... ... ... ... ... ... ... ..A ... ...
H.perryi           ... ... ... ... ... ... ... ... C.. ... ... ..C .A. ... ... ...
                                                                                144
S.m.malma          GAA AAA CTC TCC CCC TAC GAA TGT GGA TTT GAC CCC CTA GGA TCC GCC
S.m.lordi          ... ... ... ... ... ... ... ... ..G ... ... ... ... ... ... ...
S.a.alpinus        ... ... ... ... ... ... ... ... ... ... ... ... ..G ... ... ...
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ... ... ... ..G ..G ... ...
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ... ... ... ... ... ... ... ... ... ... ... ... ..G ..G ... ...
S.leucomaenis      ... ... ... ... ... ... ... ... ... ..C ... ... ..G ... ... ...
S.fontinalis       ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.namaycush        ... ... ... ... ... ... ... ... ... ... ... ... ... ..G ... ..T
H.perryi           ... ..G ..A ..T ..A ... ..G ..C ... ... ... ... ... ... ... ...
                                                                                192
S.m.malma          CGC CTG CCC TTT TCC CTA CGC TTC TTC CTA ATC GCC ATC CTA TTC CTC
S.m.lordi          ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.alpinus        ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.leucomaenis      ... ... ... ... ... ..G ... ... ... ... ... ... ... ... ..T ...
S.fontinalis       ... ..A ... ... ... ... ... ... ..T ... ... ... ... ... ..T ...
S.namaycush        ... ... ... ... ... ... ... ... ... ... ... ... ... ..G ... ...
H.perryi           ... ..A ..A ... ... T.. ... ... ..T ... ... ... ..T ..G ... ..T
                                                                                240
S.m.malma          CTA TTT GAC CTA GAA ATT GCC CTC CTC CTT CCA TTG CCC TGG GGA GAT
S.m.lordi          ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.alpinus        ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ... ... ... ... ..A ... ...
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ... ... ... ... ... ... ... ... ... ... ... ... ... ..A ... ...
S.leucomaenis      ..G ... ..T ... ... ... ... ... ... ... ... ... ... ..A ..G ...
S.fontinalis       ... ... ..T ... ... ... ... ... ... ... ... ... ... ..A ..G ..C
S.namaycush        ... ... ... ..G ... ... ... ... ... ... ... ... ... ... ... ...
H.perryi           ... ... ..T ..T ... ..C ... ... ... ..C ..C C.. ..T ... ... ..C
                                                                                288
S.m.malma          CAA CTT ACC ACC CCA GCC CTT ACA CTT GCC TGA TCC ACT GCC GTG CTT
S.m.lordi          ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.alpinus        ..G ... ... ... ... ..T ... ... ... ... ... ... ... ... ... ..C
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..C
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ..C ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ..C
S.leucomaenis      ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.fontinalis       ... ..C ... ... ... AA. ... ... ... ... ... ... ... ... ..A ..C
S.namaycush        ... ..C ... ... ... ... T.. ... ... ... ... ... ... ... ... ...
                                                                                336
S.m.malma          GCC CTC CTC ACT CTA GGC CTA ATC TAT GAG TGA ACC CAG GGG GGC TTA
S.m.lordi          ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.a.alpinus        ... ... ... ... ... ... ... ... ... ... ... ... ..A ... ... ...
S.a.erythrinus     ... ... ... ... ... ... ... ... ... ..A ... ... ..A ... ... ...
S.a.taranetzi      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.confluentus      ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
S.leucomaenis      ... ... ... ... ... ... T.. ... ... ... ... ... ..A ..A ... C..
S.fontinalis       ... ... ..T ... ... ... T.. ..T ... ... ... ... ... ... ... ...
S.namaycush        ... ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ...
H.perryi           ... ... ..T ... ... ... T.. ... ... ..A ... ... ..A ..A ... ...
                                      351
S.m.malma          GAA TGA GCC GAA TAG
S.m.lordi          ... ... ... ... ...
S.a.alpinus        ... ... ... ... ...
S.a.erythrinus     ... ... ... ... ...
S.a.taranetzi      ... ... ... ... ...
S.confluentus      ... ... ... ... ...
S.leucomaenis      ... ..G ... ... ...
S.fontinalis       ... ... ... ... ...
S.namaycush        ... ... ... ... ...
H.perryi           ..G ... ... ... ...
```

Fig. 6. Aligned sequences of the ND3 gene of the mitochondrial genome. Identical bases are indicated by (.).

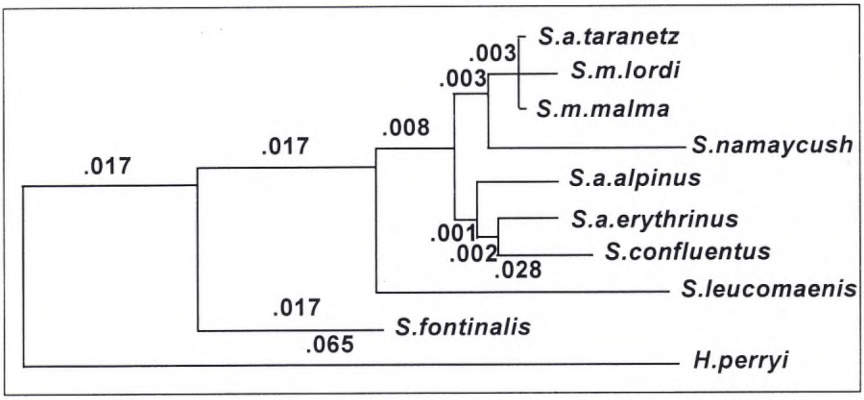

Fig. 7. Neighbor-Joining tree based on 351bp of the ND3 gene of the mitochondrial DNA in charrs. Tree was produced using the MEGA program (Nei, 1993) and numbers are the Kimura genetic distances which are cumulative.

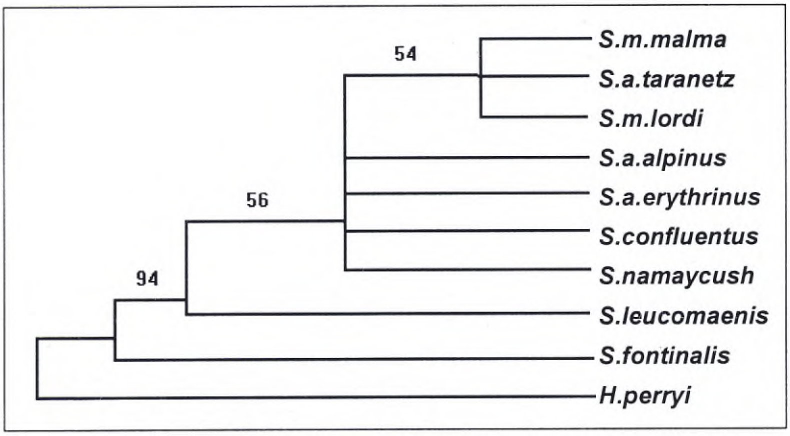

Fig. 8. Maximum parsimony consensus tree based on 351 bp of the ND3 gene of the mitochondrial DNA in charrs. Tree was produced using branch and bound aligorithm of the PAUP (Swofford, 1993) program and the numbers are bootstrap values.

between "alpinoid" like and "malma" like forms has occurred repeatedly throughout the range of the *S. alpinus-S. malma* complex.

Chromosome data supports Behnke's view that *S. malma* is a distinct species. Southern *S. malma* has a different karyotype (2n=82) from *S. alpinus* in North America and Europe (2n=78) (Cavender 1984), and these two species are reproductively isolated wherever they occur sympatrically (reviewed in Behnke 1984). Chromosome studies on Asian forms (Viktorovsky, 1978, Cavender and Kimura, 1989, Frolov and Miller 1991) have shown that the southern "*S. malma*" has a karyotype (2n=82) similar to the southern form in North America, but the northern form has a karyotype (2n=76, 78) more like *S. alpinus* (2n=78). Unfortunately *S. m. malma* from the Noatak River have not been karyotyped. If it has the same karyotype as the Asian northern form, this would support the independent origin of the northern and southern forms of *S. malma*.

Our genetic data support the subspecific status of the two members of *S. alpinus* from western North America, but indicate that there is a very close genetic relationship between the members of the *S. alpinus-S. malma* complex in Alaska. The data from both the mitochondrial ND3 gene and the nuclear 5' external transcribed spacer suggest that the *S. m. malma* from the Noatak River are more closely related to *S. alpinus taranetzi* from south central Alaska than they are to the southern *S. malma*. The ITS1 data suggest that the southern *S. malma* may be more closely related to *S. a. erythrinus* than to the northern *S. malma*, but more sequences of these regions need to be obtained from additional individuals from each subspecies to confirm this. Allozyme data (Crane 1991) supported a close relationship between charr from the north slope of Alaska (presumably *S. m. malma*) and *S. m. lordi* of southern Alaska, but they did not examine charr from the Noatak River. In future work we plan to sequence the ITS1 and 5' ETS of the ribosomal DNA from additional individuals from populations of *S. malma* at intervals along the Alaskan coast in order to clarify these relationships.

Behnke (1980) has suggested that *S. albus* from the Kamchatka River, Russia may be related to *S. confluentus* from North America. It is very similar morphologically to the stone charr, *S. kronicus* from Krontosky Lake which has a karyotype like *S. confluentus* (Victorovsky 1978, reviewed in Cavender and Kimura, 1989, Phillips et al. 1989). A phylogenetic analysis of *S. albus* using 60 craniological characters (Glubokowsky and Cheresnov 1982) placed *S. albus* as a sister species to the Asian northern *S. malma*. Our results support their findings and suggest that the specimen we studied from the Kamchatka River is a member of the *S. alpinus-S. malma* complex and closely related to the northern *S. m. malma* from the Noatak River in Alaska. We were not successful in amplifying the 300bp segment of the 5'ETS in *S. confluentus* with the primers which work for members of the *S. alpinus-S. malma* group, suggesting that it has a different sequence in the region recognized by the primers. The sequence of this portion of the 5' ETS in *S. albus* was very similar to that for *S. a. taranetz* and *S. m. malma*. In addition the sequences of the ITS1 and ITS2 in *S. albus* were very similar to other north Pacific charrs, especially the charr from the Noatak River in Alaska, and differed at many sites from *S. confluentus*. Behnke (1980) has suggested on the basis of morphological data that *S. albus* is closely related to *S. kronicus* which was shown to have a karyotype very similar to *S. confluentus* from North America (Cavender 1984). In the future we hope to design new primers for the 5' ETS which will work in all of the charrs and examine this region in both *S. confluentus* and *S. kronicus* to determine if they are sister species.

Previous mitochondrial data was based on restriction maps (Grewe et al. 1990) and on the sequence of a 289 bp portion of the cytochrome b gene (McVeigh and Davidson 1991). There were very few differences among members of the *S. alpinus-S. malma* complex and *S. confluentus* in either mtDNA data set, but a large genetic distance between these species and *S. leucomaenis* from Japan. Our data on sequences from the ND3 gene are in agreement with the previous results in this respect. A major discrepancy between the data based on nuclear genes and mitochondrial genes is the relationship of *S. confluentus*, which is a sister species to *S. leucomaenis* in the trees based on nuclear genes and karyotype data, but places within the *S. alpinus-S. malma* complex in the trees based on mitochondrial genes (reviewed in Phillips et al. 1994). These results suggest that hybridization with transfer of the maternally inherited mtDNA has occurred between *S. confluentus* and a member of the *S. alpinus-S. malma* occurred in the recent past. Hybrids between *S. malma* and *S. confluentus* have been reported recently from British Columbia (Eric Taylor, U. of British Columbia, personal communication). Another descrepancy between the phylogenies based on nuclear genes and the one obtained using sequences of the mitochondrial ND3 gene is the close relationship between members of the *S. alpinus-S. malma* complex and *S. namacyush* found in the latter case. This is an interesting finding in light of recent reports of hybridization between *S. namaycush* and *S. alpinus* in the Canadian high Arctic (Wilson and Hebert 1993).

Intraindividual and intraspecific variation in rDNA

For interspecific comparisons, it is desirable to use sequences which do not have significant intraspecific variation. In previous phylogenetic studies using the internal transcribed spacers in charrs we found that most intraspecific variation was confined to variability in "runs" of the same base, e.g.: CCCCCC vs. CCCC etc. This type of variation may be due either to polymerase error or the slippage mutations which are relatively frequent, so we have eliminated these sites from our phylogenetic analysis. Because rDNA is present in multiple copies, there is also a possibility that intraindividual variation could occur if the sequence of some of the repeating units differed from others in the same individual. In a previous study in which we sequenced the ITS1 from 12 lake trout of 4 different stocks (Zhuo et al. 1994) we found a limited amount of intraindividual variation. Although all 12 individuals had the same consensus sequence, there was a variable PvuI site present in some individuals of each population. This was detected when the ITS1 was amplified and cut with the PvuI restriction enzyme. In addition there were a couple of sites at which faint secondary bands were seen in several individuals suggesting the possibility that some of the repeating units had a different base pair at that site. In the present study we found evidence for intraindividual variation in the ITS1 in the *S. albus* sequence which had both an A and a C at positions 390 and an A and a G at 493. The C and G nucleotides were chosen for interspecific sequence comparisons (Fig. 2) because they were the darkest bands in both positions. Intraindividual variation in the ITS1 was never seen in any of the *Oncorhynchus* species which have the rDNA at only one chromosomal site. Since all lake trout and some populations of Arctic char have the rDNA at multichromosomal locations, they may be more likely to have intraindividual variation. In the present study we found intraindividual variation in the 5' ETS in *S. albus*, *S. a. taranetzi*, and *S. m. malma*, but not in the the Norwegian *S. a. alpinus* or the southern *S. malma lordi*. Variation was found in only one clone from the high Arctic *S. a. erythrinus*. *S. m. lordi* is known to have the rDNA at only one chromosomal site (2 NORs/cell), and the average number of NORs is 2.3/diploid cell in *S. a. erythrinus* (Phillips et al. 1989).

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Otolith Microchemistry of Charr - Use in Life History Studies

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Abstract

Life history of anadromous Arctic charr *Salvelinus alpinus* (L.) can be studied by tracing growth and migratory patterns of individual fish otoliths. In the present study, wavelength dispersive electron microprobe analyses were used to map strontium-calcium (Sr/Ca) concentration profiles across the surfaces of otoliths from two individual Arctic charr from Labrador, Canada and Spitsbergen, Norway to demonstrate the application of such investigations to define Arctic charr life histories. These analyses, in combination with age and growth data (also derived from otolith structure) document that Sr/Ca concentration ratios are related to external environmental factors and clearly show salinity migrations.

Keywords: Arctic charr, otolith, strontium/calcium, microchemistry, migrations.

Introduction

Arctic charr are an anadromous fish having a large range of phenotypic plasticity allowing them to take advantage of many different niches. Data on Arctic charr movements into oceanic habitats is limited in comparison with other salmonid species (Jensen and Berg 1977, McDowall 1988). The degree of anadromy is variable, migrant and non-migrant forms coexist and individuals can make transitions between life-history forms depending on environmental pressures (Nordeng 1983). Individuals may spend from one to eight years after hatching entirely in freshwater (Dempson and Green 1985) before migrating out to sea during the summer months. Subsequently, individuals may migrate to oceanic waters every year throughout the rest of their lives or skip migrations entirely during the years in which they spawn (Johnson 1980).

Through chemical examination of otoliths, it is possible to document the past environmental conditions encountered by an individual. The monomineralic structure of otoliths makes them favorable to strontium-calcium (Sr/Ca) concentration ratio analyses. The strontium content of hard parts of anadromous fishes has been found to be different in freshwater and seawater life stages (Bagenal et al. 1973, Casselman 1982, Radtke et al. 1988, Kalish 1990, Secor 1992, Reiman et al. 1994) and can be used to reconstruct migratory histories in diadromous fishes.

This study demonstrates the use of chemical analysis of otoliths in the study of migrational patterns in Arctic charr. In particular, age data (derived from otolith structure) are combined with chemical analyses of otoliths to allow determination of the length of oceanic stay, hydrographic conditions encountered, time of return to fresh water, length of freshwater stay and the respective growth in each specific period.

Methods and materials

Provision of samples

Sagittal otoliths of Norwegian Arctic charr were collected by M. A. Svenning in 1990 from a fish with a standard length of 415 mm from Lake Vårflusjøen on the island of Spitsbergen in Svalbard, Norway (79°40' N, 14°20' E, Svenning 1993). Canadian Arctic charr sagittae were collected from a fish with a standard length of 395 mm by J. B. Dempson in 1984 from the Ikarut River, Hebron Fjord, Labrador (58°08'N, 63°06'W, Dempson and Kristofferson 1987).

Preparation of otoliths for analysis

Protocol followed Radtke et al. (1990) with small deviations. The sagittal otoliths were mounted on one inch diameter glass disks using petrological epoxy then ground to reveal a section through the core region. This surface was highly polished using 0.3 and 0.05 µm alumina paste, rinsed with distilled water and ethanol, and carbon coated (250-300 Å thickness).

Analytical conditions

Samples and standards were analyzed by a Cameca Camebax SX-50 fixed crystal X-ray wavelength dispersive electron microprobe using an accelerating voltage of 15 kV, with a 5 µm diameter focused beam current of 10 nA. Strontianite and calcite were used as standards for calibration of strontium and calcium respectively. Characteristic X-rays for strontium and calcium were counted for 30 seconds and background measurements were recorded for 15 seconds at each sample location. X-ray intensities were corrected and ratios of atomic concentration computed using the ZAF method (Reed 1975). Measurement error was typically in the range of 3.5 to 4.5% for strontium and 0.5 or 0.6% for calcium. Strontium-calcium concentration ratios were multiplied by 10^3 for presentation.

Correlation of microprobe analyses to otolith structure

Following elemental analyses, otoliths were prepared for optical examination (Radtke et al. 1985). Marks left by the electron beam were visible under both transmitted and reflected light. Distances were measured along the microprobe scan line from the core to the beginning and end of each opaque and hyaline zone (Radtke et al. 1985). The positions of opaque and hyaline zones were then correlated to elemental analysis points. Relative ages at particular elemental analysis points could then be assigned.

Results

The concentration ratios of strontium and calcium varied across the otolith with distance from the core. When the distances and widths of the respective charr annuli are overlaid on the Sr/Ca profiles, a prodigious insight into each individual becomes evident (Figs. 1 and 2).

The beginning portion of the Sr/Ca profiles associated with the first years of non-migratory freshwater existence showed little or no strontium. The Spitsbergen charr otolith contained a small peak (Sr/Ca <1.0) at the very core after which the Sr/Ca ratio remained at 0.0 through the region of the otolith corresponding to the first four annuli (Fig. 1). The Labrador sample also showed a small initial peak with a Sr/Ca ratio of 1.4 followed by a region corresponding to the first three annuli (Fig. 2) where the Sr/Ca ratio remained very low, varying between 0.0 and 1.0. Strontium-calcium ratios for the Labrador charr during the freshwater residence period were consistently higher than the corresponding values from the Spitsbergen charr and are likely due to regional differences in water chemistry between rivers in Labrador and Spitsbergen.

Oceanic migration appeared to have begun after 5 years for the Spitsbergen charr and after 4 years for the Labrador charr. At these points there was an abrupt increase in the Sr/Ca ratio from levels near zero to levels near three or four. The Sr/Ca profile for the Spitsbergen charr showed three subsequent strontium peaks indicating that the fish made a total of four sea migrations, that of the Labrador sample shows four subsequent strontium peaks indicating that the fish made a total of five sea migrations. An obvious correlation appears in the later years of each fish's life between high Sr/Ca ratios and the position of opaque zones representing periods of rapid growth during the summer.

Discussion

As strontium is found in freshwater at relatively low levels very little is available for incorporation into the otolith structure. The non-migratory period is reflected in low (<1.0) Sr/Ca ra-

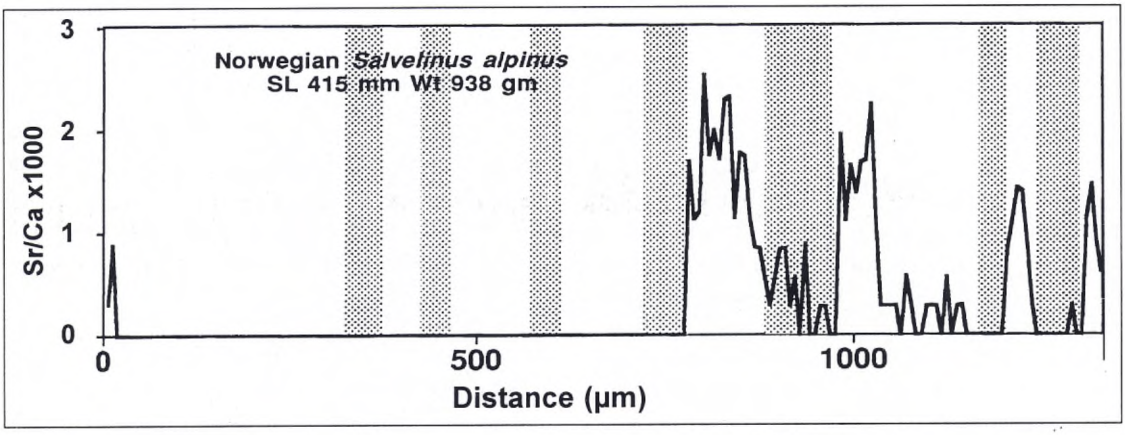

Fig. 1. Composite microprobe profile of Sr/Ca concentration ratios and opaque and hyaline areas of the Norwegian adult Arctic charr, *Salvelinus alpinus*, from Lake Vårflusjøen. Fish was estimated by annuli enumeration to be 8 years of age and higher ratios indicate this fish migrated to oceanic waters after approximately 5 years of growth. Electron microprobe data revealed the cyclic nature of Sr/Ca ratios as associated with age.

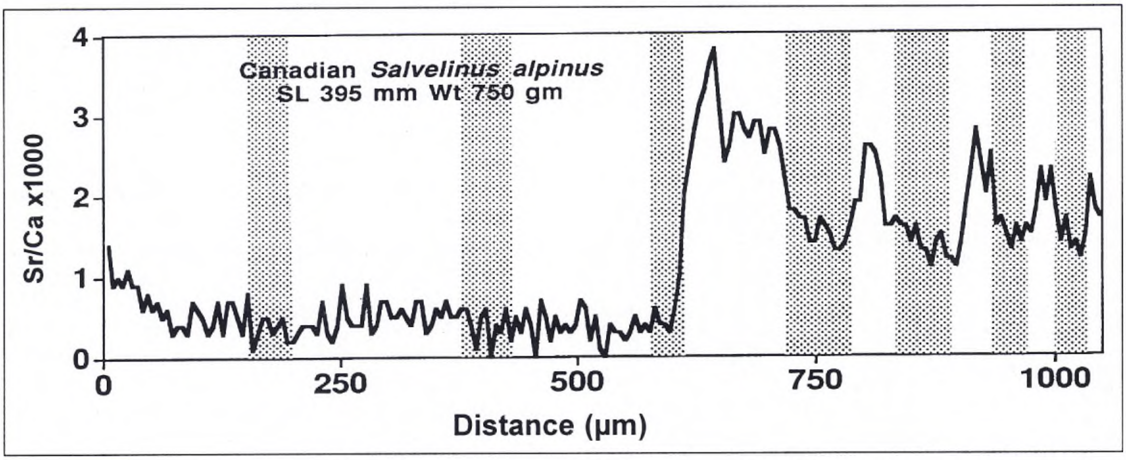

Fig. 2. Composite microprobe profile of Sr/Ca concentration ratios and opaque and hyaline areas of the Canadian adult Arctic charr, *Salvelinus alpinus*, from Labrador. Fish was estimated by annuli enumeration to be 8 years of age and higher ratios indicate this fish migrated to oceanic waters after approximately 4 years of growth.

tios in both the Spitsbergen and Labrador charr examined in this preliminary study. Forays into the ocean, with its much higher concentration of strontium, result in a higher incorporation of strontium into the otolith structure. The first sea migration results in an abrupt increase in Sr/Ca concentration ratios (Figs. 1 and 2). The first migration occurred in the fourth year for the Labrador charr and the fifth year for the Spitsbergen charr. None of the fish examined missed any annual oceanic migration subsequent to the first.

The initial strontium peak was higher than peaks associated with migrations in subsequent years. The reasons are not clear, but one possible explanation is that these regions correspond to the period of osmoregulatory stress during the first sea run when the fish is developing a tolerance for higher salinities. In subsequent years the fish would physiologically be better adapted to changes in salinity, and strontium would be incorporated into its otoliths at lower levels during summer growth. Spawning is another possible drain on both strontium and calcium, but there may be other factors responsible (Radtke and Shafer 1992).

The length at which first sea migrations occur may be estimated by relating the position of the first strontium peak to a particular annual ring or opaque zone. Using a liberal assumption of a linear relationship between otolith growth and fish length one can estimate length at the point when a fish first enters sea-water. Interestingly I found that both charr investigated first ventured out to sea at a length of 24.5 cm.

Another result implied by this study is that strontium incorporated in the tissues during sea-water migrations of adult female Arctic charr can be passed on to their progeny through egg material. This 'residual' strontium can be incorporated into the otoliths of offspring resulting in high Sr/Ca ratios (Kalish, 1990). This technique may be used for determining the identity (migratory or resident) of the previous generation and ultimately shows the possible heritability of migratory behavior. Both charr analyzed here had elevated Sr/Ca concentrations in their otolith core areas that may reflect this type of inherited strontium signal from a migratory maternal origin.

We emphasize that this research is in need of further scrutiny and development, but we feel that with continued progress this technique holds great promise for providing answers to many important questions in charr biology.

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Evidence for Two Morphotypes of Arctic Char (*Salvelinus alpinus* (L.)) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada[1]

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Abstract

Lake Hazen (82°N, 70°W) on Ellesmere Island is the largest, most northern polar lake in the world. Arctic char (*Salvelinus alpinus*), the only fish present in the area, exhibits phenotypic diversity within Lake Hazen. Biological evidence, in particular length-age relationships, suggests the presence of two distinct growth forms for both sexes. Morphological variation confirms that two morphotypes of char are present in Lake Hazen. One morphotype is slower growing, attains a smaller size, is characterized by dark coloration, and exhibits elongate pelvic and anal fin rays as well as other less obvious morphological differences. The other morphotype is faster growing, attains a larger size, is characterized by lighter coloration, and exhibits normal fins. Previous workers have made the assumption that the faster-growing form is anadromous and the slower-growing form remains in the lake. However, direct evidence to support this assumption is lacking. An alternative hypothesis is that the morphological and life history variation may be associated with segregation and specialization into different habitats within the lake, similar to situations observed elsewhere for Arctic char.

Keywords: Meristic, morphometric, variation, high Arctic, body size.

Introduction

Arctic char (*Salvelinus alpinus*) exhibits a wide range of phenotypic diversity within water bodies throughout its geographic range. Generally, many populations inhabiting areas with access to the sea exhibit a large anadromous form and a small form that passes its life history in freshwater (Johnson 1980). Both forms mature sexually and both may participate in the same spawning events. Such formation of small and large pairs of morphotypes within a population is pervasive throughout the Salmonidae (Gross 1984).

In situations of large and diverse lacustrine environments in which anadromy is unlikely or impossible, Arctic char populations likewise have differentiated into several forms. Although small and large-size pairs are typical, there may be as many as four forms specialized for different habitats within the lake (e.g., Thingvallavatn, Iceland) (Jonsson et al. 1988). Although not widely studied, it appears that in addition to differences in body size, these forms usually exhibit morphological differences that include variation in color pattern, size and shape of body parts, as well as specializations for the particu-

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lar life style followed and habitat occupied (Sandlund et al. 1992, Hindar and Jonsson 1993).

Despite the general acknowledgement of great taxonomic diversity within the Arctic char species complex (e.g., Johnson 1980), only a few examples of such variation have been sufficiently well-studied to enable a general understanding of the causes and the implications of such diversity. Furthermore, most such studies have been conducted on European populations (e.g., Norway, Klemetsen and Grotnes 1980, Jonsson and Hindar 1982; Svalbard, Hammar 1985, Svenning 1993; Iceland, Jonsson et al. 1988; Scotland, Walker et al. 1988). In North America investigations to date have typically focused upon comparison of diversity of char found in separate water bodies rather than the diversity present within particular systems. For some systems migratory anadromous and non-migratory forms have been documented (e.g., Johnson 1980). In other situations, bimodality in size has been noted within the migratory, anadromous fish (Johnson 1980 and references therein) or within non-migratory land-locked populations (Parker and Johnson 1991). However, for these situations in particular, and for North America generally, there have been no comprehensive investigations of the diversity of Arctic char within particular water bodies despite the general knowledge that such diversity regularly is present. Also, where preliminary investigations have been conducted (e.g., Nauyuk Lake, Canada) (Johnson 1980), they have generally focused upon populations near to the southern portion of the distribution of the species complex. Such studies also have only superficially investigated the morphological or genetic diversity present. Thus, this present study is significant in that it investigates in depth the morphological diversity of Arctic char within a particular water body at the northern extreme of the geographical distribution of the species - a situation of relative physical and biological simplicity.

Lake Hazen, at the northern end of Ellesmere Island in the Canadian high Arctic is the largest body of freshwater in the world that is entirely north of the Arctic Circle (Johnson 1990). The only fish species present is Arctic char. As a result of scientific investigations in 1958 (International Geophysical Year), two growth forms of char were noted in the lake (Hunter 1960). It was assumed that the larger of the two was anadromous (migratory) and the smaller was a lake resident (non-migratory). A second expedition to Lake Hazen occurred in 1981. The length and age frequencies from the 1958 and 1981 samples have been summarized by Johnson (1983). For both sexes three size groups were identified: 1) very small fish (mean length 30 mm) comprised of 0+ and 1+ age classes, 2) an intermediate-sized group (mean length 330-340 mm) ranging in age from 9-26 years (mean age in 1958 for fish under 400 mm was 16.3 years; for 1981, 17.9 years), and 3) a group of larger fish of various sizes up to 770 mm ranging in age from 11-32 years (mean age in 1958 for fish over 400 mm was 19.8 years; for 1981, 20.8 years). Three possible explanations for these size distributions were noted (Johnson 1983): 1) large fish present in summer catches from the lake represent anadromous individuals that did not go to sea that year, 2) large fish may represent non-spawning individuals that had already returned from the sea, and 3) large fish have become cannibalistic thus do not necessarily go to sea. That is, the underlying assumption once again was that the larger growth form likely represented some variation of an anadromous, migratory life history type and the smaller form represented a non-anadromous type. The very small fish were presumed to represent immature components of both forms.

Despite the work noted above for the char of Lake Hazen, no detailed description has occurred of the forms nor investigation of their interrelationships, possible origins, or implications to the evolutionary history and potential of this species complex. The present study is thus a preliminary step to a comprehensive series of ecological and evolutionary investigations of these char. The specific aims of this contribution are to: 1) verify the previous findings of two growth forms, 2) fully investigate the morphological (morphometric and meristic) variation present, and 3) develop criteria useful for the identification of individuals to the respective form. This study formulates an hypothesis of morphological distinctness and origin of the forms that will be tested in future work examining different character systems.

Materials and Methods

Study area and collection information

Lake Hazen (81°50'N, 70°25'W) is a 542 square kilometer, deep (to 280 m) lake located entirely north of the Arctic Circle, about 1000 kilometers from the North Pole (Fig. 1). Glacial meltwater from the Grant Land Ice Cap is the major source of water input and the area is extremely dry with about 25 mm of annual precipitation. Despite this very northern situation, a mountain range to the north of the lake acts as a large solar receiver making the area a thermal oasis in a true polar desert (Johnson 1990). The lake remains ice covered in all but the warmest years and due to its great depth has a relatively stable water temperature near 3°C. The Ruggles River, the only outflow to the sea, remains partially open all year. However, in all seasons except the short summer this water freezes to build large masses of overflow ice throughout the lower length of the river and on the sea ice of Chandler Fjord (Greely 1886).

Biologically the lake is very simple. There are no macrophytes and phytoplankton productivity is just within the lower detection limits of the C^{14} method. For July to August, 1958 a mean of 39 mg $C \cdot m^{-3} \cdot day^{-1}$ was recorded (Johnson 1990). Zooplankton productivity is also low (McLaren 1964). Thirty-four species of benthic invertebrates are known (Oliver 1963) and the only fish species is Arctic char.

Arctic char were collected in June, 1992 at four sites within Lake Hazen proper (Fig. 1): 1) near the inflow of Blister Creek (N=54), 2) Henrietta Nesmith Glacier (N=53), 3) near the inflow of Mesa Creek (N=48), and 4) at the outflow to Ruggles River (N=52). Six additional fish were obtained at two other sites (Gilman River and Hazen Camp). All fish were captured by either multi-mesh nylon multifilament gill nets set under the ice or angling through the ice with lures. Additional reference is made to samples collected in 1958 and 1981 as described by Johnson (1983).

Biological data

Fork length (FRL, nearest mm, Fig. 2A) and weight (nearest g) were taken in the field from fresh fish. Remaining biological variables such as sex, degree of maturity, and gonad weight were taken from frozen fish returned to Winni-

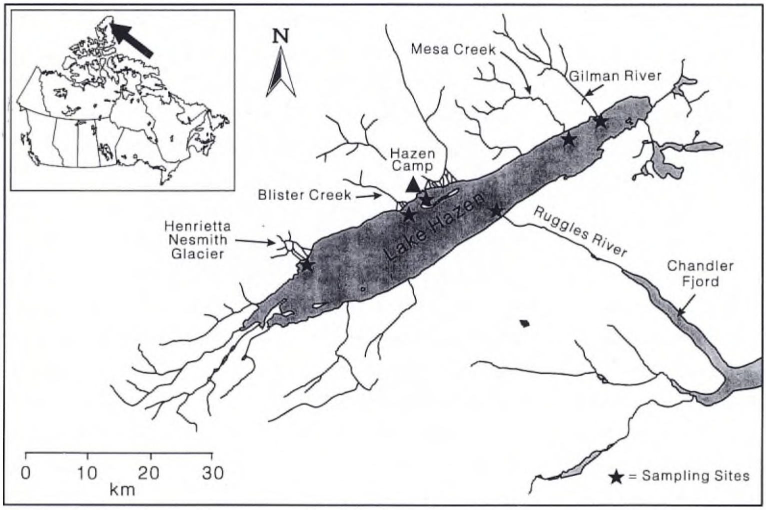

Fig. 1. Map of Lake Hazen showing the sampling sites.

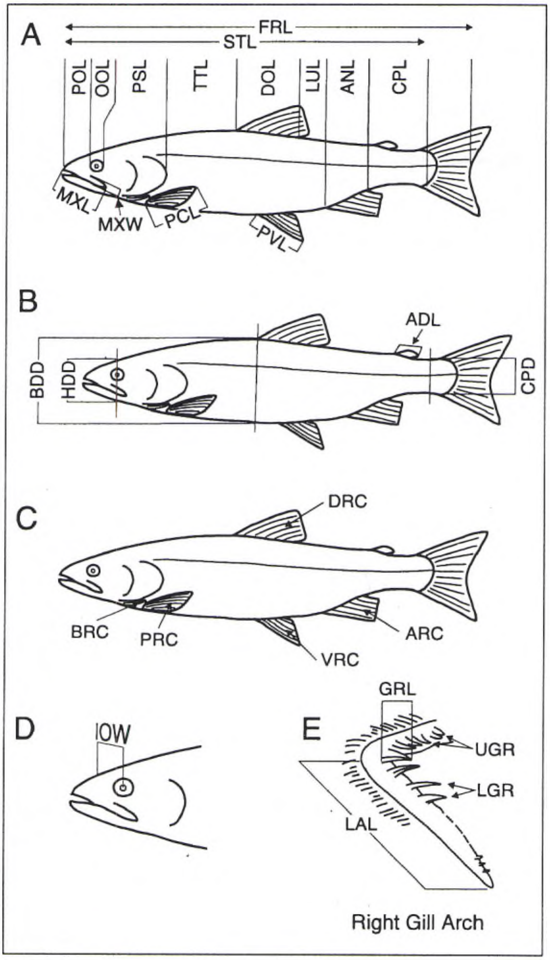

Fig. 2. The morphological variables recorded for each fish. See the text for description of mensuration and explanation of acronyms.

peg and processed for morphological data (see below). Otoliths were removed from the thawed fish during routine processing. Ages were determined from sagittal otolith cross sections by modifying the techniques described by Barber and McFarlane (1987) and Kristoffersen and Klemetsen (1991). One otolith from each fish was cut with surgical bone-cutting forceps through the nucleus, along the dorso-ventral axis. The exposed surfaces were ground and then polished with metallurgical lapping films, 30 and 0.3 µm grit, respectively. Each half was burned in an alcohol flame. The burned halves were supported on plasticine on microscope slides. Under a dissecting microscope the burned cross sectional surfaces were coated with vegetable oil and examined with reflected light. Ages were determined using criteria described by Nordeng (1961) and Chilton and Beamish (1982).

For this study, in order to confirm the presence of two growth forms, ages were determined for only 106 fish (about one-half of the total 1992 sample). The remaining half of the sample was used for a study investigating parasites of the forms. Ages for these fish will be determined at a later date and future studies will address age, growth and other biological characteristics of the entire 1992 sample in comparison to those of previous years (1958 and 1981).

Morphological data

Three types of morphological data were collected from all fish: 1) external qualitative data, 2) meristic counts, and 3) morphometric measurements. The qualitative criteria were used to classify fish to form for further analysis and consisted of general body size, general body form, dorsal and ventral non-spawning body color, paired fin color, relative length of the anterior rays of pelvic and anal fins, presence of parr marks, and sexual maturity based upon visual examination of the gonads. Using these criteria, four categories of fish could be designated: Juveniles, Small, Large, and Unknowns (see Results for complete descriptions). These categories were used both a priorily to designate groups for some statistical analyses or a posteriorily to observe the presence of groups in other analyses (see below).

Meristic counts (N=8) (Fig. 2C and E) consisted of principal ray counts for pectoral (PRC), pelvic (VRC), dorsal (DRC) and anal (ARC) fins. Counts of branchiostegal rays (BRC), upper (UGR) and lower gill rakers (LGR) (middle raker included in lower count), and pyloric caecae (PYL) were also made.

Morphometric measurements (N=19) (Fig. 2A, B, D, and E) using the following procedures were made to 0.1 mm with digital calipers. The body was divided into areas defined by particular features and the size of the part was measured. Measurements made parallel to the longitudinal body axis were: 1) preorbital length (POL) - the distance from the tip of the snout to the anterior margin of the orbit, 2) orbital length (OOL) - the distance from the anterior to the posterior fleshy margin of the orbit, 3) postorbital length (PSL) - the distance from the posterior margin of the orbit to posterior bony margin of the operculum, 4) trunk length (TTL) - the distance from the posterior margin of the operculum to the origin of the dorsal fin, 5) dorsal length (DOL) - the distance from the origin to insertion of the dorsal fin, 6) lumbar length (LUL) - the distance from the insertion of the dorsal fin to the origin of the anal fin, 7) anal length (ANL) - the distance from the origin to insertion of the anal fin, and 8) caudal peduncle length (CPL) - the distance from the insertion of the anal fin to the caudal flexure (corresponds to the origin of the caudal fin rays on the hypural plate). Measurements made parallel to the dorso-ventral body axis were: 9) head depth (HDD) - the distance centred mid-pupil from the top of the head to the bottom of the jaw with mouth closed, 10) body depth (BDD) - the distance from the origin of the dorsal fin vertically to the belly without compression, and 11) caudal peduncle depth (CPD) - the narrowest vertical distance along the peduncle. 12) The interorbital width (IOW) was measured across the body axis between the bony margins of the orbits. The remaining variables were measured along the axis of the body part as follows: 13) maxillary length (MXL) - tip of the snout to the end of maxilla (thus includes some premaxilla also), 14) maxillary width (MXW) - widest measure across the maxilla, 15) pectoral fin length (PCL) - origin of the pectoral fin to the tip of the first ray, 16) pelvic fin length (PVL) - origin of fin to the tip of the longest ray, 17) adipose fin length (ADL) - origin of the fin at the body to the posterior tip of the lobe, 18) length of middle gill raker (GRL) - distance from the origin on the arch to the tip, and 19) lower arch length (LAL) - the distance from the base of the middle gill raker to the bottom of the lower gill arch. Unless the area was damaged, all measurements and counts were taken from the left side of the fish except as follows: gill raker counts, gill raker length, and lower arch length were all taken from the first gill arch on the right side. In order to standardize morphometric data for size variation, a standard size measure (STL) was taken to the nearest 1.0 mm - distance from the tip of the snout to the end of the caudal peduncle as described above.

Data analysis

Meristic and morphometric data were analyzed using both univariate and multivariate statistical procedures. To examine the validity of assigning the Arctic char into two groups, principal components analysis (PCA) was used to summarize the variation. In this case, for illustrative purposes only, the individuals were identified to their respective form a posteriorily using the qualitative identifying criteria. In this usage, PCA provides an independent test of the reality of the groups. It should, however, be noted that failure to find groups in such an analysis does not lead to the conclusion that groups do not exist - it merely means that the variables examined did not differentiate any groups. Procedures testing the statistical null hypothesis of equality of the two forms required a priori designation of the form. This was accomplished using the qualitative criteria to classify individuals as Large, Small, Juveniles or Unknowns (see below). Univariate testing consisted of comparison of mean values using analysis of variance (ANOVA). Multivariate testing consisted of comparison of groups using discriminant analysis (DA).

Meristic data can be used directly in statistical analyses. Morphometric data must first be standardized in order to adjust for the effects of size biases in the samples, and to dampen the overwhelming effect of differences in the absolute sizes of body parts. This allows differences due to shape (i.e., relative size) of various body parts to be more clearly seen. This standardization was accomplished by calculating the residuals from the common-within-groups regression line of the body part versus STL (Reist

1985). The residual method is more accurate and theoretically sound than other methods for adjusting size (Reist 1986). Analysis of covariance is used to create the appropriate regression line from which residuals are estimated. This process also results in the estimated mean value (LSMean) for the body part standardized to the overall mean size (standard length, STL, Fig. 2) of all fish. Using this method, size-free shape variates resulted which were then analyzed using univariate and multivariate analyses (ANOVA, PCA, and DA). For PCA results, in order to include the Unknowns, the residual standardization involved three groups (Small, Large, and Unknowns), which had the following mean standard lengths respectively - 317.3 mm (*N*=49), 424.4 (113), and 270.3 (12). The overall mean value of STL from which the residuals for PCA were calculated was 383.6 mm. For DA results, the residual standardization involved only the Small and Large (means above) standardized to the overall STL=392.2 mm (*N*=162).

Results

Qualitative characteristics of the forms

Variation was evident in external characteristics such as body and fin color, body form, presence of parr marks, and relative length of the anterior pelvic and anal fin rays. Four groups were definable according to the following criteria. 1) Juveniles were not sexually mature fish which, unlike other forms, retained parr marks. These fish were excluded from further analysis. 2) Small individuals were characterized externally by generally small size, a tendency to have a terete body form, dark brownish to gray body color dorsally and rosy belly ventrally (non-spawning condition), gray paired fins with dull white leading edges, and much elongated first and second pelvic fin rays and first anal fin ray. The latter characters tended to make the distal margins of the fins somewhat emarginate rather than rounded or straight. Some of the Small individuals exhibited a slight hump in the lateral body profile immediately posterior to the head. 3) Large individuals exhibited a more robust and rounded body form, light gray back and white belly, orange or pale paired fins with white leading edges, and short typical-looking pelvic and anal fin rays. No tendency to a body hump was observed. In most cases, the variation in these characters was limited. Thus, through the combination of all these qualitative characters most individuals could be assigned to the Large or Small categories. 4) Some individuals from the entire data set could not be unambiguously classified using these criteria. These individuals were treated as Unknowns in the following analyses (Principal Components), scored using results derived from the analysis (Discriminant Analysis), or not considered when conducting the analysis (computation of group mean values, analysis of variance, computation of least square means).

Using these external criteria in combination with sexual maturity information (see below), from the entire sample of 207 fish analyzed from Lake Hazen, the following numbers of individuals were identified to one of the four groups described above: 1) Juveniles - 33 fish (16% of 207), 2) Small morphotype - 49 fish (23%), 3) Large morphotype - 113 fish (55%), and 4) Unknowns - 12 fish (5%).

Sex ratios and ecological notes

Both sexes were represented within each of the above groups as follows: 1) Juveniles (*N*=33 total) - 11 males (33%), 14 females (42%), and 8 unidentifiable (25%), 2) Small (*N*=49) - 26 males (53%) and 23 females (47%), 3) Large (*N*=113) - 70 males (62%) and 43 females (38%), and 4) Unknowns (*N*=12) - 7 males (58%) and 5 females (42%). Some morphological differences between the sexes were apparent. These will be described in detail elsewhere and do not negate the observations made herein on the samples pooled by sex (see also below).

All capture sites were relatively nearshore in shallow water. Three sites (Blister Creek, Henrietta Nesmith Glacier, and Mesa Creek) were at areas of inflow of summer meltwater; the lake site at the Ruggles River was near the year round open water outflow of the lake. Both

Large and Small forms of mature char and Juveniles were captured at all four sites. However the proportions differed between sites as follows: 1) Blister Creek (*N*=54) - Small = 33% (*N*=18), Large = 35% (19), Juvenile = 20% (11), Unknown = 7% (4); 2) Henrietta Nesmith Glacier (*N*=53) - Small = 17% (9), Large = 66% (35), Juvenile = 7% (4), Unknown = 9% (5); 3) Mesa Creek (*N*=48) - Small = 2% (1), Large = 67% (32), Juvenile = 29% (14), Unknown = 2% (1); and 4) outflow at Ruggles River - Small = 40% (21), Large = 52% (27), Juvenile = 8% (4), Unknown = 0% (0).

Detailed examination of stomach contents and parasite loads of the two adult forms are planned but not yet completed and will be reported elsewhere. However, general impressions during field work and fish processing strongly suggested that the Large form is cannibalistic and has a higher incidence of parasitism.

Growth evidence for two forms

Examination of the plot of fork length against age for the 1958 fish suggested the presence of two growth trajectories within the data (Fig. 3A). This was also present in samples of fish from 1981 (not illustrated). Examination of the growth relationship for the sub-sample of 1992 fish aged for this study confirmed the presence of two distinct growth forms (Fig. 3B). A posteriori designation of form indicated very little overlap between the Large and Small fish (Fig. 3B). Only one Small specimen overlapped the Large group and three Large fish overlapped the Small group. Most individuals that were not sexually mature were in an area of the plot that suggested they could mature into either of the two forms. Four of the Unknowns were distributed across both the Small and Large forms and the Juvenile group.

Computation of the length-age regressions for the two forms suggested substantive differences in the growth rates (Fig. 3B). For Large fish the regression equation statistics were intercept = 272.4 and slope = 11.42 (R^2=0.398) and for Small fish the statistics were intercept = 236.9 and slope = 5.81 (R^2=0.182). Analysis of covariance indicated that the slopes were not significantly different (*P*=0.43), likely due to the scatter of the points (Fig. 3B). However, the intercepts were significantly different between

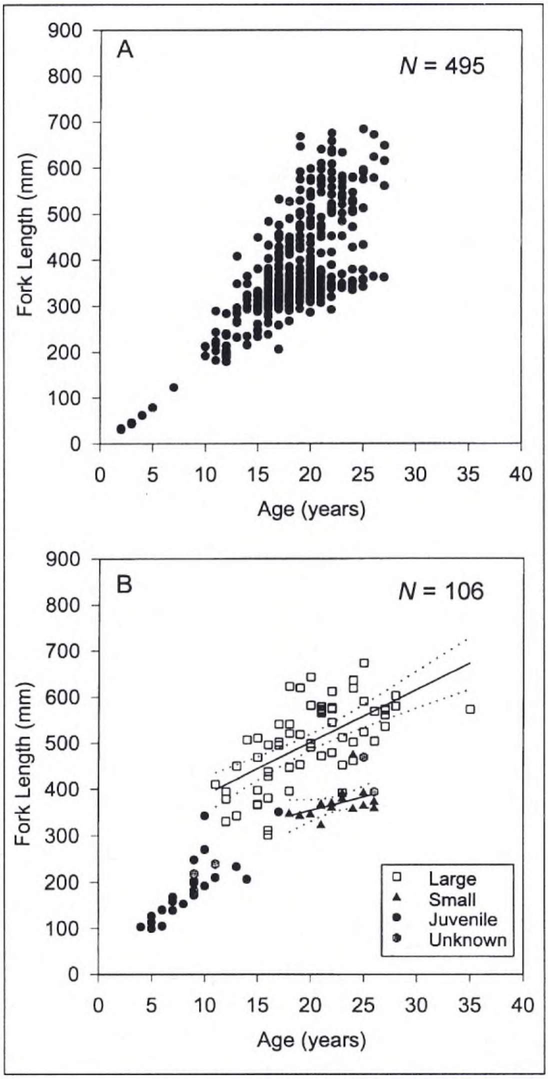

Fig. 3. Length-age relationships for both sexes combined of 1958 (**A**) and 1992 (**B**) Arctic char samples. The 1992 data are a random representation of approximately one-half the sample obtained. Individuals were identified to form a posteriorily and curves calculated separately (see text). Dotted lines represent 95% confidence limits of the regression.

Table 1. Meristic variation in the two forms of Arctic char. Variable acronyms are given in the text. Standard (Std.) and unstandardized (Unstd.) coefficients for the Discriminant Axis and the coefficients of Principal Components 1 and 2 are given. Significance (Sign.) of the ANOVA test for difference in character means is designated as NS = non-significant and ** = $P<0.01$.

Variable	Mean		Sign.	Discriminant		Principal	
	Large	Small		Std.	Unstd.	1	2
DRC	10.7	10.8	NS	-0.414	-0.626	0.542	0.577
ARC	9.5	9.4	NS	0.345	0.573	0.603	0.321
PRC	14.4	14.3	NS	0.097	0.170	0.614	-0.328
VRC	9.5	9.6	NS	-0.098	-0.190	0.345	-0.223
BRC	10.7	10.7	NS	0.004	0.006	0.271	0.483
UGR	10.2	10.3	NS	-0.128	-0.169	0.345	-0.390
LGR	15.5	15.2	NS	0.444	0.507	0.495	-0.338
PYL	38.2	35.5	**	0.833	0.179	-0.252	0.228
λ	-	-	-	0.118	-	1.656	1.145
constant	-	-	-	-	-12.150	-	-
%	-	-	-	100	100	20.7	14.3

forms ($P<0.0001$). This, in combination with a distinct gap in the distribution of points on the plots (Fig. 3B) indicated that two growth forms are present in the char of Lake Hazen. Overlap of growth trajectories of each sex was evident within both the Small and Large forms, but detailed analysis of this is deferred to a subsequent study.

Meristic evidence for two forms

With respect to univariate tests of the hypothesis of equality of Large and Small char, mean character values were not significantly different for all but one character (Table 1). The exception was pyloric caecae, for which Small fish exhibited a mean value of 2.7 less than did the Large fish.

Principal component analysis of the eight meristic variables for 166 fish, i.e., Small, Large, and Unknowns revealed the following (Table 1, Fig. 4A). Principal component one (PC1) was a contrast between high positive loadings for pectoral, anal and dorsal rays, and lower gill raker numbers and a negative loading for pyloric caecae (Table 1). This component accounted for 21% of total variation. Principal Component two (PC2) was a contrast between high positive loadings for dorsal and branchiostegal rays and negative loadings for upper and lower gill rakers and pectoral ray counts (Table 1). This component accounted for a further 14% of total variation. In examining the bivariate plot of PC1 and PC2 scores, no grouping with respect to a posteriorily designated forms was apparent (Fig. 4A). Furthermore, Unknown individuals were distributed throughout the plot.

Multivariate examination of the hypothesis of equality of the Large and Small group centroids using discriminant analysis indicated that the two groups were significantly different ($P=0.034$, df=8) prior to the extraction of the discriminant function. The best discriminating variables were pyloric caecae and lower gill raker number (positive values) contrasted with dorsal ray count (negative value) (standardized coefficients, Table 1). A plot of the discriminant scores indicated a large degree of overlap of the two forms (Fig. 5A and B). However, there was a definite tendency for Small char to score towards the negative end of the axis (group centroid = -0.518) relative to the more positive scores of Large fish (group centroid = 0.225) (Fig. 5A and B). A posteriori classification accuracy was moderate (69% correct overall). This resulted from the tendency to mis-classify Small char as Large char (for $N=47$ Small char, 17% were correctly classi-

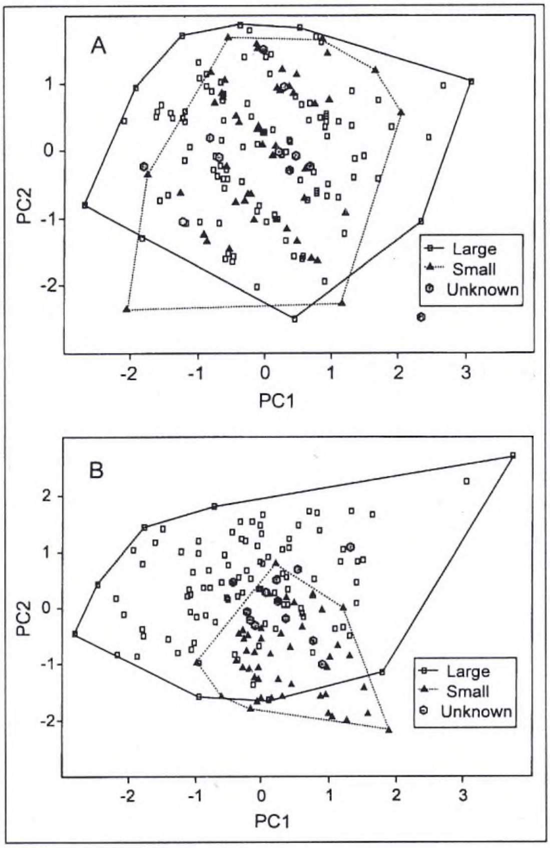

Fig. 4. Plots of scores for the first two Principal Components (PC) for meristic (A) and morphometric (B) data. Form was designated a posteriorily. Boundaries enclose all individuals of that form.

fied, 83% were mis-classified), rather than from mis-classification of Large (for N=108 Large char, 92% were correct and 8% incorrect). That is, most Small char substantially overlapped the distribution of Large char in meristic discriminant space.

The discriminant results above were based upon the categorization of individuals to one of the two known categories (Small or Large). As noted previously, using the qualitative criteria for grouping, 12 individuals could not be assigned to the appropriate category. Using the unstandardized discriminant coefficients and the constant (Table 1) with the raw data for these individuals in a linear function, the scores were calculated for these individuals. These scores were distributed throughout the distribution of both forms but tended towards the Large (Fig. 5C).

For male fish, testing for meristic differences between forms indicated that two variables (PRC and LGR) were significantly different (ANOVA, $P<0.05$). For females, only the pyloric caecae count was significantly different between forms (ANOVA, $P=0.012$). The pattern of sex-related variation did not significantly alter the interpretation of the multivariate pattern observed between forms in the PC analysis (Fig. 4A), as confirmed by the DA (Fig. 5).

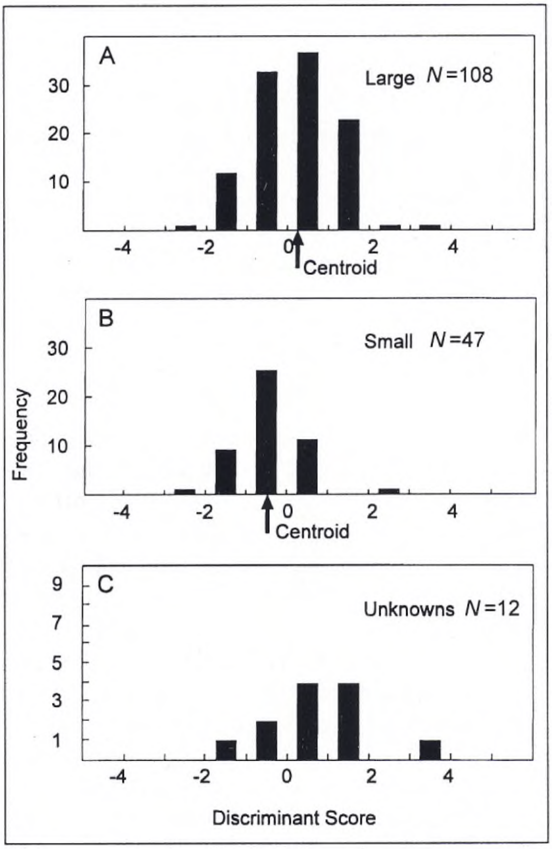

Fig. 5. Histograms of meristic discriminant scores for a priorily designated Large (**A**) and Small (**B**) forms and (**C**) Unknowns computed from unstandardized coefficients from Table 1.

Morphometric evidence for two forms

With respect to univariate tests of the hypothesis of equality of Large and Small chars, four variables were significantly different ($P<0.05$) - caudal peduncle length, pectoral fin length, pelvic fin length, and lower arch length (Table 2). A fifth variable (gill raker length) was almost significant ($P=0.0524$). Large char had relatively longer caudal peduncle and lower arch lengths, but relatively shorter pectoral and pelvic fin, and gill raker lengths than did Small char (LSMeans, Table 2).

Principal component analysis of the 19 morphometric variables for 159 fish (Small, Large, and Unknowns) for which complete data were obtained revealed the following (Table 2, Fig. 4B). Principal component one was a contrast between high positive loadings for maxillary length, postorbital length, pectoral length, head depth, and preorbital length and negative loadings for trunk length and lumbar length (Table 2). This component accounted for 21% of the total variation. Principal component two was a contrast between high positive loadings for caudal peduncle length, anal length, maxillary width, and body and head depths and negative loadings for pelvic fin length, pectoral fin length, lumbar length, gill raker length, and adipose fin length (Table 2). Upon examination of the bivariate plots of PC1 and PC2 scores, some grouping with respect to a posteriorily designated

Table 2. Morphometric variation in the two forms of Arctic char. Variable acronyms are given in the text. Means are the least-square mean (LSMean) estimated from the common-within-groups regression lines of the variable against standard length. Standard (Std.) and unstandardized (Unstd.) coefficients for the Discriminant Axis and the coefficients of Principal Components 1 and 2 are given. Significance (Sign.) of the ANOVA test for difference in LSMeans is designated as NS=non-significant, $*=P<0.05$, and $***=P<0.001$.

	LSMean		Sign.	Discriminant		Principal	
Variable	Large	Small		Std.	Unstd.	1	2
POL	22.6	21.8	NS	-0.197	-0.065	0.607	0.215
OOL	12.3	12.3	NS	0.044	0.044	0.297	0.131
PSL	53.2	54.3	NS	-0.064	-0.025	0.675	-0.167
TTL	96.4	94.6	NS	0.015	0.002	-0.652	-0.051
DOL	45.8	47.5	NS	0.056	0.016	0.412	-0.056
LUL	63.3	64.0	NS	0.280	0.067	-0.349	-0.452
ANL	32.1	32.0	NS	0.147	0.053	0.235	0.525
CPL	63.7	61.3	*	0.335	0.087	-0.138	0.713
HDD	42.5	41.7	NS	-0.050	-0.018	0.655	0.329
BDD	75.1	73.3	NS	-0.147	-0.024	-0.031	0.387
CPD	26.5	26.9	NS	-0.125	-0.082	0.222	0.181
IOW	29.4	28.2	NS	-0.198	-0.044	0.261	0.149
MXL	38.0	39.4	NS	0.064	0.026	0.815	-0.150
MXW	5.9	5.6	NS	-0.181	-0.204	0.340	0.505
PCL	68.9	82.4	***	0.412	0.065	0.668	-0.534
PVL	57.5	72.2	***	0.782	0.131	0.567	-0.614
ADL	15.9	16.8	NS	0.300	0.159	-0.067	-0.205
GRL	5.2	5.8	≈*	0.327	0.335	0.060	-0.263
LAL	35.8	33.7	*	-0.266	-0.090	0.401	0.311
λ	-	-	-	2.719	-	3.968	2.548
constant	-	-	-	-	-0.382	-	-
%	-	-	-	100	100	20.9	13.4

forms was apparent (Fig. 4B). Although overlap was evident, Large char, with the exception of a few outliers, tended to score from +1 to -3 on PC1 and from -1 to +2 on PC2. Conversely, Small char tended to score between zero and +2 on PC1, and zero and -2 on PC2. That is, unlike the similar situation for meristic data, divergence between the forms was observed in the morphometric data. The greatest degree of separation was evident on PC2. On this component, Large fish exhibited greater relative sizes for the positive coefficients that contributed to PC2. Conversely, for the negative coefficients contributing to PC2, the Small fish exhibited larger relative mean sizes of body parts. Unknown individuals generally overlapped the distributions of both Large and Small char to some extent (Fig. 4B).

Multivariate examination of the hypothesis of equality of the Large and Small group centroids using discriminant analysis indicated that the two groups were significantly different ($P<0.0001$, df=19) prior to the extraction of the discriminant function. The best discriminating variables were pelvic fin length, pectoral fin length, caudal peduncle length, and gill raker length (positive values) contrasted with lower arch length, interorbital width, and preorbital length (negative values) (standardized coefficients, Table 2). A plot of the discriminant scores indicated minimal overlap between the two forms (Fig. 6A and B). The group centroids were quite different - Large char =-1.123 and Small char= 2.389. A posteriori classification accuracy was very good (96% correct overall). Four of 100 Large char and two of 47 Small char were misclassified.

Scores calculated from unstandardized coefficients (Table 2) for the 12 Unknowns were primarily distributed in the area of the axis occupied by the Large form (Fig. 6C). One individual scored near to the Small centroid.

For male fish, testing for morphometric differences between forms indicated that 11 variables (POL, DOL, CPL, BDD, IOW, MXL, CPL, PVL, ADL, GRL, and LAL) were significantly different (ANOVA, P<0.05 or less). For females, five variables (CPL, MXL, PCL, PVL, and LAL) were significantly different between forms (ANOVA, P<0.05 or less). The pattern of sex-related variation did not alter the interpretation of the multivariate pattern observed between forms in the PC analysis (Fig. 4B), as confirmed by the DA (Fig. 6).

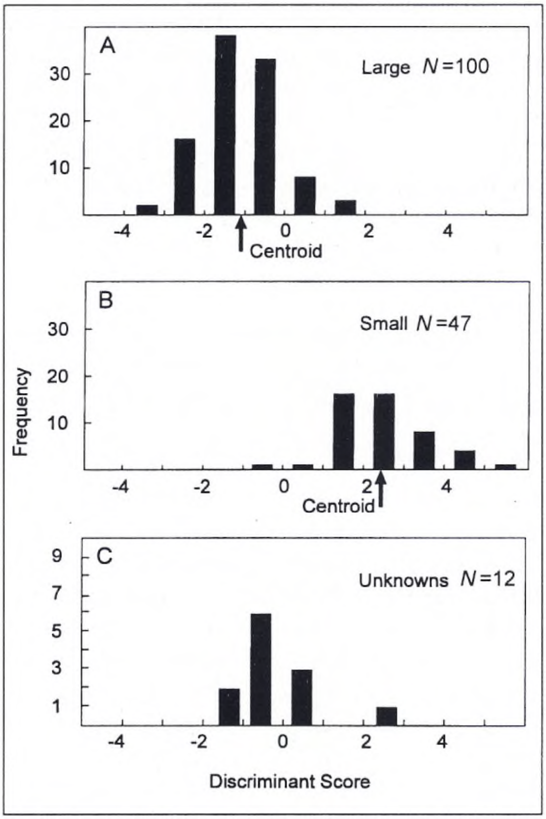

Fig. 6. Histograms of morphometric (residual) discriminant scores for a priorily designated Large (**A**) and Small (**B**) forms and (**C**) scores for Unknowns computed from unstandardized coefficients from Table 2.

Discussion

Variation in growth

In general, the growth of both forms of char in Lake Hazen, measured as length at age, is relatively slow in comparison to populations from more southerly locations in North America. For example, char in Lake Hazen are about 200 mm at age 10 whereas most populations enumerated by Johnson (1980) ranged from about 300 to 600 mm; for age 15, the comparison is about 400 mm for Large fish to 400-700 mm; and for age 20, the comparison is about 500 mm for Large fish to 540 - 640 mm. Char in Lake Hazen (especially the Large form) are also relatively old in comparison to those elsewhere - e.g., large numbers greater than 20 years whereas for 15 stocks summarized by Johnson (1980) only four had any fish older than 20. Both the small size and relatively older ages of the fish are consistent with the lower productivity of this far northern lake.

The presence of two growth trajectories within the adult segment of the population in all samples (1958, 1981, and 1992) confirms the existence of two distinct growth forms of char in Lake Hazen. Generally, it appears that fish which ultimately will become Large individuals are initially longer than the Small fish at the point of divergence of the forms. This is supported by the observed difference in intercepts predicted from the within-form regressions. This initial divergence is further accentuated by a greater growth rate in Large fish as evidenced by a steeper slope to the regression line. Thus, despite apparently sharing a similar growth rate during early ages (up to about seven or eight years), rapid divergence in growth occurs at about age nine (as evidenced by increased variability in size-at-age). This divergence both continues and is exacerbated (i.e., different slopes) to result in quite separate growth forms. Such differences in growth possibly accrue from differences in life history between the forms. These life history differences may be due to one or more of the following factors differentially distributed between the forms: a) anadromy, b) cannibalism, or c) segregation into energetically marginal habitats. Presence of smaller char in the guts of the few Large fish examined to date and the appearance of much greater rates of parasitism in Large fish tend to support cannibalism as the proximate explanation. Further examination of these possibilities is warranted.

The great similarity in growth trajectories for samples separated by 34 years (i.e., at least one complete population cycle) suggests a situation of great stability in the char population of this lake. Thus, the effects of human perturbation on this system are likely quite low. The situation in Lake Hazen is likely representative of the undisturbed state for high Arctic populations of Arctic char in North America. The apparent temporal stability of the fish population further suggests great stability in the ecological circumstances of this system. This, in turn, has likely created a situation favourable for either the divergence of local populations into different forms or for the maintenance of such forms once having arrived from elsewhere (see below).

Variation between sexes

Sexual dimorphism in morphology is apparent in many fishes and is present to a limited degree within both the Large and Small forms of Arctic char in Lake Hazen. It is possible that some degree of the difference between the two forms is the result of such sexual dimorphism and the slight differential representation of sexes in the present samples. However, the morphological differences between the forms exist independently of sex because such differences remained when the sexes were examined separately. Many of the differences observed between the forms were in body parts possibly associated with reproductive behaviour - e.g., elongation of pelvic and anal fin rays in the Small form. Further examination of these possibilities is merited.

Morphological variation and functional consequences

The presence of qualitative differences between forms in appearance and in lengths of pelvic and anal fin rays as well as in quantitative morphological characters all substantiate the observed differences in growth discussed above. Therefore, it is concluded that two forms of char definitely exist within Lake Hazen.

The substantive difference in pyloric caecae numbers between these two forms within this lake is greater than the variation typically observed in such characters among geographically disparate populations (see McPhail 1961). This difference, as well as the morphometric differences observed, all indicate that these two forms diverge widely from each other. This, in turn, suggests a high degree of ecological specialization either as migratory types, differential predators, or as ecological forms associated with particular habitats in the lake.

For example, univariately (although not statistically significant in all cases), Large fish tended to have relatively longer sections of the body both towards the anterior and the rear of the body. Longer anterior sections would allow for enhanced ability to consume large prey thus support a piscivorous life style either as cannibals or as anadromous predators. Longer posterior body sections would enhance long distance swimming ability and acceleration characteristics (Webb 1974), both of which are consistent with a predatory life style. Conversely, the more terete body form, the elongate paired fins and anal fin (and thus greater relative surface area) will enhance the maneuverability of the Small form, thus may represent adaptations useful in avoiding predation from the Large fish. Darker, presumably more cryptic, coloration of the Small form is consistent with this argument. The same number of gill rakers that are both longer and arrayed along a shorter arch in the Small form suggests differences in diet between the forms. Small fish would be better able to prey upon the seasonably available invertebrates than would Large fish. These interpretations of the morphological differences between the forms lead to predicted differences in diet. Thus, Large fish are predicted to be piscivores and/or cannibals, and Small fish are predicted to prey primarily on invertebrates (at least during periods of seasonal availability).

Differences in diet between the forms are also suggested by the substantive difference in numbers of pyloric caecae. Piscivorous species of fish as well as more piscivorous individuals within a species generally exhibit greater numbers of pyloric caecae than non- or less piscivorous counterparts (Nikolsky 1963). For piscivorous forms of char from Kamchatka, a similar situation exists (Reshetnikov 1961). Thus, the greater number of pyloric caecae observed in Large char is consistent with a piscivorous diet.

From the above, it is most likely that the observed morphological differences have practical consequences for the life history of the forms. Thus, it is likely that the life histories of the two types differ to a substantial degree. However, more direct observation of the life history of each form is required to decide between the various possibilities.

Explanation for the bimodality

Considerable diversity of Arctic char is known from within lacustrine environments. Often this consists of dwarf and normal growth pairs (e.g., Klemetsen and Grotnes 1980, Svedäng 1990), which may or may not be morphologically distinct as well (e.g., Hindar and Jonsson 1982, 1993; Jonsson and Hindar 1982). Ecological segregation and a tendency to behave somewhat like good species often complements the growth and morphological differentiation (e.g., Walker et al. 1988). Occasionally, diverse assemblages of morphotypes occur in ecologically diverse habitats (e.g., four closely related morphs in Thingvallavatn, Iceland (Magnusson and Ferguson 1987)). The phenomenon of pairs or multiple morphotypes within single water bodies seems more prevalent in Europe than North America (Johnson 1980). Thus, if the situation described for Lake Hazen is in fact due to similar causes, it represents one of the few examples described for North America. Whether the seeming paucity of this occurrence in North America is simply due to a lack of study or whether a biological explanation is relevant remains unknown at present.

Griffiths (1994) summarizes seven classes of possible explanations for size bimodality in lacustrine populations of Arctic char which are neither exclusive nor individually sufficient to explain the diversity. Some of these (e.g., piscivory, intra- and inter-specific competition, and alternative life styles) are primarily environmentally based and concerned with maintenance of bimodality. Alternatively, allopatric and sympatric speciation, and genetic inertia are primarily genetically based and address the ultimate origin of the bimodality. Because many of the data are not yet available to test between these alternatives and the various possibilities within several of the genetic explanations, detailed examination of these is deferred to future studies.

Variation in Unknowns

The observed variation of Unknowns was neither continuous nor precisely intermediate to the Small and Large forms. Rather, for the variables which differentiated the known forms best, the Unknowns as a group generally tended to resemble the Large form. Two explanations are possible. First, the Unknowns may simply represent individuals which may ultimately become Large in all but one case, but which have not yet grown or matured to the point where the distinguishing character values are obvious. Alternatively, the Unknowns may represent intergrades or hybrids between the two forms. The former expectation would be more likely if genetic evidence distinguishing the forms is not found. If genetic distinctions are apparent, depending upon the degree, the latter explanation would gain credence. Further detailed examination of these questions is warranted.

Conservation and protection of the forms

Because we have no clear idea as to the mechanisms of origin or maintenance of the two forms in Lake Hazen, extreme caution is warranted to ensure human activities do not present threats to these char. Despite the distant geographical location, the Arctic char of Lake Hazen are exploited by anglers to an unknown degree. The number of each type of fish taken is unknown but is likely fairly low in comparison to other more southern locations in North America. However, the primary productivity of Lake Hazen is likewise extremely low (Johnson 1990) and in many respects Lake Hazen may represent a closed system in which energy cycles primarily within the system. Thus, the ability of these char populations to withstand even limited regular human perturbation is unknown. Regardless of the ultimate answer to the various questions outlined above (e.g., anadromous or not, two genetically distinct forms or not, or two environmentally induced forms or not), the Small and Large forms of char of Lake Hazen represent one of the few documented cases of this phenomenon in North America and one of the most northerly documented cases in the world. Therefore, appropriate regulation of human impact as well as increased scientific understanding are both warranted.

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Immersion Mass-Marking of Otoliths and Bone Tissue of Embryos, Yolk-Sac Fry and Fingerlings of Arctic Charr *Salvelinus alpinus* (L.)

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Abstract

Two methods of mass labelling of otoliths and bone tissue were tested and compared: by osmotic incorporation of different tetracycline solutions at fertilization and by rapid immersion (few minutes) of eyed eggs, yolk-sac fry and fingerlings in a hyperosmotic solution (5% sodium chloride) of tetracycline hydrochloride or oxytetracycline (1%). The optimal duration of immersion (maximal labelling with minimal mortality) was determined. As *Salvelinus alpinus* was reared for more than one year it was possible to study, under an U.V. light microscope, the effectiveness and persistence of tetracycline fluorescent marking of whole otoliths and caudal vertebrae.

Keywords: Arctic charr, embryos and fry, mass-marking, tetracycline, osmotic shock.

Introduction

Artificial propagation of Arctic charr has been carried out for many years in subalpine lakes like Lake Leman without knowledge of its impact. However, limited marking experiments with external (Champigneulle and Escomel 1984) or internal tags (Champigneulle et al. 1987, Rubin and Buttiker, 1993) have been used for a first estimation of the impact of stocking with charr juveniles of 3 to 5 cm in Lake Leman (Champigneulle et al. 1988, Champigneulle and Gerdeaux 1993, Rubin and Buttiker 1993). These studies demonstrated that 51 to 89% of captured spawners of the 1983 to 1985 cohorts came from artificial propagation of fingerlings.

Marking bony structures in fish with fluorochromes such as tetracycline antibiotics was pioneered by Weber and Ridgway (1967) and Meunier (1972, 1974). Administration of tetracyclines can be by injection, dietary intake or immersion, and marks can be detected by fluorescent microscopy of calcified tissues (otoliths and vertebrae). Immersion is the only practical procedure for embryos and fry which are too young to feed or too small to inject (Tsukamoto 1985, Dabrowsky and Tsukamoto 1986, Nagiec et al. 1988). However, the relatively long exposure times (12 to 48 hours) and the quantities of tetracycline needed require large-scale facilities when mass-marking is carried out. A recent improvement in this technique is the osmotic incorporation of tetracycline at the time of egg fertilization in salmonids (Ruhlé and Grieder 1989, Ruhlé and Winecki-Kühn 1992), and the simultaneous osmotic shock and immersion for the vital mass labelling of elvers (Alcobendas et al. 1991, 1992) or coregonids (Rojas-Beltran et al. 1995).

The main purpose of this paper is to test and compare the applicability, and to report refinements, of these two mass-marking methods for eggs, eleuteroembryos, and fry of *Salvelinus alpinus,* including the development of multiple marks.

Material and methods

Origin of eggs

Eggs and milt were obtained from our delayed (temperature and photoperiod manipulation) hatchery broodstock (Gillet and Breton 1992). Each ovulating female was anaesthetized in 2-phenoxyethanol (0.3 ml L^{-1}). Ova were fertilized with a mixture of sperm from several males and diluted in DIA 532 (Billard 1977). After hardening, twenty minutes later, eggs were transferred into incubation trays. Different batches of eggs from six females were incubated separately at 6°C ±1 (Tables 1 and 2).

Mass-marking procedures

In marking experiments by osmotic incorporation at fertilization (Ruhlé and Grieder 1989, Ruhlé and Winecki-Kühn 1992) ova and milt (pool from five males) were mixed in dry conditions, then were immediately imersed for 30 or 60 min, in different solutions of tetracycline hydrochloride (TC) or oxytetracycline (OTC) buffered pH 8 (TRIS, glycine and NaOH) concentrations (1 to 8 g L^{-1}) (Table 1). Dead eggs were counted and removed twice a week and cumulated mortality rates were calculated at 6 and 35 days. A batch (5.5, Table 2) of eggs labelled at fertilization in 4 g L^{-1} buffered pH 8

Table 1. Synopsis of marking experiments by osmotic incorporation at fertilization in Arctic charr.

Date	Batches	*N*	Solution (concentration) g L^{-1}	Immersion duration (min)	Instant mortality (%) (6 days)	35 day cumulative mortality (%)
17.03.93	1.1	1804	TC (4)	60	0.28	44
	1.2	2191	TC (2)	60	0.05	30.5
	2.3	2240	TC (4)	60	1.07	42.1
	2.4	2516	TC (2)	60	0.79	33.6
29.03.93	control	419			0.96	34.4
	3.1	290	OTC (8)	60	0.82	82.4
	3.2	300	OTC (4)	60	2.0	50.7
	3.4	323	OTC (2)	60	1.24	37.8
	3.5	360	OTC (1)	60	1.39	49.2
	3.6	290	OTC (8)	30	0.35	61.7
	3.7	277	OTC (4)	30	0.73	38.6
	3.8	355	OTC (2)	30	1.13	40.6
	3.9	301	OTC (1)	30	0.67	51.2
	3.10	285	TC (8)	60	3.51	62.1
	3.11	288	TC (4)	60	1.04	36.1
	3.12	333	TC (2)	60	0.0	22.8
	3.13	369	TC (1)	60	0.82	50.1
	3.14	221	TC (8)	30	1.36	53.4
	3.15	307	TC (4)	30	0.65	36.2
	3.16	238	TC (2)	30	1.68	34.0
	3.17	290	TC (1)	30	0.0	24.5

Table 2. Synopsis of marking experiments by bathing in a hyperosmotic solution (5% sodium chloride) with 1% tetracycline hydrochloride for Arctic charr.

Date	Batches	*N*	Stages at mass marking Total length (mm)	Immersion duration (min)	Temp. °C	Instant mortality (%) (24 h)	Cumulative mortality (%) at (day)
05.05.93	control	100	eyed eggs			2	19 (21)
	4.1	100		5	7.5	0	10 (21)
	4.2	100		10		0	6 (21)
	4.3	100		17		0	6 (21)
05.05.93	control	583	Yolk-sac fry			0.0	0.7 (16)
	5.1	795	at 1-3 days	3.5	7.5	0.0	0.3 (16)
	5.2	644	Hatching	2		0.0	1.1 (16)
	5.3	525	16	5		0.0	0.8 (16)
21.05.93	control		Yolk-sac fry			1.4	35 (58)
	5.1		at 18 days	3.5	8.5	8.4	32.6 (58)
	5.2		2/3 resorption	5		7.3	41.2 (58)
	5.3		17.5	7		9.2	51.4 (58)
01.07.93	control		fry at 59 days			0.9	52.1 (203)
	5.1		30	3.5	9.5	3.8	50.4 (203)
	5.2			2.5		3.0	60.9 (203)
	5.3			2		4.0	69.5 (203)
	5.4	150		3		2.7	33 (132)*
23.11.93	control		204 days			0.0	52.1 (224)
	5.1		fingerlings	3.5	8.0	0.0	50.7 (224)
	5.2		72	2.5		0.0	61.0 (224)
	5.3			5		0.0	69.7 (224)
	5.5	981		7		0.08	61.3 (202)**
30.12.93	control	10	eyed eggs			10	10 (35)
	6.1	10		10	6.0	10	20 (35)
	6.2	10		15		10	10 (35)
	6.3	10		20		0	0 (35)
	6.4	10		30		10	10 (35)

* Accidental total mortality on 04.10.93.

** Batch initially labelled by osmotic incorporation at fertlization.

TC solution for 60 min was reared for more than one year in order to make comparisons with batches labelled by short term immersion (2 to 30 min) in a hyperosmotic solution (5% of NaCl) of 1% TC. In order to improve the TC penetration, the advanced eyed eggs, when the otoliths were visible, were immersed for a longer time (5 to 30 min) than the fry or the juveniles (2 to 7 min, Table 2). Survival of these marked batches and unmarked control batches was accurately monitored. The same batches (5.1, 5.2, 5.3 and 5.5) were used in multiple marking experiments and compared with the initial control batch (Table 2).

Rearing procedure

The different batches were reared separately up to 213 days, then pooled in a 250 L tank supplied with water pumped from a depth of 36 m in Lake Leman (5.5°C in winter and 10°C in summer). Fish were fed and reared with dry trout pellets as described by Gillet (1991), Guillard et al. (1992) and Gillet and Breton (1992).

Mark detection

Marks were detected with a Zeiss Axiovert 35 inverse microscope with reflected fluorescent light and two sets of filters (U.V.-G35, FT395, LP420 and Blue 450-490, FT510, LP520). After extraction by dissection, whole otoliths were examined without grinding for all fish. In some cases we used trypsin to extract the otoliths (Rojas-Beltran and Vincent 1993). Otoliths and, in some cases (batches labelled at 59 or 204 days, Table 2) vertebrae, were mounted directly on glass slides using "Tesa" non toxic (without solvent, washable in water) transparent glue (no fluorescent in U.V. light) and observed with 50x, 100x or 200x magnification.

Results

A total of 13,578 Arctic charr eggs was mass-marked by osmotic incorporation at fertilization (Tables 1, 2) and 2,554 individuals were mass-marked by immersion in hyperosmotic tetracycline solution at stages from the eyed egg stage to the fingerlings of 72 mm (mean total length), aged 204 days (Table 2).

Unfortunately, the quality of eggs and milt, especially for marking experiments at fertilization, was very poor, maybe due to the late time of stripping and the strong variability in the quality of the eggs (C. Gillet, pers. comm.). However no major differences in mortality of eggs at 6 days of mass-marking (Table 1) by osmotic incorporation at fertilization were observed (only the batch 3.10 exhibited a mortality of more than 3%). For each experimental condition (TC or OTC and 30 min or 60 min, Table 1), the batch bathed in a strong concentration (8 g L^{-1}) exhibited a significantly higher mortality (Chi-squared test; $P<0.01$; df=1) than that for each of the other batches.

The embryos withstood a relatively long (5 to 30 min) immersion in hyperosmotic solution (5% NaCl) very well with low (0 to 10%) instantaneous mortality rates (Table 2). The yolk-sac fry withstood better short immersions (2 to 7 min) at hatching than yolk-sac fry at the 2/3 of resorption (18 days), or than small prefed fry at 59 days (Table 2). However, the 204 days fingerlings (mean length 72 mm) withstood very well immersions up to 7 min. Most of the mortality after 24 h of labelling was due to handling rather than osmotic shock.

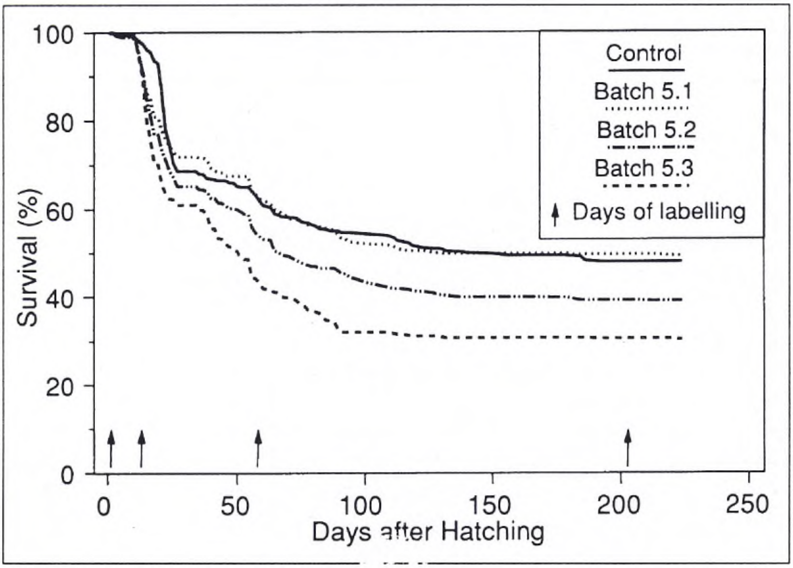

Fig. 1. Long term (224 days) comparative survival of different Arctic charr batches mass-marked at four stages (arrows) by bathing in a hyperosmotic solution (5% NaCl) with 1% Tetracycline. For stages and immersion duration for different batches, see Table 2.

Long-term survival (up to 224 days after hatching) in the control did not differ significantly (Chi-squared test; $P>0.05$; df=1) from 3.5 min (5.1) immersion labelled batches (Fig. 1). However, a lower survival was detected for longer immersion batches (39.1% for batches 5.2 and 30.5% for 5.3) and 38.7% for 5.5 batch initially labelled at fertlization (Table 2).

235 individuals (79 mass-marked at fertilization and 156 by short immersion with osmotic shock) were examined for fluorescent-mark retention and readability results (Table 3).

In batches labelled at fertilization, the fluorescent marks (mark position: 0) were detected on whole otoliths (Fig. 2a) in fry of less than three months and quality of marks was poor when compared with the rapid immersion method and closely related to the concentration of TC or OTC solution and the duration of immersion (Tables 1,3).

Optimal immersion times (maximal labelling with minimal mortality) were determined to be 20 min in a 5% NaCl hyperosmotic, 1% tetracycline solution for advanced "eyed" eggs (mark position: 0; Table 3; Fig. 2d) and 3.5 minutes for fry at hatching (mark position: 1; Table 3; Fig. 2b-e). Despite a short time (only 16 days) between the first and second mass-marking, the two otolith fluorescent marks were excellent and clearly distinguishable over one year in all batches (Table 3; Fig. 2b-e). On the contrary, the TC marks in sagitta otoliths in third (fry at 59 days) and fourth (fingerlings at 204 days) mass-labelling were rather poor and variable for all unground material. However, in fourth mass-marking, excellent fluorencent marks were observed in the centrum on vertebrae (Table 3; Fig. 2c).

In hyperosmotic solution, very good and distinguishable otolith labelling (Fig. 2d) was obtained in advanced "eyed" eggs with relatively long immersion (20 to 30 min).

In all of the short-term immersion batches, the two first marks retention and persistence in

Table 3. Tetracycline labelled controls for different batches mass-marked at fertilization (F) or by rapid immersion method with mark retention in otoliths and/or centrum of vertebrae. The marks position is given as follows: (0) Nucleus labelling in egg stage, (1) at hatching, (2) 16 days after, (3) 59 days after and (4) 204 days after.

Experimental batches	Total length (mm)	Age at sampling (days)	*N*	Number and position of TC marks						
				0	1	2	3		4	
							Oto.	Vert.	Oto.	Vert.
2.3 F	16-19	1-15	27	27						
1.2 F	17	1-3	8	8						
3.9 F	16-17	1-15	8	8						
3.11 F	16-17	1-15	8	8						
4.2	16-178	1-3	8	8						
6 pool	39-50	113	12	12						
5.4	53-70	132	12				12			
5.5 F	56-72	122	18	6						
5.5 F	55-200	202-359	10	0						10
5.1	53-83	204	20		20	20	14	4		
5.2	61-82	204	22		22	22	4	6		
5.3	67-90	204	20		20	20	8			
5.1	62-83	213-224	14		14	14	4	4	4	14
5.2	55-87	213-224	14		14	14	2	6	2	14
5.3	57-85	213-224	14		14	14	2	4	2	14
5 pool	115-222	381	20		20	20	12	16	6	20

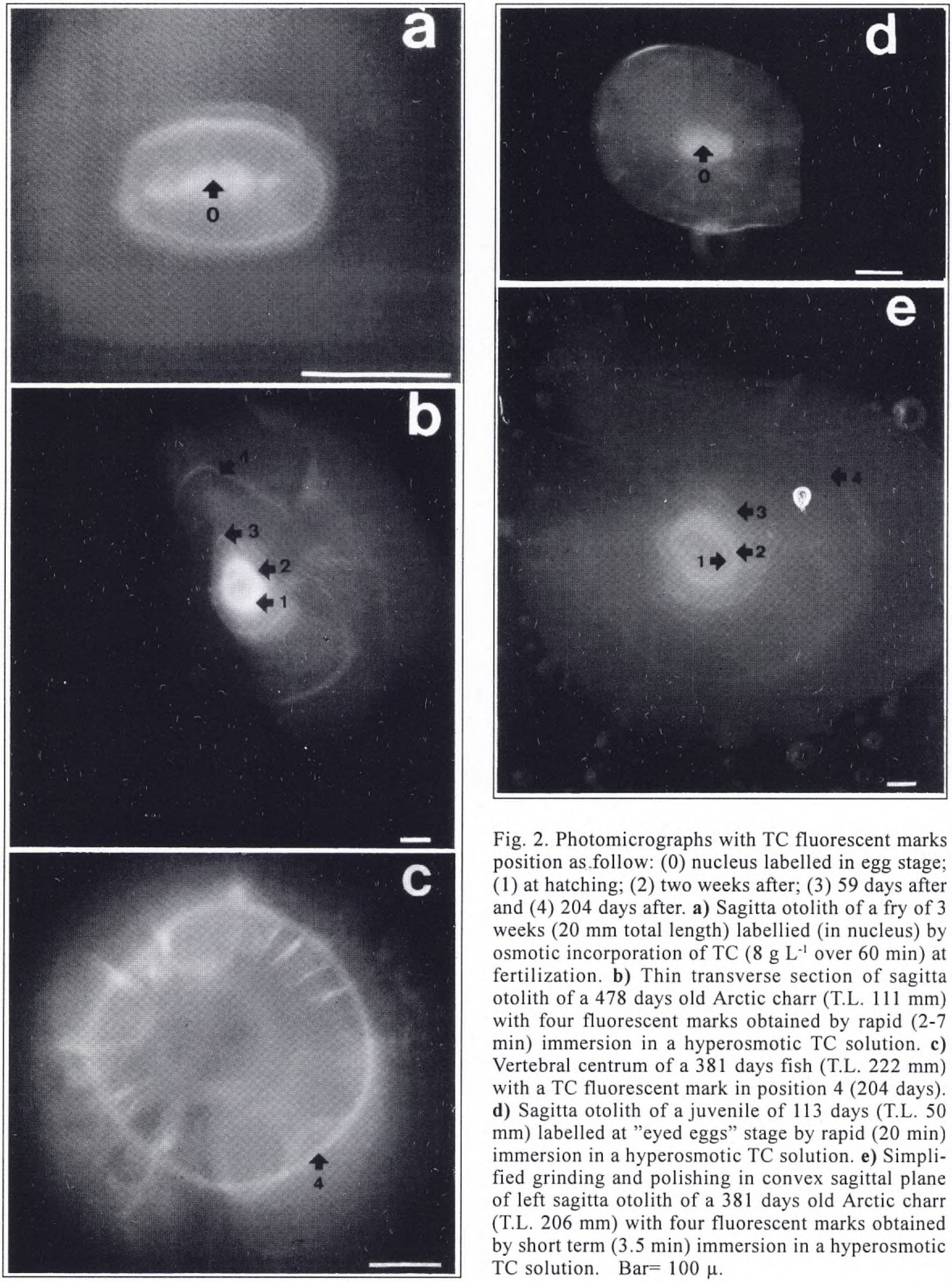

Fig. 2. Photomicrographs with TC fluorescent marks position as follow: (0) nucleus labelled in egg stage; (1) at hatching; (2) two weeks after; (3) 59 days after and (4) 204 days after. **a)** Sagitta otolith of a fry of 3 weeks (20 mm total length) labellied (in nucleus) by osmotic incorporation of TC (8 g L^{-1} over 60 min) at fertilization. **b)** Thin transverse section of sagitta otolith of a 478 days old Arctic charr (T.L. 111 mm) with four fluorescent marks obtained by rapid (2-7 min) immersion in a hyperosmotic TC solution. **c)** Vertebral centrum of a 381 days fish (T.L. 222 mm) with a TC fluorescent mark in position 4 (204 days). **d)** Sagitta otolith of a juvenile of 113 days (T.L. 50 mm) labelled at "eyed eggs" stage by rapid (20 min) immersion in a hyperosmotic TC solution. **e)** Simplified grinding and polishing in convex sagittal plane of left sagitta otolith of a 381 days old Arctic charr (T.L. 206 mm) with four fluorescent marks obtained by short term (3.5 min) immersion in a hyperosmotic TC solution. Bar= 100 μ.

sagitta otoliths examined whole was 100% for fish reared up to more than one year (115 to 222 mm total length). However, in the oldest individuals, a better distinction between the four TC marks was obtained by a rapid grinding and polishing on the convex sagittal plane of the sagitta otoliths (Fig. 2e).

Discussion

Mass marking by rapid immersion with osmotic shock in Arctic charr was found to be more efficient, consistent and easier to apply than mass labelling by osmotic incorporation at fertilization. Better results in fluorescent marks examined in whole otoliths were obtained for the advanced "eyed" stage (when otoliths are present) and newly hatched fry than for prefed fry and fingerlings. However, excellent fluorescent tetracycline marks were obtained in the centra of vertebrae of fingerlings (40 to 90 mm T.L.) but not in intermediate fry (25-30mm total length) at 59 days maybe due to vertebral centra being not fully ossified at this age (Nagiec 1979).

With the osmotic shock technique, all individuals were labelled and the observation of the two first marks in whole otoliths was possible without special preparation in more than one year old Arctic charr in our experimental batches. However, for elvers this direct observation is possible over 5 years (F.J. Meunier, pers. comm.). Moreover, fluorescence in 59 or 204 days mass-labelling batches will be expected to appear far out from the nuclear area of the sagitta. The poor recovery of these later otolith marks may be due partly to the thicker and less transparent outer areas of growing sagitta. In this case, a grinding and polishing to approach the nuclear region of sagitta were necessary to detect the third and fourth TC marks (Fig. 2b-e). As in Ruhlé and Grieder (1989) and Ruhlé and Winecki-Kühn (1992), we observed that in larger otoliths which require grinding for examination, the thin fluorescent nuclear layer may be lost, leading to erroneous negative results. It is for this reason that we recommend for larger fish (mass-marked at fingerling stage) the extraction of some caudal vertebrae in order to detect TC marks in their centrum (Fig. 2c).

For coregonids (Rojas-Beltran et al. 1994) with long-term immersion TC technique (6-18 hours), the percentage of retention marks is more variable, more difficult to practice at a large scale and seems to be less persistent than the short term immersion hyperosmotic technique.

The rapid immersion in hyperosmotic TC solution technique presented here for Arctic charr has a promising potential for vital mass-marking at precocious stages to study their development in nature over one year. Further research will examine the use of other fluoromarkers with the osmotic shock technique.

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The Effects of Stocking Density on Survival and Growth of Wild-caught Arctic Char

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Abstract

Wild-caught Arctic char, *Salvelinus alpinus*, from Møkkeland lake, northern Norway suffered greater degrees of fin damage and mortality when held at low (30 kg m^{-3}) than when held at high (150 kg m^{-3}) stocking density. Most (70-90%) of the Møkkeland char held at low stocking densities had damaged fins, whereas less than 10% of the fish stocked at a density of 150 kg m^{-3} showed signs of caudal fin injury. The high incidence of fin damage amongst the char held at low density may suggest that levels of aggressive encounters were high in these fish. Char stocked at 90 kg m^{-3} showed levels of fin damage intermediate between the groups stocked at lower and higher densities. Rates of weight loss were greater in the char stocked at low density than in the groups held at higher stocking densities, suggesting that the energetic costs of engaging in aggressive behaviour may have been high for the fish held at 30 kg m^{-3}. The combination of energy losses arising from participating in aggressive encounters, and the injuries sustained therefrom, probably account for the high rates of mortality observed in the Møkkeland char stocked at low density.

Keywords: Arctic char, stocking density, aggressive behaviour, mortality.

Introduction

Char species have been produced for stock enhancement and sport fishery purposes in several countries for many years. Recently, however, the realisation that the Arctic char may be in decline in certain areas (Maitland 1992) and the increased interest in 'farming' and 'sea ranching' operations has led to some intensification of studies relating to rearing techniques for this species (Jobling et al. 1993b, Heggberget et al. 1994).

The fish characteristics required for successful stock enhancement and 'sea ranching' operations may differ from those deemed desirable when producing fish directly for the table in intensive farming operations. Long-term rearing in a hatchery environment, which may result in domestication, can have negative consequences upon fish destined for release (Utter et al. 1993). There is, however, little information about how wild-caught char respond to being held in hatchery environments (Heggberget et al. 1994). It would be of benefit to know how wild-caught fish adapt to being held in captivity for shorter or longer periods of time if it is envisaged that a period of hatchery-rearing is to be incorporated into a 'sea ranching' programme.

Previous studies have shown that hatchery-reared Arctic char usually perform poorly when held at low stocking density (Jobling et al. 1993b), and the poor growth performance is probably linked to high levels of agonistic behaviours displayed by char stocked at low densities (Christiansen and Jobling 1990, Winberg 1993). Levels of agonistic behaviour are reduced in char exposed to water currents (Adams et al. 1995), and growth performance may be improved by exposing the fish to flowing water (Christiansen and Jobling 1990). Similarly, numbers of agonistic encounters tend to decline, and growth performance improves with increasing stocking density (Brown et al. 1992, Jørgensen et al. 1993). Thus, it was predicted that exposure of wild-caught char to water currents and/or stocking at high density would be useful strategies to be adopted when holding such fish in captivity. Consequently, as part of a larger programme aimed at investigating the possibility of using Arctic char in 'sea ranching' operations an experiment was conducted in order to examine the responses of wild-caught char to being held at different stocking densities within a hatchery environment.

Materials and Methods

The experiment was carried out using wild-caught Arctic char from Møkkeland lake, northern Norway. Prior to the start of the experiment the fish had been maintained in holding tanks at stocking densities of 150-200 kg m^{-1} for a period of six months. During this time the fish were weaned on to dry pellet feed. Only healthy fish that were in good condition were selected for use in the experiment. Two weeks before the start of the experiment approximately 600 juvenile fish within the size range 19-23 cm fork length were selected from a larger population. Two hundred and seventy of these fish were tagged with numbered FTF-69 fingerling tags (Floy Tag & Mfg, Seattle), enabling tagged fish to be recognised individually. Char were then distributed among six tanks of 100 L capacity to give duplicate tanks at each of three stocking densities. Each of the 30 kg m^{-3} groups comprised 34 charr, all of which were tagged. The 90 kg m^{-3} groups held 78 fish, with 50 tagged individuals per group, whereas each of the 150 kg m^{-3} groups held 165 individuals, 50 of which were tagged.

The water flow to each tank was adjusted to generate a circumferential current of approximately 30 cm s^{-1}, this current speed being chosen on the basis of the results of previous studies showing that exposure of Arctic char to flowing water leads to reduced levels of 'bite-mark' damage (Christiansen and Jobling 1990). The water temperature was held at 2°C throughout the course of the 63 day experiment (18.10.93-23.12.93), and the photoperiod was simulated to match the natural photoperiod at Tromsø (70°N). The fish were offered dry pellet feed (pellet 4; Felleskjøpet A/S) in excess, with feed being provided continuously by means of automatic disc feeders. Mortalities were recorded on a day to day basis. Dead fish were removed, but were not replaced, so the numbers of fish within the tanks suffering mortality decreased with time.

At 21 d intervals during the experiment feed intake was monitored using X-radiography (Jobling et al. 1993a). Following provision of the marked feed the fish were anaesthetized (80 ppm benzocaine) and X-ray photographed. Individual fish were then recognised by their tag numbers and these fish were weighed to the nearest 0.1 g, and fork length measured to the nearest 0.1 cm. The fish were then examined for signs of fin damage. Following development of the X-ray plates they were examined, and numbers of fish that had been feeding were recorded.

At the end of the experiment all the tagged fish were weighed and length measured. The analyses of changes in weight and condition (Condition Factor = [Body weight/Fork length^3] • 100) were carried out using the data collected for fish that retained their tags throughout the entire experiment, and for which complete records were available.

Chi-squared goodness of fit tests were used for the analysis of possible differences in the frequencies of fish with fin damage. Growth data were not normally distributed, and non-parametric tests (Kruskal-Wallis and Mann-Whitney) were used for examining possible differences among treatments. Differences at $P<0.05$ were considered significant.

Results and Discussion

There were no within-treatment differences in the frequencies of fish with fin damage, but proportions of fish with fin damage were significantly higher in the groups of charr stocked at 30 kg m^{-3} than in the groups held at higher stock-

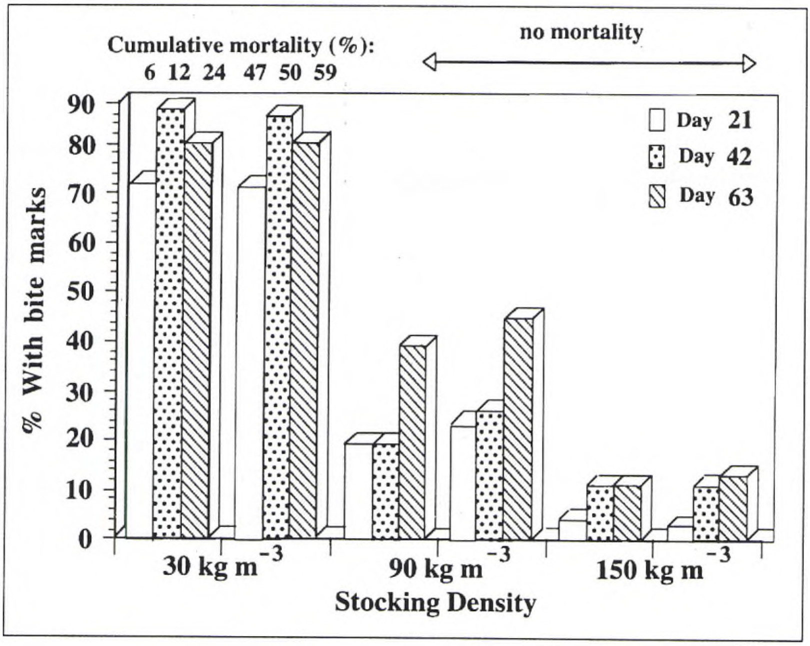

Fig. 1. Proportions of char with damaged caudal fins at various times (21, 42 and 63 days) after establishment of groups held at stocking densities of 30, 90 and 150 kg m^{-3}. Data relating to cumulative mortality within groups are also shown.

ing densities. Differences were apparent when the first registration was made, 21 d in to the experiment (Fig. 1). At this time over 70% of the fish stocked at the lowest density showed signs of caudal fin damage, whereas in the high density groups (150 kg m^{-3}) less than 5% of the fish had injuries to the fins. Proportions of fish with damaged fins increased with time in the groups stocked at intermediate and high density, and by the end of the experiment proportions of fish with fin damage were approximately 40% in the groups stocked at 90 kg m^{-3} and 10% in the groups of charr held at 150 kg m^{-3} (Fig. 1).

Thus, percentages of fish with fin damage were clearly negatively correlated with stocking density. However, in contrast to the findings of studies conducted on hatchery-reared Arctic char of the 'Hammerfest strain' held at low density (Christiansen and Jobling 1990, Christiansen et al. 1991) exposure of the low density groups of Møkkeland char to water currents was not found to be particularly efficacious in reducing the numbers of fish with fin damage. Adams et al. (1995) demonstrated that exposure to water currents led to reductions in levels of agonistic behaviour in hatchery-reared progeny of wild-caught Arctic char from Loch Insh, Scotland, and percentages of fish with fin damage have previously been used as an indirect indicator of levels of aggressive activity within the group (Christiansen and Jobling 1990, Christiansen et al. 1991). Consequently, it seems that increasing stocking density may be an effective way of reducing aggression in wild-caught Møkkeland char, as has been found in previous studies on Arctic char from other geographic areas (Brown et al. 1992, Jørgensen et al. 1993), whereas exposure of the fish to flowing water may not.

Few fish were observed to feed during the course of the experiment, but when feed intake was monitored on day 63 there was a clear trend towards percentages of feeding fish being higher (15%) in the groups stocked at 150 kg m^{-3} than in those held at lower stocking densities (5% in both 30 kg m^{-3} and 90 kg m^{-3} groups). The fact that few fish fed led to there being considerable loss of weight in all groups, irrespective of stocking density. Overall weight loss amounted to 19% of initial body weight in the fish stocked at 30 kg m^{-3}, 17% in the char held at 90 kg m^{-3} and

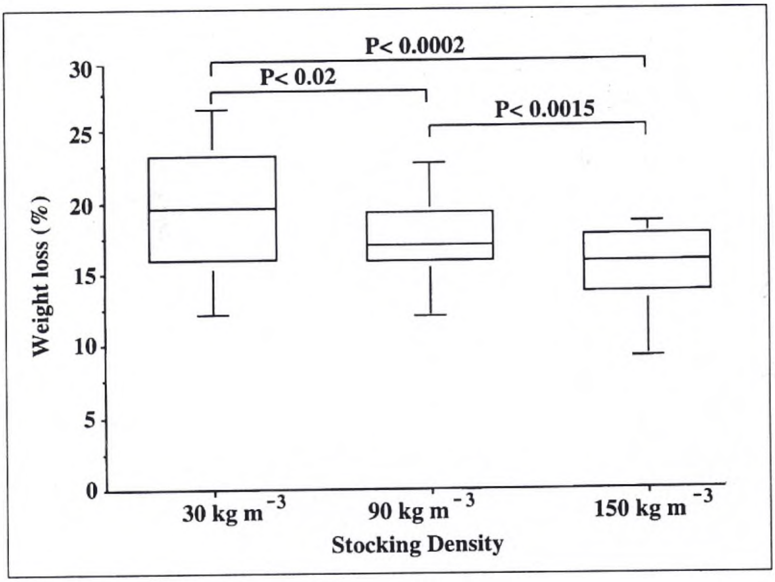

Fig. 2. Box-and-whiskers plots showing the weight losses (% of initial body weight) of char held at stocking densities of 30, 90 and 150 kg m^{-3}. Numbers of fish monitored were 40 at 30 kg m^{-3} and 100 at each of the other stocking densities.

15% in the 150 kg m^{-3} groups, with these differences being highly significant (Fig. 2).

Similarly, condition factor, which can be used as an indicator of nutritional status, also decreased as time progressed. Decline in condition was, however, more rapid in the char held at 30 kg m^{-3} and 90 kg m^{-1} than in those stocked at the highest density (Fig. 3). At the time of the first measurement, made 21 days into the experiment, there were significant differences in condition between fish stocked at 150 kg m^{-1} and those stocked at lower densities. These differences were maintained with the passage of time. There were no significant differences in condition between fish stocked at 30 and 90 kg m^{-1}. These results suggest that energy reserves were being depleted most rapidly by the fish held at the lowest stocking densities, and may indicate that the energetic costs of engaging in agonistic behaviour are high. In this respect, the results of the current study are in agreement with previous findings: several workers (Haller and Witten-

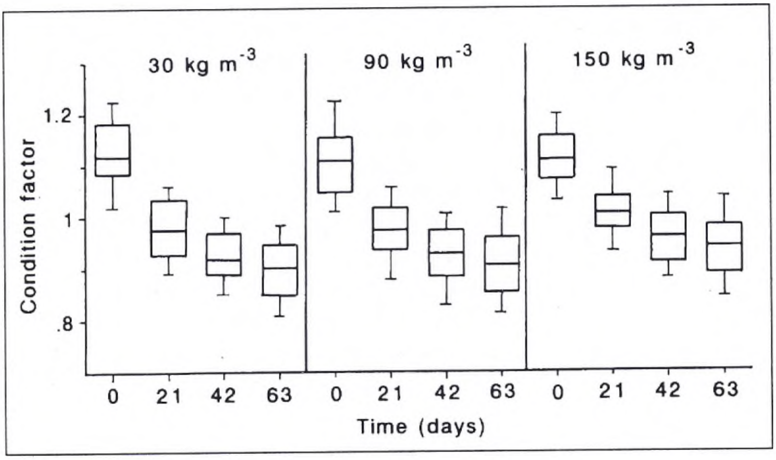

Fig. 3. Box-and-whiskers plots showing the changes in condition factor with time in groups of char held at stocking densities of 30, 90 and 150 kg m^{-3}. Numbers of fish monitored were 40 at 30 kg m^{-1} and 100 at each of the other stocking densities. Significant differences in condition between fish stocked at 150 kg m^{-1} and those held at lower densities were found on days 21, 42 and 63. No significant differences were observed between groups stocked at 30 and 90 kg m^{-1}.

berger 1988, Abbott and Dill 1989, Christiansen and Jobling 1990, Christiansen et al. 1991, Haller 1991a,b, Winberg 1993) have found evidence that the costs of aggressive behaviour are high, possible costs of engaging in such behaviour being increased energetic expenditure, suppression of feed intake and reduced growth.

Taken together, the results of the present study suggest that levels of aggression were higher in the wild-caught Møkkeland char stocked at low density than in groups held at higher stocking densities. High energetic costs associated with engaging in aggressive behaviour may have resulted in rapid depletion of the energy reserves in the char stocked at low density. A combination of the energy depletion that resulted from high frequencies of aggressive interactions, and the injuries sustained by fish participating in aggressive activities probably account for the high rates of mortality observed in the Møkkeland char stocked at low density (Fig. 1).

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Population Structure in Landlocked Spitsbergen Arctic Charr. Sustained by Cannibalism?

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Abstract

Arctic charr, *Salvelinus alpinus* (L.), is the only freshwater fish species on Svalbard. Charr populations demonstrate a great ecological plasticity, showing various adaptations to harsh environments. With few exceptions, most studies within the wide geographic range of the Arctic charr, underplay the importance of cannibalism and it is often claimed that cannibalism in these species is of little or no significance. Based on the observed stomach contents and annual growth of charr in Lake Arresjøen, Svalbard (Spitsbergen), we devised a simple model in which fish mortality and the occurrence of small prey-fish in the diet of larger fish was varied. Our results indicate that cannibalism may be a main force in structuring the age- and length-class distribution of charr in this lake, and we propose that cannibalism may be a key factor regulating the fish population structure in Arctic and high mountain lakes in general.

Keywords: Arctic charr, cannibalism, population structure.

Introduction

The Arctic charr, *Salvelinus alpinus* (L.), has a Holarctic distribution, with the widest geographic range of any salmonid species (Hammar 1985). It is the only freshwater species on Svalbard and many lakes in the archipelago contain charr (Lönnberg 1899, Dahl 1926, Gullestad 1973, 1975, Hammar 1982, 1985, Svenning 1993). Charr populations demonstrate tremendous ecological plasticity, showing various adaptations to harsh environments. In landlocked lake systems on Spitsbergen, sympatric populations seem to be present (Hammar 1982, Svenning 1993). Traits such as age-at-maturity may vary markedly between charr populations, and the multiplicity of life-history tactics often results in bimodal length-frequency distributions (Johnson 1976, 1980, 1981, Power 1978, Svenning 1993). In Lake Arresjøen, Svalbard, two size modes of charr coexist, with the large-sized form preying upon smaller fish (Svenning 1993). It has been suggested that cannibalism is common amongst large fish in most landlocked charr populations on Svalbard (Svenning 1992).

Cannibalism in Arctic charr has been reported from several other areas (Klemetsen and Østby 1967, Skreslet 1973, Klemetsen and Grotnes 1980, Klemetsen et al. 1985, Sparholt 1985, Riget et al. 1986). With few exceptions, however (see Le Cren 1965), most studies underplay the importance of cannibalism in general (e.g. Lorenz 1966, Maynard Smith and Price 1973). Dawkins (1976) states that cannibalism is a rare phenomenon and a process of little importance in shaping ecological systems. In Arctic charr and brown trout, a 5% proportion of conspecifics in the diet of larger fish has often been considered insignificant (e.g. L'Abée-Lund et al. 1992).

Arctic charr were sampled with gillnets and funnel traps in Lake Arresjøen in 1990 (Svenning 1992), 1993 (Svenning and Fevolden in manus) and 1994 (Svenning unpublished data). Based on the observed stomach contents and annual growth of charr in Lake Arresjøen, we present a simple model in which fish mortality and the occurrence of small fish in the diet of larger fish are varied. We hypothesize that cannibalism is the main factor structuring the charr population in Lake Arresjøen.

Material and methods

Study area

Svalbard comprises a group of four large, barren islands (Spitsbergen, Edgeøya, Barentsøya and Nordaustlandet), and a number of smaller islands. The climate on Danskøya, on the northwestern coast of Spitsbergen, is typically Arctic. The average monthly air temperature is above 0 °C only in June, July, August and September, with the highest average temperature, 5 °C, being recorded in July. Lake Arresjøen is situated on Danskøya and is located about 250 m from the coast in a low valley at an elevation of 15 m above sea level. Unlike most lakes on Svalbard, Arresjøen receives little run-off from glaciers, and surface drainage is poor. Permafrost seals the subsoil and snow-melt provides a flush of water only in late spring. Arresjøen is a small, (0.35 km^2) oligotrophic lake with a maximum depth of 36 m. The lake is ice-covered for about 10 months each year to a depth of 1.5-2 m. In August (1990, 1993, 1994) the water column was completely mixed, with temperatures ranging from 6.3 to 6.5 °C at the surface, and 6.1 to 6.3 °C at the bottom. During the same period, transparency, measured with a 25 cm secchi disk, was 7.5-8.5 m.

Sampling

Charr were sampled from Lake Arresjøen in the beginning of August 1990, 1993 and 1994. Fish were captured with electrical fishing gear and bottom gillnets in 1990, while pelagic gillnets were used in 1993. In 1994 we also captured fish with funnel traps, and the population size of younger charr was estimated using mark- and recapture methods (Svenning unpublished data). All sampled fish were measured, weighed and classified with respect to sex, stage of maturity, color of flesh and parasite infection (Svenning 1993). Otolith preparation, reading and measurements, were performed as described in Svenning et al. (1992). The food items were identified and their relative contribution to stomach fullness estimated (Svenning 1993). The method used was similar to the points method of Hynes (1950), but employed a percentage scale. The average degree of fullness for each prey item is expressed as a percentage of the average degree of total fullness in the sample.

The charr population in Lake Arresjøen

The Arctic charr in Lake Arresjøen are landlocked, i.e. ascendence from the sea is not possible. The charr in the lake are either unexploited or have been exploited very little by man. There was no significant difference in length- and age distribution, or in growth pattern, between charr captured in 1992, 1993 and 1994, and data for all sampled fish, shown in Figs. 1, 2 and 3, are therefore combined (Svenning and Fevolden in manus). There was a bimodal length- and age distribution, with no fish between 180 and 260 mm (Fig. 1), and only three fish between 11 and 15 years of age (Fig. 2). The length-at-age data show that the charr in Lake Arresjøen have very low growth rates during the first 10 to 15 years, with annual length increases of 10 to 15 mm (Fig. 3). The few charr between 11 and 15 years were between 16 and 18 cm, while all fish older than 15 years were greater than 25 cm in length. The oldest fish captured was 31 years old, and the largest fish was 55 cm.

Diet

In gill net catches from Lake Arresjøen, small charr made up about 16 to 23% of the diet of the sampled fish. The rest was chironomids (75-82%), zooplankton (<1%) and trichopterans (<2%). The prey-charr observed in stomachs of the large charr ranged from 7 to 13 cm in length and 6 to 11 years in age (Svenning 1993).

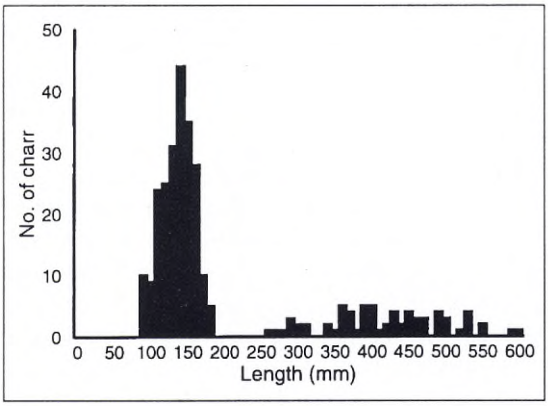

Fig. 1. Length distribution of Arctic charr sampled with gill nets in Lake Arresjøen in August 1990, 1993 and 1994.

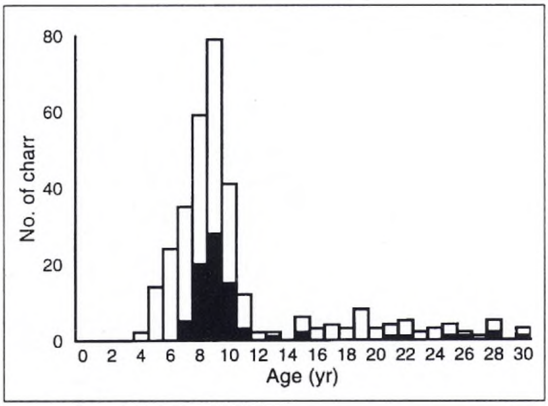

Fig. 2. Age distribution of Arctic charr sampled with gill nets in Lake Arresjøen in August 1990, 1993 and 1994. Open columns represent immature fish and black columns show mature fish.

The Model

In order to predict the consequences of cannibalism from larger Arresjøen charr (age >15 yr) on the charr population structure in the lake, one must know the food consumption of the cannibals and the age structure of the population. The food consumption can be estimated from the growth increase of larger fish, combined with the amount of fish in the diet (or the frequency of cannibalism), i.e. the feeding rates. The age structure is a direct consequence of the annual mortality. The impact of cannibalism can therefore be estimated without knowing the absolute number of fish in each year class. The spread-

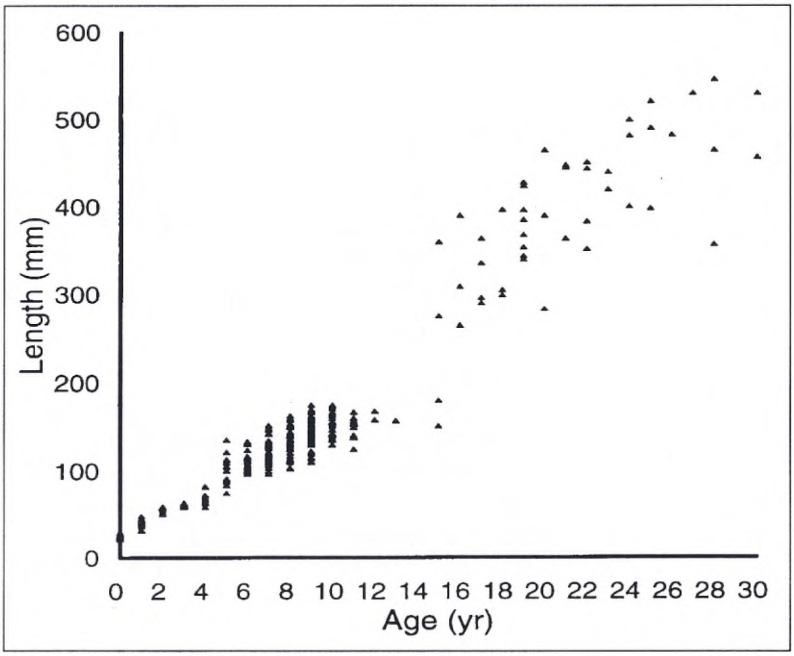

Fig. 3. Length-at-age for Arctic charr sampled with gill nets and by electrofishing in Lake Arresjøen in August 1990, 1993 and 1994.

sheet, Quattro Pro (Vers. 6.0), was used to model the charr population structure, by varying feeding rates (amount of prey fish in the larger charr's diet) and the annual mortality in age-classes older than age five years.

Feeding rates

The larger charr in Arresjøen (> age 15) increased their weight by an average of 71 g per year (linear regression, N=45, r=0.83). The calorific values for prey-charr are approximately 6.5 kJ/g (Christiansen 1991) and those for chironomids are probably similar (Øyvind Schnell, Univ. of Bergen, Norway, pers. comm.). Based on laboratory studies with Arctic charr (fed to excess with dry pellets, in which 1 g of pellet contains 22-24 KJ/g), an intake of 19.2 KJ/g (0.8 g pellet) is necessary on average for a single charr to increase its weight by 1 g (Malcolm Jobling, Univ. of Tromsø, pers. comm.). Consequently, in order to increase its weight by 71 g per year, a large Lake Arresjøen charr would consume at least 210 g of fish or chironomids per year, i.e. the food coefficient value should be at least 3.0.

Mortality rates

Mark- and recapture experiments with funnel traps in 1993 and 1994 (Svenning unpublished data), in which 1,500 charr were individually tagged and 5,000 additional charr were tagged by fin clipping, gave a population size estimate of 17,000 (±1,450) "catchable" charr (age 5-14). The average mortality of these age-classes was calculated to be approximately 0.3 ± 0.15. In our model we have varied the mortality of charr aged from 6 to 9 from 0.1 to 0.6 per year, and fish older than age 16 to vary between 0.05 and 0.15, while the mortality (M) of fish aged from 10 to 16 was calculated from the formula:

$$M_a = (M_{6\text{-}9}-(M_{6\text{-}9}-M_{>15}))/6, \text{ for } 9 < a < 16,$$

where M_a is mortality at age a, and $M_{6\text{-}9}$ and $M_{>15}$ are mortality at age 6-9 and at age >15 respectively.

Table 1. The correlation between fish diet and mortality due to cannibalism in Arctic charr in Lake Arresjøen, given two different food coefficient values. Fish diet is the average amount of fish observed in the diet of larger charr, including all fish with stomach contents. Mortality in small charr (age 6-9) is set to 0.35 and mortality of large charr (age >15) is set to 0.1.

Food coefficient	Mortality due to cannibalism (%)	Fish diet (%)
3	10	1.3
	50	6.7
	100	13.3
5	10	0.8
	50	4.0
	100	8.0

Results

Using the following values, our model demonstrates that all mortality amongst the younger charr (age 6-9) in Lake Arresjøen is due to cannibalism (Table 1): a food coefficient value of 3.0; mortality of 6 to 9 year old charr of 0.35; mortality for larger charr (age >15) of 0.1; and

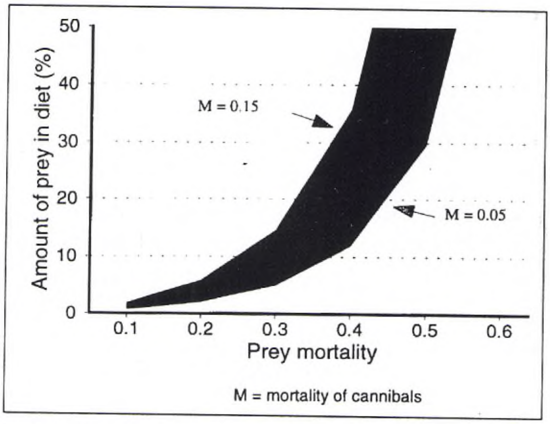

Fig. 4. The estimated relationship between prey mortality (age 6 to 9 years) and the amount of prey-fish (%) in the diet of larger charr in Lake Arresjøen. The mortality of larger charr (cannibals) are varied from 0.05 to 0.015.

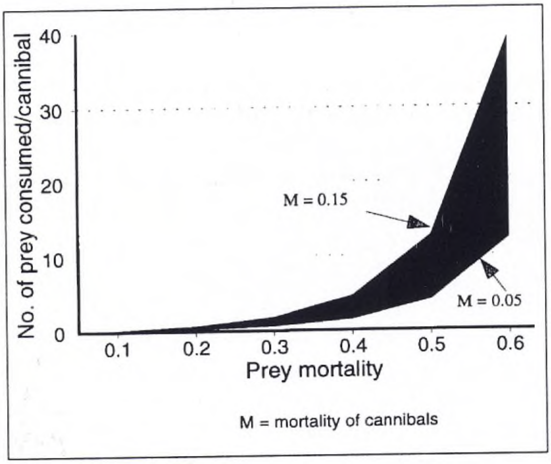

Fig. 5. The estimated relationship between prey mortality (age 6 to 9 years) and the average number of prey-fish consumed per large charr in Lake Arresjøen. The mortality of larger charr (cannibals) are varied from 0.05 to 0.015.

a proportion of 13.3% conspecifics in the diet of larger charr. By increasing the food coefficient value to 5.0, only an 8% proportion of conspecifics in the diet of larger charr was required for cannibalism to account for all the mortality of younger charr (Table 1). The mortality of fish aged 10-15 is calculated in accordance to the formula given above (see Material and methods).

Figs. 4 and 5 demonstrate the correlation between mortality and fish diet, when we assume (in the model) that all mortality (100%) of younger charr (age 6-9) is due to cannibalism. The food coefficient value is set to 3.0 on both occasions. With a mortality of larger charr of 0.05, an increase of prey mortality from 0.2 to 0.5 is associated with an increase in fish diet from 2.0 to 29.6% (Fig. 4). With a mortality of large charr of 0.15, the same increase would be from 5.8 to 91.8% (Fig. 4).

Assuming that all mortality is due to cannibalism, and the mortality of smaller and larger charr are set to 0.35 and 0.1 respectively, only 3.1 prey-charr of 9 g each are eaten by an average large fish in a year (Fig. 5). Or, similarly, if only 8% of the large population are cannibals (Table 1), each will consume 23 charr with an average weight of 9 g. By increasing the mortality of smaller charr to 0.45 in the model, an average large fish will consume 7.7 prey-charr a year. By assuming only a fraction of the population are selective cannibals, these would make up 32% or 19% of the population, with food coefficient values of respectively 3.0 or 5.0. This means that an average annual consumption of 25-100 g charr per large charr, give mortality rates in the range of 0.20-0.50 for small charr (age 6-9).

Discussion

The results obtained by the simple model presented here for the charr population in Lake Arresjøen, document that cannibalism may be a major force in structuring the age- and length-class distribution of charr in this lake. Given approximately 10 to 15% of conspecifics in the diet, all mortality of younger charr may be caused by cannibalism. In back of the widespread occurrence of cannibalism reported in Arctic charr (Klemetsen and Østby 1967, Skreslet 1973, Klemetsen and Grotnes 1980, Klemetsen et al. 1985, Sparholt 1985, Riget et al. 1986, Svenning 1992, 1993), we therefore propose that cannibalism may be a key factor regulating the fish population structure in Arctic and high mountain lakes in general.

The gradual increase in annual growth rates for the age-classes 11 to 16 years (Fig. 3), may be related to a gradual increase of charr in the diet. The annual absolute weight increment per fish is low for all size and age-classes of charr in Lake Arresjøen. However, the cannibalistic charr have a much higher weight increment than the small, chironomid-feeding charr. In our calculations we have used a food coefficient of 3.0 in most of the analyses for piscivorous charr; this is a very modest figure when compared to several piscivorous species (Backiel 1971). In laboratory studies of cannibalistic brown trout, food coefficient values in the range 2.9 to 7 have been obtained at temperatures of 8 to 16 °C (Forseth and Jonsson 1994). Additionaly, free living fish are likely to use more energy searching for prey than laboratory fish which are fed to satiation. Thus, our food coefficient of 3.0 probably underestimates the food intake. Nevertheless, according to our model, an average annual consumption of 25 to 100 g charr per cannibal, making up only 10 to 20% of the annual food consumption, would yield mortality rates in the range 0.20 to 0.50 for the age-classes which are preyed upon. In Lake Arresjøen, the proportion of charr in the diet of the larger charr varied between 14 and 24% by weight in 1990, 1993, and 1994 (Svenning 1993, Svenning and Fevolden in manus). These values lie within the range which may explain the population age structure by our model. The low number and weight of charr consumed per cannibal are compensated for by a relatively high number of cannibals. Even small increases of charr in the diet of the cannibals, could increase the annual mortality of the age-classes preyed upon to a level too high to sustain recruitment to the cannibalistic fraction of the population, i. e. the observed stable population structure in Lake Arresjøen could collapse.

A 5 to 15% proportion of conspecifics in the diet of fish has been found in several studies (Frost 1954, Kipling et al. 1970, McCormack 1970, and L'Abée-Lund et al. 1992). In populations with much faster growth rates than the charr in Lake Arresjøen, the annual food consumption must also be considerably higher. A 5 to 15% fraction of fish in the diet would substantially increase the total consumption of fish per piscivorous charr. For example in Lake Takvatn, if smaller charr (6-13 cm) make up 8% of the diet (food coefficient value=3.0) of larger fish (>20 cm), all mortality of smaller charr (age 2-4) can be explained by cannibalism (Svenning 1993).

Although most available habitats in Lake Arresjøen have been fished with gill nets that are effective at capturing fish between 18 and 29 cm, the number of captured charr in this length range is very small (Svenning 1993). The total catch consists of a high number of small fish (<18 cm), few fish of intermediate size (18-30 cm) and quite large numbers of fish greater than 30 cm in length (Svenning 1993), giving a bi-modal length distribution. The scarcity of charr of intermediate size has also been observed by Hammar (1982) for Lake Arresjøen. Thus, the size- and age-structure of Arctic charr in Lake Arresjøen seems to have been stable over a long period of time, and challenges the explanation that the missing age-groups are caused by a previous reduction in recruits. Similar observations of a bi-modal length distribution have been reported for other Arctic populations of whitefish, lake trout and landlocked charr (Hunter 1970, Klemetsen et al. 1972, Skreslet 1973, Johnson 1976, Power 1978, Sparholt 1985).

The catch curve of charr in age-classes between 16 and 30 from Lake Arresjøen indicates a very low annual mortality rate. By assuming that the catch curve is biased due to variation in catchability, i. e. that the number of old and large charr is overrepresented due to increasing gill net catchabilities with fish size, the actual mortality rate may be higher. However, as the charr reach ages up to at least 31 years (Svenning 1993), the annual mortality within the age-classes 16-30 years has to be very low, unless the number of 16 year old recruits are substantial. The low number of captured fish in age-classes 12-15 years does not support this hypothesis.

Theoretically, a reduction in the number of piscivores could lead to an increased consumption of charr by those remaining in the population, followed by an increased individual annual growth rate. However, the increase in annual growth rate for the piscivorous charr in Lake Arresjøen, combined with a low fraction of fish in the diet, may indicate that small charr have a low vulnerability to predation by piscivorous fish. Therefore, a reduced number of large cannibals may not be compensated for by increased growth rate, and the fraction of large fish in the population will probably be heavily reduced even by a low fishing mortality.

Both Johnson (1976) and Power (1978) point out the danger which may arise when exploitation of northern salmonid populations increases to the point that the reserve of old fish in the stock are depleted. Power's concern was mainly based on the theoretical risks of unsuccessful reproduction in the hostile Arctic environment. To ensure the long-term survival of a species, he suggests that a high number of reproducing year-classes may be needed. It is, however, also probable that intensive exploitation may lead to increased recruitment, at least as a short term effect in allopatric populations of Arctic charr and brown trout. In low-productive Arctic and high-alpine lakes the growth and recruitment rates for fish probably balance on a knife's egde. Therefore, increased recruitment may easily result in decreased growth rates, and a population consisting of small-sized individuals. In this context, cannibalism may be of special importance due to its effect on the population dynamics, and may also be a prerequisite for high growth rates in low-productive systems. Thus, removal of large fish by exploitation may concurrently remove the recruitment control of the population, which may change a population characterized by fast-growing, large individuals, to individuals with stagnation in growth at much shorter lengths.

Annual recruitment to the stock of large, cannibalistic Arctic charr in Lake Arresjøen is low, probably around 10% of the stock (Svenning 1993). To maintain a population structure which includes large fish, fishing mortality rate should not exceed this annual recruitment rate to the cannibalistic fraction of charr. By gillnetting, a fishing mortality around 10% will easily be exceeded, even with a low fishing effort. Therefore, we would suggest angling only, in combination with bag limits. If gillnetting is to be allowed, a corresponding bag-limit must be applied. By utilizing such management the quality of the catch and the fishery may outweight the low quantity of harvested fish.

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Migration of Anadromous White-Spotted Charr, *Salvelinus leucomaenis*, in southwestern Hokkaido, Japan

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Abstract

Using data from trap catches in the River Furuu, southwestern Hokkaido, and from commercial catches in coastal waters of the Sea of Japan, it is thought that white-spotted charr (*Salvelinus leucomaenis*) perform an upstream migration in spring/summer from May to early July. The tagging experiments indicate that most charr descend to the sea in spring after overwintering in rivers, but some migrate to the sea in late autumn or early winter without overwintering. The migration distance at sea of the autumn-migrating charr was longer (maximum 70 km from the river mouth) than that of spring-migrating charr (10 km).

Keywords: white-spotted charr, *Salvelinus leucomaenis*, northern Japan, migration, sea-overwintering.

Introduction

White-spotted charr (*Salvelinus leucomaenis*) are generally distributed in northern Japan and their anadromous populations occur chiefly around all of Hokkaido (Inamura and Nakamura 1962, Goto 1992). Despite low commercial value, this species is important not only as a target for recreational fisheries (Nakata 1991) but also as the predator of chum salmon (*Oncorhynchus keta*) fry (Kubo 1946).

Shibata (1938), Gritsenko and Churikov (1976), and Yamamoto and Nakano (1994) reported migrations of the anadromous white-spotted charr in southwestern Russia and in northern Japan. These results suggested similar migration patterns with anadromous charr descending to the sea in spring and ascending rivers in summer, and migrants overwintering in the rivers. However, migration of charr at sea and the biology of white-spotted charr in southwestern Hokkaido have never been examined.

The aim of this paper was to present information about migrations of anadromous white-spotted charr in rivers and in the Sea of Japan off southwestern Hokkaido, and to deal with their overwintering at sea. Data from the literature on anadromous species of *Salvelinus* were also compared.

Materials and methods

Traps to catch anadromous charr were located in the lower- and middle reaches of the River Furuu (43°08' N, 140°26' E), and were operated from June to October in both 1992 and 1993. The river is about 12 km in length and flows into the Sea of Japan at Kamoenai, southwestern Hokkaido (Fig. 1). In 1992, the mean 10-day water temperatures of the River Furuu ranged from 1.2 (mid-February) to 15.6 °C (late July) 1.5 km upstream from the river mouth. One trap was set 0.9 km upstream from the mouth and was centered on the stream with a weir placed

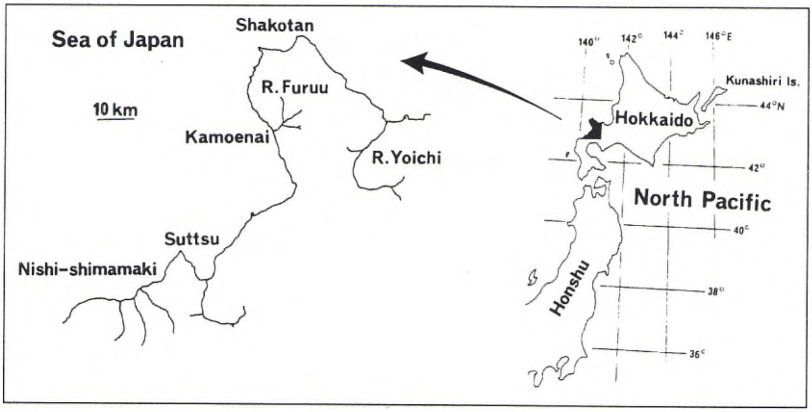


Fig. 1. The study area in southwestern Hokkaido, Japan.

across the stream to guide fish into the trap. The other three traps were fixed on fish ways of dams situated in three branches 4-7 km upstream from the mouth. These traps were thought to be capable of trapping all sizes of ascending charr (>20 cm), however, it was thought that some migrants ascended through the weir of the lower trap when the water flow of the river increased.

In 1992, the trapped fish were counted daily, measured for fork length to the nearest millimetre, and tagged with a numbered dart tag at the base of the dorsal fin. Anadromous charr were distinguished from resident charr by external appearance such as the silvering of the body and the size of spots (Yamashiro 1963, Nakata 1991). Fork lengths of anadromous charr which were released in the summer of 1992 ranged from 21 to 56 cm and the length distribution had three peaks at 30, 37, and 45 cm (N=496). These fish were recaptured in the river using the traps, a cast net, and electrofishing gear from June 1992 to September 1993, and additional charr were tagged and released during this period. In the spring of 1993, charr with tags caught from Kamoenai coast were also examined at Kamoenai Fisheries Cooperative.

To elucidate the fluctuating amounts of anadromous charr in the Sea of Japan, 10-day landings during 1991-93 off the Suttsu and Nishi-shimamaki coasts (Fig. 1) were investigated from the market data of the Suttsu and Nishi-shimamaki Fisheries Cooperatives, respectively, located 50 and 80 km away from Kamoenai. These were done because exact landing data were not available at Kamoenai, and because charr were incidentally caught with set nets that were installed off the Suttsu and Nishi-shimamaki coasts for commercial fisheries from late March to December.

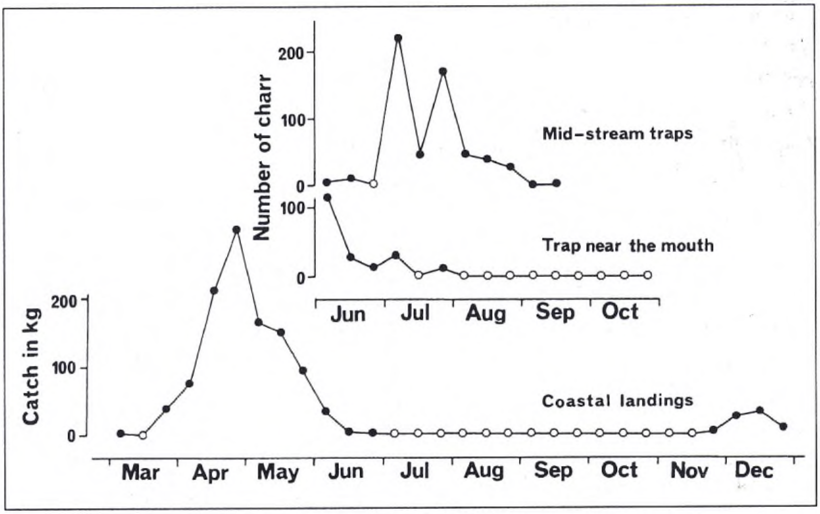
Results

Catches from coastal waters and traps in the river

Ten-day coastal landings averaged from 1991 to 1993 rapidly increased from late March to late April, and showed a peak in late April, but declined in May and June (Fig. 2). Charr disappeared in the sea during summer and autumn, however, fish were caught from late November, and catches increased a little in December (Fig. 2). Exact data from charr landings of Kamoenai coast were unavailable but these landings seemed to show the above tendencies.

Ten-day catches, in the lower trap near the river mouth operated from June 1, rapidly decreased from early June, then fish were hardly caught from mid-July through October (Fig. 2). Trap data in May were unavailable because the water flow increased with the snow melt. Midstream traps caught numerous fish from early July (Fig. 2). Daily trap catches tended to increase when it rained, however, detailed information such as the water flow was not available.

Fig. 2. Average ten-day catch of white-spotted charr in 1991-1993 in the Sea of Japan off the coasts of Suttsu and Nishi-shimamaki (bottom) and ten-day changes in catch of charr with traps in the middle and lower reaches of the River Furuu in 1992 (top). Open circles indicate no catch.



Movements of tagged white-spotted charr

A total of 522 charr were tagged from June 1992 to April 1993 in the River Furuu, and 46 charr were recaptured in the river surveys and by commercial/recreational fisheries in rivers and at sea by September 1993.

Among 496 charr released in the summer of 1992, two fish were found in the Sea of Japan off Shakotan located 30 km away from Kamoenai in January 1993 and the other two fish were found, respectively, in February and March 1993 in the lower reaches near the mouth of the River Yoichi located 70 km away from Kamoenai along the coast (Figs. 1 and 3).

During the winter surveys, no charr with tags were caught in the River Furuu, but anadromous charr without tags that seemed to have ascended in the previous summer were frequently caught in the river. From late March to early April, three tagged charr were recaptured near the mouth, and many anadromous charr were observed as schools in pools 0.9-1.5 km upstream from the mouth (Fig. 3). Of 26 charr which were tagged and released from these schools in April 1993, and of 496 charr released in the previous summer, 5 and 13 charr respectively were recaptured by set nets off the Kamoenai coast within 0-10 km from the mouth of the River Furuu from April 22 to June 2 (Fig. 3). No tagged charr were recaptured at sea after June 3.

One tagged charr which was released in the lower reach of the River Furuu in early April 1993 returned to the lower reach on June 3 (Fig. 3). Moreover, five tagged charr which were released in the summer of 1992 returned to the middle reaches of the River Furuu in July and September 1993 (Fig. 3).

Discussion

On the basis of coastal landings and trap catches, the present study indicates that anadromous white-spotted charr commence an upstream migration in the beginning of June and/or in May, and that they maintain their ascent in June and early July. It is likely that the ascent by a majority of the migrants concludes in late July and that they remain in streams between summer and mid-autumn and then descend to the sea. However, based on the coastal landings and tagging experiments, the descents of anadromous charr seem to occur at two different times: most of the seaward migrations take place in mid-April after overwintering in fresh waters but some descend streams in late November or December and overwinter at sea (Fig. 3).

Shibata (1938) noted that white-spotted charr enter the sea in May and return to rivers in Au-

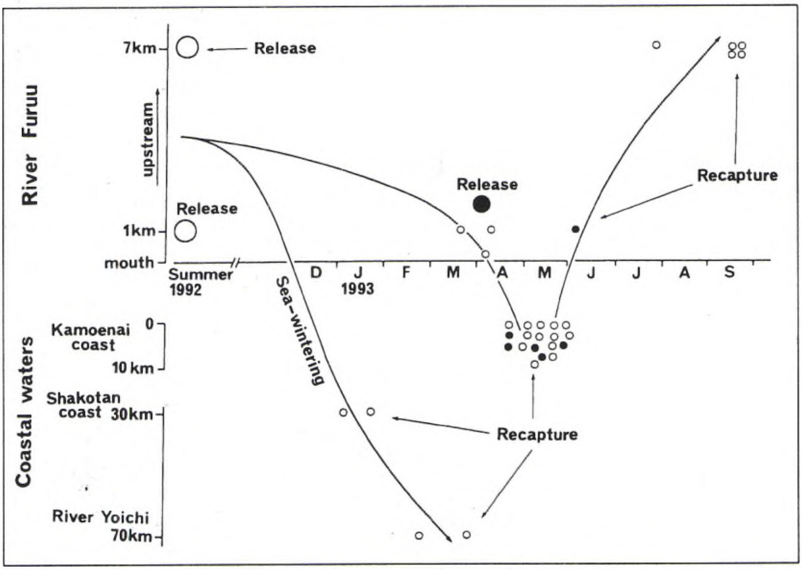


Fig. 3. Movements of white-spotted charr tagged and released in the River Furuu. Large circles show locations of release, and open and filled small circles recaptures of fish released, respectively, in the summer of 1992 and the spring of 1993.

gust in Kunashiri Island situated approximately 40 km from the coast of eastern Hokkaido (Fig. 1), one of the Kurile Islands. Gritsenko and Churikov (1976) showed that the same species conducts a downstream and upstream migration in spring/summer and in summer, respectively, in northern Sakhalin. Yamamoto and Nakano (1994) revealed that this species descends streams in spring, returns in summer/autumn and overwinters in the streams in northern Hokkaido. These results are different from those of the present study: the charr of the River Furuu ascend the stream one or two months earlier (May to early July) than the other populations, and some of the River Furuu overwinter at sea. In winter, set-net fisheries are not operated off the coasts of southwestern and southern Hokkaido, but many recreational anglers fish sea-inhabiting charr on the shoreline of southwestern Hokkaido. This fact strongly supports the thesis that white-spotted charr overwinter at sea in this region.

Anadromous Dolly Varden (*Salvelinus malma*) and anadromous Arctic charr (*S. alpinus*), which occur in more northern areas than white-spotted charr, are not known to overwinter at sea (Grainger 1953, Armstrong 1970, 1974, 1984). It is considered that the seawater adaptability of salmonids is associated with photoperiodic changes (Finstad et al. 1989, Arnesen et al. 1991) and with low water temperatures (Finstad et al. 1988, Sigholt and Finstad 1990). In addition, the timing of seaward migration has been shown to vary with different stocks were also shown (Thorpe 1988, Mayama et al. 1989). In the present study, some white-spotted charr overwintered at sea in southwestern Hokkaido but charr of northern Hokkaido and of Kunashiri Island remained in streams in winter (Shibata 1938, Yamamoto and Nakano 1994). In Hokkaido, winter sea temperatures (5-9 °C) off southwestern Hokkaido are higher than those (0-5 °C) off northern and eastern Hokkaido (Table 1). These differences in migration behaviour may be partly caused by seasonal changes in sea-water adaptability varying among each stock of Hokkaido as well as by the sea-water tolerance being affected by sea temperatures in winter.

Although charr that entered the sea in the spring moved within 0-10 km from the mouth, sea-overwintering charr travelled a maximum of about 70 km. It is probable that anadromous white-spotted charr in southwestern Hokkaido travel relatively short distances like the other anadromous *Salvelinus* species previously discussed (Moore 1975, Armstrong 1984, Kristof-

Table 1. Monthly changes in surface sea temperature (°C) off the coasts of Kamoenai, southwestern Hokkaido, Wakkanai (45°42' N, 141°40' E), northern Hokkaido, and Rausu (44°03' N, 145°12' E), eastern Hokkaido, in 1992.

	Jan	Feb	Mar	Apr	Mar	Jun	Jul	Aug	Sep	Oct	Nov	Dec
SW Hokkaido	6.8	5.8	6.8	8.6	11.2	14.5	19.0	21.1	20.6	16.1	11.7	9.2
N Hokkaido	2.9	1.5	2.7	5.9	9.9	14.4	19.3	19.8	17.3	13.7	9.0	4.7
E Hokkaido	1.1	-0.2	0.1	2.6	6.2	10.3	14.9	17.9	16.6	13.9	9.5	4.2

ferson et al. 1984, Dempson and Kristofferson 1987). In the present study, efforts to catch and to discover tagged fish were different among localities, and therefore to elucidate the migration routes and homing of white-spotted charr, more numerous data should be obtained from tagging experiments.

The present study demonstrated the sea-overwintering of white-spotted charr in southwestern Hokkaido. However, it has not yet known why the differences in the migration behaviour of white-spotted charr occur; some overwintering at sea and others overwintering in rivers. An aim for the future is to examine the seawater adaptability in relation to water temperatures, day-length, season, age and maturity of the anadromous white-spotted charr from respective populations in Hokkaido.

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Present and Future Charr Research: Reactions of a Salmon Biologist

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Introduction

What are the important questions in charr ecology now? The symposium papers highlighted many of these, and suggested many others, some of which I will try to explore here.

Genetics and speciation

The tools available for exploring genetic variety seem to be proliferating fast, and it is encouraging to see that the inherent genetic variety can now be measured in charr (Davidson et al. unpubl[1]., Ferguson and Liskauskas 1995, Hartley et al. 1995, Hirai et al. unpubl., Nilsson and Schmitz 1995, Phillips et al. 1995, Skulason and Snorrason unpubl., Wilson et al. unpubl.). But the attempts to establish genetic relationships between groups show a bewildering variety of results. According to the method adopted, and perhaps to the sample size, statistical trees can be drawn which show different degrees of relationship, and not always the same groupings of species. Does this mean that the whole group of charrs shares a very large amount of variety, and that there are not yet any adequate methods of quantifying enough of that variety to provide dependable measures of interrelationships? Are we also too myopic in concentrating our attention too closely on charr, or even on salmonids? The geneticists alluded to findings in human genetics (Ferguson et al. 1995): are we making sufficient use of the advances in molecular genetics in other groups? It seems that we should continue to explore the nature of genetic variation in these fishes, and particularly to search for ways of revealing the nature of genetic regulators of developmental processes.

The broad affiliations of different geographic groups of charr have been accounted for by the suggestion of multiple refuges and recolonisations after glaciation periods (Davidson et al. unpubl., Ferguson et al. 1995, Hartley et al. 1995, Svenning and Borgstrøm 1995, Wilson et al. unpubl.). Much of this sounded like speculation. The precision with which groups of charr can be separated biochemically contrasts with the imprecision of information on location and timing of residence and duration in the refuges (also of possible routes of colonisation from the refuges to the present areas of distribution). Is this because there is genuine lack of knowledge of these, or are we failing to communicate with the geologists and glaciologists? Communication may be quite good in limited geographical areas like Svalbard (Svenning and Borgstrøm 1995) - but how good is it when considering the refugia in, for example, northern Canada (Davidson et al. unpubl., Wilson et al. unpubl.)?

Ksenia Savvaitova's (1995) quotation from Mayr, about the charr species complex being a nightmare for systematists, but a paradise for evolutionary biologists - this is the real source of fascination in charrs, and leads directly into consideration of life-histories.

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[1] Some references are to unpublished oral and poster presentations. Abstracts are found in the Book of abstracts from the symposium and the titles appear in the references (editors' comment).

Life histories, ecological and parasitological interactions

There are several striking similarities between charr and Atlantic salmon *Salmo salar* L., but several differences. Both charr and salmon are distinguished by their remarkable biological flexibility, and I was delighted with the extremely pragmatic and flexible way in which Dr Savvaitova treated their taxonomy. But that flexibility shows itself in different ways. Both groups of species possess developmental plasticity (Johnson 1995, Klemetsen et al. unpubl., Reist et al. 1995, Savvaitova 1995, Skulason and Snorrason unpubl., Thorpe 1986, 1989, 1992), but whereas salmon use this rather aggressively to solve their problems (Thorpe et al. 1992), charr seem to avoid their problems rather than solve them directly. For example, in every case of interactive segregation that was discussed, it was the charr rather than the competing species that seemed to be displaced - by brown trout *Salmo trutta* in Windermere (Elliott and Baroudy 1995), by cutthroat trout *Oncorhynchus clarki* in British Columbia (Northcote 1995), by white suckers *Catostomus commersoni* in Canada (Dubois et al. unpubl., Héroux and Magnan unpubl., Venne and Magnan unpubl.), and by whitefish *Coregonus* spp. in Scandinavia (Langeland 1995). This is a very economical way of acting. The readiness to make such ontogenetic shifts seems to characterise a certain prudence in charrs (Amundsen 1995).

All life-history strategies are solutions to the problem of successful reproduction in variable environments, and so should be interpreted in relation to reproductive success (fitness). Niko Tinbergen (1963) set out a scheme of questions which had to be answered if we were to understand a behaviour pattern. These questions were:

- how did it evolve?
- how does it develop in the life-time of the species?
- how is it controlled?
- what is its adaptive advantage?

Applying these to the variety of life-history patterns in charr, I make the general assumption of a marine origin for salmonids, using freshwater as a protected but relatively unproductive environment for reproduction and as a nursery for the young, with ultimate radiation further into freshwater (Thorpe 1982). In the case of charr this has been a gradual but not irreversible specialisation, so that partial return to the marine environment is still possible when profitable (Thorpe 1994a, Berg 1995, Chernitsky et al. 1995, Christensen unpubl., Gudkov 1995, Jonsson et al. unpubl., Reist et al. 1995, Rikardsen unpubl., Strand et al. unpubl., Takami 1995). So I would disagree with Lionel Johnson's assumption that charr show a "lack of specialisation to live in the ocean" (Johnson 1995). The freshwater environment is relatively specialised and temporary compared with the more generalised and less variable marine pelagic environment. It is therefore more probable that natural selection in the freshwater environment rather than in the marine environment would induce specialisation in the fish (Thorpe 1988).

As to the ontogenetic development of life-history strategies in charr, Bjøru and Sandlund (1995) quoted that "a stunted charr was an unhappy charr." I think it would be, if it knew that was what it was being called. But what is a stunted charr? Is it really a slow-growing animal, or is it a fast growing one, which achieves maturity quickly at a small size (Klemetsen et al. unpubl), and so doesn't need to grow any bigger? In that case it is a winner, and not a loser, and so should be a happy charr.

This is not such a trivial point. David Policansky (1983) pointed out that fishes reproduce as soon as they are able to do so developmentally. The implication of that statement is that growing is secondary to reproducing, and can be regarded as what the fish does with surplus energy when it cannot mature (Thorpe 1986, 1994b). I suggest that is what is represented by the results of some of the experiments designed to try to reduce the proportion of charr maturing over winter (Pålsson unpubl., Petursdottir and Pålsson unpubl., Ugedal et al. unpubl.). At higher temperatures some of the immature charr (that is, those that had opted to postpone maturation) were growing faster than were the maturing charr at lower temperatures.

Sergei Alekseyev's (1995) studies examined the subtle differences in relative developmental timing - heterochrony - which lead to morphological differentiation, and imply genetic differences between the types which possess these different physiological rates. As solutions to fitness problems, these are genetic responses to specific environmental constraints.

Other ontogenetic responses involved niche shifts, which more often than not involve migrations of one form or another (Hammar unpubl., Jonsson et al. unpubl.). Downstream migration, and the return migration in autumn and at maturity, occurred in some (e.g. Chernitsky et al. 1995) but not in all populations, and within those populations in some but not in all individuals (Christensen unpubl., Gudkov 1995, Rikardsen unpubl.). Since migration is a general biological response to adversity (Taylor and Taylor 1977), it is appropriate to ask what was wrong with the animal's current habitat, such that it needed to leave it (Thorpe 1989b)? In one paper the question was posed another way: were the fish that left the benthic and entered the pelagic environment the winners or the losers (Klemetsen and Dahl-Hansen 1995)? I believe they have to be seen as proximate losers, but ultimate winners. For example, in Takvatn, before the population was severely reduced, juvenile fish left the benthic habitat and moved into the pelagic as smolts, and then much later, they moved to the more energetically rewarding littoral as they became adult (Klemetsen et al. 1989). After thinning of the Takvatn population, these "smolts" moved directly from the benthic to the littoral habitat, suggesting that the pelagic was a poor compromise for them (Klemetsen and Dahl-Hansen 1995).

This raises the question as to what was the internal motivation for movement from the benthic environment, and the more general question about the hormonal control of seasonal developmental changes in charr, which was Tinbergen's third question. Apart from a projected study on the differences in activation of insulin-like growth factor (IGF-1) in smolting and non-smolting charr in Japan (Hirai et al. unpubl.), I see little evidence of endocrinological studies: why? Charr contrast with salmon in tending to return to fresh water in winter (Berg 1995, Chernitsky et al. 1995, Jonsson et al. unpubl., Takami 1995, Yamamoto and Nakano unpubl.): why? Do they share the same patterns of seasonality of hormonal change evident in other salmonids? What is the annual pattern of prolactin production? Do charr produce so much prolactin in the late summer that they regain their freshwater regulation systems and are driven to select lower salinities? What about the acclimation systems of very small migrants (e.g.Vesturdalsa 1+ migrants at 4-8cm: Jonsson et al. unpubl.): do they behave like ocean-type sockeye salmon *Oncorhynchus nerka* (age 0+) in Alaska, and move gradually up a salinity gradient from fresh water to full sea water over a period of about 3 months (Heifetz et al. 1989)?

The ability to respond to prey at relatively low light intensities enabled charr species to survive competition with more dominant species which were less successful at such low light levels (Northcote 1995). The charrs' ability to shift from generalist to specialist feeders in response to competition (Amundsen 1995) is a feature of their flexibility, but at the margins of their distribution prey size may be critical, and seasonal and habitat shifts may be obligatory (Hammar unpubl.).

It was very refreshing to read a parasitologist discussing his animals in ecological and evolutionary terms (Curtis 1995). The charr seemed to deal with their parasites in a characteristically gentle manner - but what was in it for the parasite? There seem to be some interesting problems there for the evolutionary biologist. The possibility that the cestodes may modify the maturation process in charr (Curtis 1995) deserves more attention, as maturation control is a topic of great interest to charr aquaculturists (Pålsson unpubl., Petursdottir and Pålsson unpubl., Sveinsson and Haraldsson unpubl., Ugedal et al. unpubl.).

Successful maturation in charr depends on how much energy reserve is used during winter, as in other salmonids (Rowe et al. 1991). Maturation was also correlated with growth rate in spring and summer (Forseth et al. 1995; Gillet

1995, Pålsson unpubl.) but no evidence was presented for a causal link between the two. The experiments to check maturation by food restriction seemed to give contradictory results (Pålsson unpubl., Petursdottir and Pålsson unpubl., Ugedal et al. unpubl.), but I suspect that much of the source of this contradiction arose from attempting to restrict the fishes too late in the maturation cycle (Rowe and Thorpe 1990, Thorpe et al. 1990, Jobling 1995).

Tinbergen's last question (1963) - what are the adaptive advantages of these differences in life-history strategy - has been tackled in one or two experimental studies, particularly by comparison of allopatry and sympatry of morphs, or of competing species (Skulason and Snorrason unpubl., Klemetsen et al. unpubl.). Such studies show the solutions adopted in the absence of competition, and how competition can be circumvented.

Skulason and Snorrason (unpubl.) proposed a way of looking at the plasticity of charr life-histories, and identified some of the major questions which should be asked in relation to polymorphism in animals. The studies in Thingvallavatn (Jonasson 1993) illustrate well how Arctic charr adapt trophically in a relatively stable system with few competing fish species.

Management

One implication for management keeps recurring: our goals in management are at odds with those of the fish. The charr seeks to reproduce at the earliest opportunity (Policansky 1983): we seek to maximise their somatic growth. This dichotomy needs to be in the mind of the manager when he is planning his manipulations. So, for example, the question of the balance of residency versus anadromy is a question of relative reproductive advantages from the fish's viewpoint (Thorpe 1993). Also, "stunting" (that is, rapid growth and short asymptotic length) has to be considered in relation to its reproductive advantages for charr.

In aquaculture it is important that the farmer rears his fish efficiently, both for his own economic good, and to ensure that environmental impacts are minimal (Thorpe and Huntingford 1992, Thorpe and Cho in press). Malcolm Jobling (1995) described ways in which conversion rate of food into charr flesh could be maximised, while at the same time achieving relatively even growth among all the fish in the population. To do this also requires control of the way in which food is offerred to those fishes (Olla et al. 1992), and control of the densities at which they are kept (Siikavuopio and Jobling 1995). If food is delivered at a fixed point, on a fixed time schedule, then a dominant fish can defend a feeding station. If the cage is saturated with food throughout its volume all at the same time, then it does not pay the dominant individuals to defend anything, and all fish, irrespective of their social rank, will get an adequate meal. Furthermore, fish do not feed all the time. Consequently it pays to devise systems in which it is the fish which determine when the food is delivered. Such self-feeding systems are being developed for salmon in Norway (Juell et al. 1994) and Australia (Blyth 1993), and for charr in Sweden (Eriksson and Alanärä 1992).

Finally, the frequent change in emphasis from describing everything in terms of population mean values, to examining the nature of individual variation by considering variances within distributions is very encouraging. For a group of people interested in the nature of variation in such flexible organisms, this is particularly important for understanding such variety.

The Future

Based on this assessment, I consider that important questions in charr ecology that should be tackled include the following:

Genetics

How do we resolve the conflicting information on interspecific groupings?

Biogeography

Where were the refugia? When were they occupied? How did colonisation proceed?

Behaviour/Ecology

Why do charr shift habitats? What is wrong?

Behaviour/Physiology

Why do charr leave the sea in winter? Why behave differently from salmon?

Physiology/Endocrinology

What is the internal motivation for movement (migration)?

Endocrinology

What are the seasonal patterns of pituitary and hypothalamic hormone production?

Conservation/Management

How do we maintain genetic continuity?

Aquaculture

How do we maximise production while minimising environmental impact?

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Guide to authors

General editorial practice

Submit the manuscript in triplicate.

All manuscripts submitted are considered for publication on the understanding that they have not been published, submitted, or accepted for publication elsewhere.

Manuscripts are submitted to reviewers for evaluation of their significance and soundness. Authors will generally be notified of acceptance, rejection, or need for revision within three months.

Decisions of the editors are final.

Manuscripts are edited to improve communication between the author and the readers.

Authors will receive one set of first proofs.

Authors are recommended to keep their papers short.

Fifty reprints are supplied free of charge. An additional number may be ordered at cost. Price list and order forms for reprints are sent with proofs.

Manuscripts

Language

Manuscripts should be in English. Linguistic usage should be correct. Write in a clear style. Avoid extensive reviews in the Introduction and Discussion. Cite only essential sources of a theory or opinion.

Title

The title should be brief and contain words useful for indexing and information retrieval.

Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article.

Keywords

Five keywords should be given for indexing and information retrieval.

Text

The first page should contain only the title and author's name and address. Begin the text on page two. The manuscript should be type-written, double-spaced with wide margins and on one side only of good quality paper. Word processor generated manuscripts should be in upper and lower case letters of typewriter quality font. Manuscripts printed by 7 x 9 or 9 x 9 dot matrix printers will not be accepted for publication or review. Underlinings in the text should be avoided. After re-submission please enclose a diskette containing the final version of the manuscript in any DOS-wordprocessing program (e.g. wp 5.1, ws, ms-world).

Illustrations

Submit each diagram, graph, map or photograph in one original and three copies. All illustrations should bear author's name. Tables and legends of illustrations should be written on separate sheets. Do not incorporate the legend in the figure itself. Tables and illustrations should be comprehensible without reference to the text.

Colour plates may be included at the author's expense.

Plan your illustrations for the smallest size possible. Figures, letters, and other symbols on illustrations should be drawn so large that they will be at least 1.5 mm high in the final print.

Units

Use SI units as far as possible.

Nomenclature

Binomial Latin names should be underlined and used in accordance with International Rules of Nomenclature.

References

In the list of references the following usage should be conformed to:

Journal

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshw. Res., Drottningholm 55: 144-171.

Book

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology. An evolutionary approach. Third edition. - Blackwell Scientific Publications, Oxford. 482 p.

Chapter

Krebs, J.R. and R.H. McCleery. 1984. Optimization in behavioural ecology. p. 91-121. - In: Krebs, J.R. and N.B. Davies (eds.) Behavioural ecology. An evolutionary approach. Second edition. Blackwell Scientific Publications, Oxford.

In the text references are given:

Svärdson (1976) or, at the end of a sentence (Svärdson 1976).

Titles of journals should be abbreviated according to the World List of Scientific Periodicals. If in doubt, give the title in full.

Do not refer to unpublished material.

Acknowledgments

Keep them short.

Symbols and Abbreviations

The following symbols and abbreviations, as well as others approved for the Systeme International d'Unités (SI), are used in this journal without definition. Any others must be defined in the text at first mention, as well as in the captions or footnotes of tables and in fiugres or figure captions. A variable divided with another variable should be noted as the following example L per min is L min^{-1}.

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h", "min", and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Prefixes

giga (10^9)	G
mega (10^6)	M
kilo (10^3)	k
milli (10^{-3})	m
micro (10^{-6})	μ
nano (10^{-9})	n
pico (10^{-12})	p

Time and Temperature

day	d
degrees Celsius	°C
hour (spell out for diel time)	h
kelvin	K
minute	min
second	s

Spell out year, month, and week.

In Table and Fig.:

year	yr
month	mo
week	wk

Weights and Measures

centimeter	cm
gram	g
kilogram	kg
kilometer	km
liter (exception to SI)	L
meter	m

Spell out hectare and tonne.

Mathematics and Statistics

all standard mathematical signs, symbols, and abbreviations base of natural logarithm	e
common test statistics (F, t, etc.)	
correlation or regression coefficient (multiple)	R
correlation or regression coefficient (simple)	r
degree (angular)	°
degrees of freedom	df
expected value	E
intercept	α
logarithm (specify base)	log
minute (angular)	'
not significant	NS
percent	%
probability	P
probability of type I error (false rejection of null hypothesis)	$P\alpha$

probability of type II error (false acceptance of null hypothesis)	$P\beta$
radian	rad
sample size	N
second (angular)	''
standard deviation	SD
standard error	SE
variance	V or var

Physics and Chemistry

all atomic symbols	
alternating current	AC
ampere	A
becquerel	Bq
candela	cd
chemical acronyms listed in Webster's dictionaries (DDT, EDTA, etc.)	
coulomb	C
dextro	D
direct current	DC
electron volt	eV
equivalent	eq
farad	F
gray	Gy
hertz	Hz
hydrogen ion activity (negative log of)	pH
joule	J
levo	L
lumen	lm
lux	lx
molar	M
mole	mol
newton	N
normal	N
ohm	Ω
ortho	*o*
para	*p*
pascal	Pa
per mille (per thousand)	‰
siemens	S
tesla	T
trishydroxymethylaminomethane	tris
volt	V
watt	W
weber	Wb

General (some are restricted)

compass directions (maps and coordinates): east	E
north	N
south	S
west	W
et alii	et al.
et cetera	etc.
filial generation	F
for example	e.g.,
international unit	IU
months (tables, figures): first three letters (Feb, Jun, etc.)	
ploidy	n
sex (tables, figures, hybrid crosses): female	♀
male	♂
that is	i.e.,

Word List

The spelling of the following words is frequently inconsisten in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

CONTENTS

Proceedings of the
Third International Charr Symposium
June 13-18 1994, Trondheim, Norway

Keynote lecture

Invited papers

Closing lecture