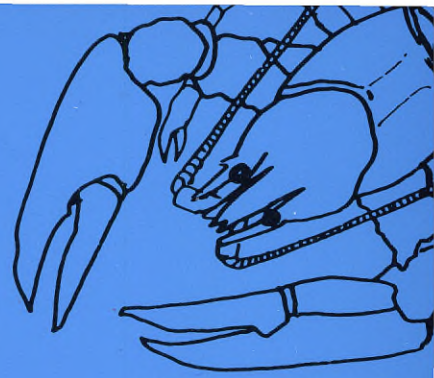




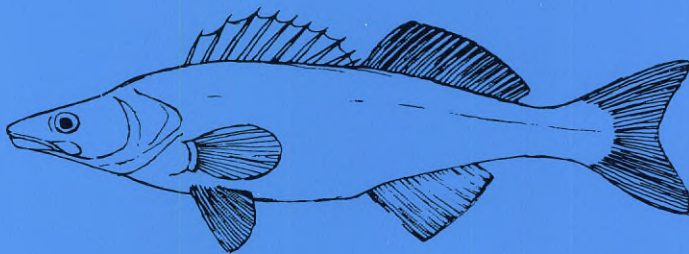
Det här verket har digitaliserats vid Göteborgs universitetsbibliotek och är fritt att använda. Alla tryckta texter är OCR-tolkade till maskinläsbar text. Det betyder att du kan söka och kopiera texten från dokumentet. Vissa äldre dokument med dåligt tryck kan vara svåra att OCR-tolka korrekt vilket medför att den OCR-tolkade texten kan innehålla fel och därför bör man visuellt jämföra med verkets bilder för att avgöra vad som är riktigt.

This work has been digitized at Gothenburg University Library and is free to use. All printed texts have been OCR-processed and converted to machine readable text. This means that you can search and copy text from the document. Some early printed books are hard to OCR-process correctly and the text may contain errors, so one should always visually compare it with the images to determine what is correct.





Nordic Journal of Freshwater Research



No 67 1992

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, evolution, genetics and limnology. The main emphasis of the journal lies both in descriptive and experimental works as well as theoretical models. 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, lack of funds for page charges will not prevent an author from having a paper published.

The journal will be issued annually.

Submission of manuscripts

Manuscripts should be sent to the Editors:
Nordic Journal of Freshwater Research,
Institute of Freshwater Research,
S-178 93 DROTTNINGHOLM, Sweden.

Deadline for No. 68 (1993) is 1 December, 1992.

Subscription information

Inquiries regarding subscription may be addressed to the Librarian:

Institute of Freshwater Research,
S-178 93 DROTTNINGHOLM, Sweden.

Annual subscription price including V.A.T. SEK 250.

Editorial Board

Magnus Appelberg, Editor, Institute of Freshwater Research, Sweden

Torbjörn Järvi, Editor, Institute of Freshwater Research, Sweden

Lennart Nyman, WWF, Sweden

Jens-Ole Frier, Aalborg University, Denmark

Hannu Lehtonen, Finnish Game and Fisheries Research Institute, Finland

Árni Ísaksson, Institute of Freshwater Fisheries, Iceland

Bror Jonsson, Norwegian Institute for Nature Research, Norway

Alwyne Wheeler, Epping Forest Conservation Centre, England

Lionel Johnson, Freshwater Institute, Canada

Lars-Ove Eriksson, Umeå University, Sweden

Anders Klemetsen, Troms University, Norway

Jan Henricson, Kälarna Experimental Research Station, Sweden

Thomas G. Northcote, University of British Columbia, Canada

ISSN
1100-4096

Nordic Journal of Freshwater Research

No 67 1992

formerly
Report of the Institute of Freshwater
Research, Drottningholm

ISSN
1100-4096

BLOMS BOKTRYCKERI AB, 1992

Contents

Tom G. Northcote	Migration and Residency in Stream Salmonids - some Ecological Considerations and Evolutionary Consequences _____	5-17
Martin-A. Svenning Astrid Smith-Nilsen Malcolm Jobling	Sea Water Migration of Arctic Charr (<i>Salvelinus alpinus</i> L.) Correlation between Freshwater growth and Seaward Migration, based on back-calculation from Otoliths _____	18-26
Björn Malmqvist	Stream Grazer Responses to Predator Odour - an Experimental Study _____	27-34
Anders Klemetsen Harald Muladal Per-Arne Amundsen	Diet and Food Consumption of Young, Profundal Arctic Charr (<i>Salvelinus alpinus</i>) in Lake Takvatn _____	35-44
Carl Folke Håkan Olsén Svante Winberg Rickard Bjerselius Lars Karlsson	Differences in Rheotactic Response and Attraction to Population - Specific Odours in Baltic Salmon (<i>Salmo salar</i> L.) Parr _____	45-51
Odd Terje Sandlund	Differences in the Ecology of two Vendace Populations separated in 1895 _____	52-60
Erik Degerman Berit Sers	Fish Assemblages in Swedish Streams _____	61-71
Trygve Hesthagen Ola Hegge Jostein Skurdal	Food Choice and Vertical Distribution of European Minnow, <i>Phoxinus phoxinus</i> , and Young Native and Stocked Brown Trout, <i>Salmo trutta</i> , in the Littoral Zone of a Subalpine Lake _____	72-76
Eva Brännäs Bo-Sören Wiklund	Low Temperature Growth Potential of Arctic Charr and Rainbow Trout _____	77-81
Anders Jonsson	Shelter Selection in YOY Crayfish <i>Astacus astacus</i> under Predation Pressure by Dragonfly Larvae _____	82-87
	Notes and Comments _____	88-101

Migration and Residency in Stream Salmonids - some Ecological Considerations and Evolutionary Consequences

TOM G. NORTHCOTE

Department of Zoology, University of British Columbia
Vancouver, British Columbia V6T 2A9, Canada

Abstract

The range of patterns in and partitioning between migratory and residential behaviour is examined for several species of salmonid fishes to determine common factors which may promote the alternate strategies. In particular, habitat characteristics, preferences, and movement versus residency of salmonid populations in North America, Europe and Asia are used to illustrate evolutionary pressures that may be shaping such behaviour. Isolated headwater resident populations of salmonids in marginal habitats may represent important sources of genetic diversity which need protection and preservation.

Introduction

The potential advantages and biological consequences of fish migration in streams has been repeatedly considered and frequently reviewed over the last several decades (Nikolsky 1963, Northcote 1967, 1978, 1984, Harden Jones 1968, 1981). Furthermore in recent years there have been several attempts to quantify relative costs and benefits of such behaviour in terms of productivity and fitness (Gross 1987, McDowall 1988, Gross et al. 1988). Rightly so, the phenomenon of salmonid migration, often involving enormous numbers of large fish moving over remarkable distances to arrive with high precision on the natal spawning grounds from which they arose, has captured much scientific attention in attempts to uncover the mechanisms involved. But the other side of the migration coin for stream salmonids often evident in the same watershed - that of residency - also can generate considerable scientific enquiry and concern over protection of local stocks and special habitats, as relevant questions are explored.

How little movement do resident populations really exhibit in streams? What environmental conditions are associated with stream residency, or perhaps even promote it? Does the extent and pattern of local movement change seasonally,

latitudinally, or over the age of the individual? Why do some individuals or even some populations of stream salmonids apparently not migrate, if the advantages in doing so seemingly are so great? And finally, what may be the evolutionary consequences and adaptive significance of adopting a stream resident rather than a migratory pattern of behaviour? These are some of the questions which I want to consider by reviewing the recent literature mainly for North American and European populations of stream char and trout, and by developing my synthesis and comments on the two contrasting phenomena.

Post-emergence dispersal and residency

Although salmonid alevins in their gravel redds undergo an initial descent and later an ascent, each having lateral components (Dill 1969, Carey and Noakes 1981, Godin 1982), these movements take place in a confined spatial scale of usually less than a metre. Even prior to hatching, trout eggs may be displaced by spates nearly a metre downstream without being washed out of stream gravels (Crisp 1989). Emergence itself is not necessarily a single fixed event, as very young fry may at first make only short exploratory movements out of the

gravel followed by reentry either on-site or a short distance downstream. Emergence may be largely diurnal [rainbow trout, *Oncorhynchus mykiss*, 10 °C (Dill 1970)], nocturnal [rainbow trout, 15 °C (Dill 1970)] or about equal between night and day [Atlantic salmon, *Salmo salar*, 10 and 15 °C (Dill 1970)].

But once the young become permanently free-swimming in a stream they are in a situation where greater movement, whether short or long distance, becomes possible. Because of their small size and limited energy reserves, the fry if away from the stream edge or bottom can be vulnerable to downstream displacement, especially if stream current velocities much exceed 10 cm s⁻¹; the higher the velocity the greater the displacement (Ottaway and Clarke 1981, Ottaway and Forrest 1983, Heggenes and Traaen 1988). Detailed stream channel experiments on dispersal rates have shown patterns of downstream movement to be more complex (Crisp and Hurley 1991a). Young Atlantic salmon (*S. salar*) had high dispersal rates at low water velocity (7.5 cm s⁻¹) and lower rates at the higher velocities tested (25 to 70 cm s⁻¹). Brown trout (*S. trutta*) had the lowest dispersal rate at 25 cm s⁻¹, a slightly higher rate at 7.5 cm s⁻¹ and increasingly higher rates at velocities above 25 cm s⁻¹. Changes in water velocity as well as day and night illumination also had important effects on dispersal rate of the young (Crisp and Hurley 1991b, Crisp 1991). Critical water velocities for displacement increase at higher temperature and fry length (Heggenes and Traaen 1988), so flow increases up to 10 times greater than base did not increase downstream movement of 6.7-16 cm brown trout in a small stream (Heggenes 1988b).

Large scale downstream migration of salmonid fry may occur shortly after their emergence in streams flowing into rearing lakes or large rivers (for examples see Northcote 1969, 1978, 1984), but for stream resident forms there seems to be much variability between species and stocks in the extent of such movement. In some, considerable numbers move appreciable distances downstream soon after emergence (Solomon 1982, Solomon and Templeton 1976, Baglinière et al. 1989). In others, dispersal is mostly but not entirely down-

stream and after about a week, fry emerging from one redd may be relatively evenly dispersed for up to 100 m or more downstream (Le Cren 1973). In still others, very few young fry apparently migrate downstream (Northcote 1969, Elliott 1987, 1989, Moore and Gregory 1988a, Northcote and Hartman 1988).

Where the stream spawning habitat is close to or juxtaposed with early juvenile rearing habitat, dispersal movements may take place over only a few metres or less. Headwater populations of cutthroat trout (*O. clarki*) in Cascade Mountain streams of Oregon provide good examples of such restricted fry movement to stream "lateral" habitat (Moore and Gregory 1988a). For a migratory brown trout population (Black Brows Beck) with a temporary stream rearing phase, the initially resident fry are heavier at given length than the first out-migrants, the latter having empty stomachs and appearing moribund (Elliott 1990). Nevertheless, the resident brown trout living above a falls in nearby Wilfin Beck begin life at a smaller size than those in Black Brows Beck because they arise from small adult females which invest about half as much energy into egg production as do those in the other stream (Elliott 1988).

Heland (1980a,b) described the outmigrant brown trout fry from an artificial stream as being smaller and having "weaker growth" than the non-migrants. Furthermore the migrants moved downstream only at night and established territorial mosaics during the day, but later than did the non-migrants. Rainbow trout resident above falls in Kokanee Creek, British Columbia, were lighter for a given length than were below falls migrants, but in another stream (Deer Creek) there were no significant differences in length-weight relationship between above and below falls trout stocks (Northcote and Hartman 1988). The smaller under-yearling redspot masu-trout (*O. rhodurus*) resident in a Japanese mountain stream evidently undergo a density-dependent downstream migration during summer and autumn (Nakano and Nagoshi 1985).

Thus there seems to be much species and stock-specific variability in the extent of migration shortly after emergence in stream-dwelling populations of trout. For those in small headwater or

above waterfall reaches, movement often may be limited to only a few metres, except for the fraction of apparently weaker early outmigrants in poor condition.

Territoriality and home range

Very shortly after emergence, young stream-resident char and trout fry establish territories which they defend at least during the day. Aggressive young-of-the-year brook trout (*Salvelinus fontinalis*) fry are 13% larger than their non-aggressive conspecifics in the same stream and area and on the same day (Grant 1990). Habitat characteristics may influence the degree of aggressiveness in brown trout juveniles inasmuch as rough stream bottom provides visual isolation between fish, resulting in smaller average territory size and presumably higher fry densities (Heggenes 1988a). In small headwater streams of the Cascade Mountains, Oregon, resident cutthroat fry on emergence establish territories in lateral habitats which they maintain at least until the end of summer (Moore and Gregory 1988a). Manipulation experiments with lateral habitat clearly demonstrate its importance in regulating fry density and downstream emigration (Moore and Gregory 1988b). Territory

size shows a strong positive regression to body size for several species of stream dwelling salmonids (Grant and Kramer 1990).

Although trout fry holding position in streams during the day set up territories, these may not be maintained during the night. Using infra-red viewing apparatus to observe distribution of rainbow trout fry in a small stream at night, I was able to record a lateral shift in fry abundance between night and day (Northcote 1962). Chapman and Bjornn (1969) showed that individual rainbow (steelhead) trout juveniles moved onshore at night in Idaho streams and rivers. As resident cutthroat fry became older and larger in Oregon streams, they held position further offshore (Moore and Gregory 1988a). Therefore territories maintained by juvenile salmonids in streams can shift diel as well as seasonally in location so the fish sequentially occupy different positions especially over their first year of growth. Seasonal and diel shifts in specific home sites have also been reported in large stream resident brown trout (Clapp and Clark 1990).

Estimates of home range size depend on stream dimensions, velocity, habitat features, salmonid species, length, and age to mention but a few of the more obvious factors. Those given for fry (Table 1) indi-

Table 1. Some recent estimates of home range for three species of stream resident trout.

Species	Stage	Home range (m)	% recapt. in home range	Stream	Source
Brown	0+	up to 370 ^a		Aberfeldy River	Jackson (1980)
Brown	1+ & older	2.4-22	55-74	Alwen River	Cane (1974)
Brown	"	c.10	up to 93	Gwyddon River	Harcup et al. (1984)
Brown	"	46	88	Llyn Teg. Wel. Dee	Woolland (1972)
Brown	"	50	66	Hengselva River	Heggenes (1988a)
Brown	"	60		Aberfeldy River	Jackson (1980)
Brown	"	98-108	62-65	Doyleston S. Branch	Burnet (1969)
Brown	2+ to 9+	45-200	97	Tverrelva River	Hesthagen (1988)
Cutthroat	0+	25-100 ^a		Wash. & Oreg.	Trotter (1989)
Cutthroat	fry to adult	200	97	Wash. streams	Fuss (1982)
Cutthroat	1+ & older	50	80	Musqueam Creek	Heggenes et al. (1991)
Rainbow	1+ & older	200	nearly 100	Estibere	Dumas (1976)

^aprobably represents initial dispersal distance

Table 2. Characteristics of three streams where resident trout movement has been studied in detail.

Stream	Mean width m	Mean depth cm	Mean flow m ³ s ⁻¹	Species	Source
Hengselva Norway	6.9	22.8	0.37	brown	Heggenes (1988c)
Gwyddon S. Wales	3.6	16.0	0.20	brown	Harcup et al. (1984)
Musqueam Brit.Col.	2.5	15.0	0.10	cutthroat	Heggenes et al. (1991)

cate ranges up to a few hundred metres but they probably incorporate the overall dispersal distance. Home ranges for yearling and older salmonids are smaller, usually a few tens of metres. Local stream substrates may be marked by intraspecific odours deposited by trout who use these cues to remain within or return to home areas (Halvorsen and Stabell 1990).

The restricted movement of stream resident trout is nicely illustrated by studies on three progressively smaller systems (Table 2). In a Norwegian river some brown trout moved downstream over 300 m, whereas those in a smaller Welsh stream did not go further than 200 m downstream. Nearly a third of all 587 cutthroat trout (mean length 12.1 cm, range 9-32 cm) recaptured in the very small Musqueam Creek, British Columbia, were taken within 1 m of their previous site, and over 63% of the recaptured fish had not moved more than 10 m (Heggenes et al. 1991). There was a slight skewness in the distribution of movement in a downstream direction, a feature also evident in the other two studies. Over the sampling period (February to the end of August) there were only small changes in the extent of movement, with slightly less movement in winter at low water temperatures and more in spring and summer at higher flows and increasing water temperatures.

Analysis of the pattern of movement by stream resident trout suggests that there is a large static fraction and a small, mobile fraction of individuals in the populations, (Solomon and Templeton 1976, Hesthagen 1988, Heggenes et al. 1991), the latter not necessarily representing just misfits and ejects but possibly also explorers and colonizers of new areas and habitats of advantage to the population in general.

Food resources, foraging and residency

The idea that the food resources of a stream and the ability of salmonids to obtain it could play a major role in setting not only their population density but also their residency has had a long history. Chapman (1966) drew together much of the earlier field and experimental work on stream salmonids relevant to this notion. Symons (1971) showed that young Atlantic salmon, through behavioural interaction, adjusted population density in response to available food. That drift prey abundance could change territory size of young rainbow trout fry residing in stream channels and thereby affect their emigration rate was demonstrated by Slaney and Northcote (1974).

Thus the stage was set for the series of experimental studies in the 1980s which related food resources and juvenile foraging behaviour to stream residency. Stream salmonids apparently exploit for long periods specific velocity sheer zones as feeding stations because these require low energy expenditure by the fish (see for example Bachman 1984, Fausch 1984). Dominant brook and brown trout hold stream positions which give them the maximum potential "profit", i.e. they select focal points on the basis of water velocity characteristics and food supply to maximize net energy gain (Fausch 1984, Fausch and White 1986). A reduction in food abundance could bring about emigration of small stream-dwelling cutthroat trout within one week (Wilzbach 1985). On the other hand Mesick (1988) found that even after 2 months of starvation brown trout could maintain residency in an experimental stream providing their condition

factor remained above about 1.3. The smaller trout did emigrate in response to short term lack of food, probably because of their higher metabolic rates and smaller energy reserves, but the larger trout did not. Mesick (1988) suggests that this may explain why the small (c. 25 mm) rainbow trout fry in the experiments of Slaney and Northcote (1974) showed an emigration response to food reduction within 2 days.

Aggressiveness directly affects the foraging success of young salmonids in streams as Grant (1990) demonstrated for young-of-the-year brook trout. The larger aggressive fry maintained a 29% larger foraging radius in their territories, and made significantly more feeding attempts per unit time than did the smaller non-aggressive fry.

Range of movement associated with foraging may increase considerably in older and larger stream resident trout (Clapp and Clark 1990). Wild brown trout adults (greater than 40 cm) in the South Branch of the Au Sable River, Michigan, ranged from as little as a few hundred metres to over 33 km. Short range foraging activity varied both seasonally as well as dielly and may be related to a size-dictated shift from drift feeding to piscivory.

Refuge migration and residency

Stream resident populations of char and trout have long been known to change their habitat at the onset of winter when conditions in areas occupied from spring to autumn become unfavorable. Cooper (1953) noted such behaviour in Michigan brook trout that moved from pools into dense cover in winter. Juvenile brook trout in Lawrence Creek, Wisconsin, moved predominantly downstream to overwinter survival areas (Hunt 1969), but after habitat improvement to increase pool area and streambank cover, such movement decreased (Hunt 1974). Similarly in two Idaho streams, there was little movement of brook trout young if the population didn't exceed the winter cover capacity (Bjornn 1971), whereas resident rainbow trout emigrated downstream to overwinter in coarse rubble of the Lehmi River which upper tributaries lacked.

A series of detailed recent studies has greatly increased our understanding of overwintering behaviour and residency in several species of salmonids. Both brook and brown trout make short movements, changing their summer habitat to occupy low velocity edge habitat with cover in winter (Cunjak and Power 1986a). Feeding decreases then and the number of trout resting on the bottom increases. Brook trout resident in tributaries have a lower rate of metabolic reserve use than do those of migratory stocks overwintering in the mainstem river (Cunjak and Power 1986b), although the physiological parameters measured had greater variability in tributary stocks (Cunjak 1988). Even though some feeding continues throughout winter, the condition factors for both brook and brown trout decline and remain low until spring (Cunjak and Power 1987), perhaps because assimilation efficiency is reduced at cold temperatures. Adult brook trout resident in high elevation Wyoming streams move into low velocity (less than 15 cm s^{-1}) areas in late autumn but remain active over the winter as shown by the radiotelemetry studies of Chisholm and Hubert (1987).

Trout (mainly cutthroat) resident in Carnation Creek on the west coast of Vancouver Island, British Columbia, make frequent short distant movements to use its small, temporary floodplain tributaries especially in early spring and late autumn (Hartman and Brown 1987). But on the inner coast of southern British Columbia environmental conditions for trout in small streams may become most severe in late summer and early autumn, when low discharge can result in isolated pools becoming low in dissolved oxygen. Such is the case in Cutthroat Creek, a tributary to Musqueam Creek entering the North Arm of the Fraser River (Northcote and Hartman 1988). At its mouth Cutthroat Creek often declines to a minimum discharge of about 1 L s^{-1} in late summer but by mid-autumn flows gradually increase, reaching a maximum in the order of 100 L s^{-1} in winter. In summer, temperature in the lower reaches of the creek may approach $20 \text{ }^{\circ}\text{C}$. The headwaters of the creek go completely dry during summer and autumn, but many of the deeper middle reach pools, though

isolated, remain partially filled by groundwater with temperatures rarely over 15 °C. Once the middle reach pools become isolated, dissolved oxygen content can become severely depleted (1-2 mg L⁻¹). Although some resident cutthroat trout young and adults survive in isolated pools throughout late summer and autumn at oxygen levels below 2 mg L⁻¹, as water level recedes cover is greatly reduced and predation, especially from raccoon, becomes severe.

Reproduction and residency

At maturity, adults of stream resident salmonid populations may migrate short distances, usually upstream, to reach favourable reproductive habitat. Such behaviour has been described for brook trout populations (McFadden 1961), as well as for both brook trout and landlocked Atlantic salmon (Leclerc and Power 1980). Adult stream resident brown trout often limit movement to a few hundred metres or less except at spawning time (Shuck 1945, Stefanich 1952, Solomon 1982). Headwater brown trout adults living above a dam on the Søre Osa river system in Norway move into small tributaries to spawn (Jonsson and Sandlund 1979). A small branch of the Scorff River in Brittany (France) supports both stream resident and migratory populations of brown trout (Baglinière et al. 1989). The resident population spawns only in the uppermost reaches of the system whereas the migratory population spawns mainly in lower reaches with some overlap between populations occasionally in the middle reaches. In one year (1977) resident trout spawned in the upper reaches before migrant spawners entered, the latter spawning first in the lower reaches with spawning migrants gradually spreading upstream into the middle reaches. In another year (1980) migrants started spawning in the lower reaches first. Thus there seemed to be some spatial separation between the spawning populations, but not temporal separation. In some streams suitable spawning sites for resident cutthroat trout occur in or very near to the

lateral habitats used for juvenile rearing so there may be little migratory movement required (Moore and Gregory 1988a). A sequence of waterfalls, cascades and rapids on each of several small interior streams in British Columbia restrict resident rainbow trout populations to short sections of spawning and rearing habitat where the only possibility for movement is downstream over barriers preventing their upstream return (Northcote and Hartman 1988); downstream movement seems to be minimal in resident populations. The resident cutthroat trout in the Musqueam Creek system (loc. cit.) can move only a few hundred meters upstream before barriers partially block access to upper reaches of the stream. Lack of suitable spawning habitat further restricts reproductive movement in these populations. Thus for several reasons stream resident trout often must spawn close to where they reside.

Resident trout and char in headwater streams, compared to their downstream counterparts, usually are smaller and less fecund, mature at an earlier age, but tend to spawn later in the season. This in general held for interior rainbow trout and coastal cutthroat trout populations in British Columbia (Northcote and Hartman 1988). It also was the case for brown trout populations in the Søre Osa river system in Norway examined by Jonsson and Sandlund (1979).

Several species of salmonids demonstrate sexual differences in the extent of reproductive migration, the females undergoing more extensive migrations than the males. This characteristic has long been known in Atlantic salmon (see for example Österdahl 1969) and also occurs in brown trout where the male to female ratio is much lower not only in the sea-going fraction of the population (Le Cren 1984) but also for the migratory part of inland populations (Crisp et al. 1984). Presumably there is a selective advantage for females to migrate to productive feeding habitats where their resultant large increase in size can be realized in higher fecundity and fitness, but this is not required in the males.

Genetic control of stream residency?

Do stream resident and migratory forms of char and trout only represent "ecophenotypes" within a single gene pool (Skaala and Naevdal 1989), or do they each represent genetically distinct gene pools, showing adaptation to special environmental conditions? This question has attracted the attention of Scandinavian salmonid biologists for some forty years (see for example Alm 1949, Svårdson and Nilsson 1964, Nordeng 1983, Skaala and Naevdal 1989, Hindar et al. 1991). In 1949, when studying streams tributary to the Arrow and Kootenay lakes in British Columbia, I first became interested in the strong selective pressure that waterfalls might direct upon the migratory behaviour of salmonids living upstream from one-way barriers to movement. But it was 20 years later before I published in part (Northcote 1969) results of initial studies on one of the streams, Kokanee Creek. Thereafter we showed that the rainbow trout from above and below a major waterfall on this system possessed meristic as well as lactate dehydrogenase (LDH) genotype differences (Northcote et al. 1970). In addition when progeny of above and below waterfall stocks from the creek were reared under the same conditions (light, temperature, space, food), not only did they demonstrate adaptive differences in directional response to water current, but also showed significant differences in growth rate and maturity which seemed to confer advantages to fish residing above waterfalls (Northcote 1981). Young rainbow trout homozygous for the above falls LDH form exhibited a more positive response to water current than did those homozygous for the form common in the below falls stock (Northcote and Kelso 1981). The above falls LDH isozyme was more efficient in lactic acid conversion than the below falls form (Tsuyuki and Willisroft 1973) and appeared to confer greater swimming stamina to young trout of the above falls form (Tsuyuki and Willisroft 1977). Together these several differences in the above falls stocks of rainbow trout under genetic control may adapt the fish for residence in high gradient headwater streams.

An intensive study including field, rearing and transplantation experiments with Arctic char from small resident, large resident, and anadromous populations of the Salangen River system, Norway (Nordeng 1983) showed that both genetic and environmental factors were involved in the control of their resident or migratory behaviour.

Much work has been done over the last decade on genetic control of migratory versus resident behaviour in brown trout populations. Field experiments conducted by Jonsson (1982) indicated that the much less migratory behaviour of an above falls stock was due to genetic differences. Nevertheless he pointed out that resident fish could arise from diadromous parents and vice versa, as Rounsefell (1958) suggested for brown trout and Nordeng (1983) for Arctic char. After a long series of studies on a migratory brown trout population in Black Brows Beck and a resident population in Wilfin Beck, Elliott (1989) concluded that there was strong evidence for genotypic differences between the stocks controlling their migratory behaviour. Skaala and Naevdal (1989) studied 10 different enzyme systems involving some 30 loci in stream resident and anadromous brown trout from three watersheds. Significant genetic differences were found between the two life history forms in all three watersheds. In two of them genetic diversity (mean heterozygosity, H) was higher in resident (8.9, 5.3%) compared to the anadromous populations (4.7, 4.0%).

Vuorinen and Berg (1989) working on 38 protein loci could find no strong evidence of genetic mixing between non-anadromous Atlantic salmon stocks (residing above waterfalls in the upper reaches of the Namsen River, Norway) and anadromous stocks, even though the latter had been stocked as fry in the headwaters since 1950. Recent mitochondrial DNA studies on sympatric populations of anadromous and nonanadromous Atlantic salmon in a Newfoundland river show them to be genetically distinct (Birt et al. 1991).

In general there is much evidence to support the idea that stream resident and migratory forms of salmonids can be genetically distinct with a number of morphological, behavioural and physiological differences which appear highly adaptive for the

two life history strategies. Strong genetic control for residency seems to be particularly well developed in populations living in habitats (headwater streams, reaches above waterfalls, or other barriers) where emigration could be disadvantageous. In more "open" stream systems where upstream access is not so restricted, genetic control seems to be relaxed so that migratory and resident individuals apparently occur within one stock, as in brown trout inhabiting the Voss River system (Jonsson 1985, 1989, Hindar et al. 1991). Nevertheless environmental conditions, particularly those affecting growth rate, can markedly alter the degree of residency expressed (Jonsson 1985, Hindar et al. 1991). Where the effects of life history pattern (e.g. migration or residency) and geographical isolation (e.g. spawning location) can be separated, the latter consistently shows larger genetic differentiation than the former (Hindar et al. 1991).

Discussion

How resident are the residents?

After emergence, underyearlings of resident trout and char populations may move up to a few hundred metres (usually downstream) before taking up territories, but for others where spawning and juvenile rearing habitat are close or even superimposed, there may be little or no appreciable movement.

Territory establishment by juveniles usually results in smaller, weaker ones being forced out of local rearing habitat, thereby producing a downstream exodus of this fraction of the population. The feeding territories initially defended over the short run (days) are only a few body lengths in size but these may be abandoned periodically or temporarily, resulting in older fish developing a home range in the order of a few metres and eventually tens of metres. Thus territory and home range size increase ontogenetically. With increasing size the juveniles "outgrow" their territories occupied as fry and shift holding position probably in relation to a trade-off between energetic benefit and predation risk (pers. comm. Dr. K.D. Fausch).

In temperate or subtemperate latitudes, there are regular as well as intermittent changes in environmental conditions which may cause stream resident salmonids to move to refuge habitat, and thereby give up one site of residence for another. Often these shifts occur just prior to the onset of winter but they may also occur at other times. Again the distances involved may not be large, some leading to lateral shifts of only a few metres in small streams.

Location of suitable sites for reproduction seems to cause the most extensive movement in resident salmonid populations, but even here the distances involved may only be a few hundred metres and sometimes much less. For some cutthroat trout populations in small streams, feeding and reproductive habitats can be virtually identical.

What conditions promote residency?

General environmental features can exert a major effect on the degree of residency developed by salmonids inhabiting streams. In populations living above barriers to upstream movement (waterfalls, rapids, dams, culverts) there usually is very limited downstream movement of young or adults (Northcote and Hartman 1988), presumably because of sharp selection against such behaviour. On a smaller scale, the type of stream bottom can be important in territory establishment so greater densities of young can be accommodated in stream sections with coarse substrate or high complexity of cover. Consequently, one might expect a higher degree of residency in populations inhabiting stream sections with these characteristics. Furthermore in streams where spawning and rearing habitats are abundant and close together, movement for the life stages involved should be low. On the other hand where these two basic requirements are sparse, and widely spaced, residents have to make more extensive movements. A similar argument could be developed for the location of refuge and rearing habitats.

An abundant food supply, through its effect on territory size, also should be an important factor in promoting residency in stream salmonids. If prey drift rates are low, as they may well be in many headwaters (low order systems where incident

light is reduced because of closed canopy, with lower temperatures and lower dissolved nutrients), then there should be selection for low trout population density. This could be accomplished by a shift towards small body size and thereby reduced fecundity, a common characteristic in headwater stream salmonids. In addition, above falls forms of trout may start free-swimming life at a smaller size because of genetically determined differences in egg weight (Elliott 1988) or in lower growth rate (Northcote 1981). In the case of the Cutthroat Creek headwaters where the trout become isolated in small pools from mid-summer to mid-autumn, food supply must become greatly reduced because invertebrate drift is stopped leaving only the small area of pool bottom and water surface (the latter receiving terrestrial inputs) as potential sources. Trout surviving in such pools became progressively more emaciated in appearance over this period.

Does residency change temporally and/or ontogenetically?

Certainly there are short and longer term changes in the propensity of stream-dwelling salmonids to remain where they are or conversely to move. Small diel shifts in holding positions of juvenile stages and even adults were noted previously, with movement from more central positions in the stream during the day towards lateral margins at night. Summer holding positions or territories are rarely the same as those used during winter either by young or older salmonids, so seasonal changes in habitat occur even though the fish remain as stream residents. As the juveniles become larger they occupy habitats with different conditions (greater depth, more adequate cover, higher velocities, for example), so there are also changes in location of residency with age. This of course becomes particularly evident at maturity when suitable reproductive habitat must be sought.

Why "stay at home"?

There are many pressures promoting residency in stream salmonids. For those populations living

above barriers to upstream fish passage, moving very far downstream could be disastrous in the sense of being able to contribute to the next generation. Once over a waterfall fish are permanently lost from the gene pool of their above falls population. In many headwater populations even upstream movement can be restricted either by series of falls and rapids in high gradient reaches or by dewatering of uppermost stream channels during low flow periods.

Energetically, it can be expensive to change residence site. Of course the benefits may outweigh the costs, as the many migratory populations of salmonids demonstrate, but this is not always so. Fish migration involves a cycle of movement (Northcote 1978), so in rivers and streams even though the downstream leg may be cheap, the upstream return rarely is. In addition to the costs of moving, many other costs must be accommodated. Frequently in their migratory cycle stream salmonids use several different habitats, if only temporarily, and these may have to be won if territories are involved. Again there are energy costs involved in physiological adaptations to new habitats. Furthermore in new habitats there can be an extended range in the type or size of predators to contend with as well as new parasites and diseases, all of which can add to the cost of moving both in terms of energy and survival. At home, movement costs should be small and the range of predators, parasites and diseases perhaps reduced.

In a broader perspective, a species which can cover a wide range of aquatic environments by partitioning its populations into resident, semi-migratory, and fully migratory forms (Jonsson 1985) may be in a stronger position for long-term survival where conditions are very changeable and often unpredictable as those in temperate and polar latitudes usually are. As alternative strategies, these different life history patterns may be in evolutionary competition (Gross 1987), though under highly changeable and unpredictable conditions I am not sure that the patterns must always confer equal fitness, as has been argued (*loc. cit.*).

Some evolutionary consequences of residency

Resident and migratory forms of stream salmonids may be geographically isolated, or at least partially so, by barriers to their upstream movement and these may have existed for several thousand years since the termination of deglaciation (Crozier and Ferguson 1986). But the two forms also occur in systems without barriers to upstream movement (Berg 1985). Hutchings (1985) considered that the long-term persistence of resident (ouananiche) and anadromous forms of Atlantic salmon must represent evolutionarily stable strategies (Maynard Smith 1982). There can be considerable variation between systems in the proportion of one life history form or the other, depending on the availability of suitable habitat for residency. Such an explanation may apply more generally, but two supposed requisites, that of fitness between individuals adopting each strategy being equal, and that of maintaining a constant proportion of both phenotypes (Gross 1987), need to be carefully considered and tested.

From an evolutionary point of view, there are several noteworthy features of resident salmonid populations in headwaters of streams. The first is that they are often reproductively isolated from both lower reach resident and migratory populations in the same stream system. They are of course isolated from headwater populations in other stream systems. Secondly they usually represent very small breeding populations. For example in an 195 m study area in upper Cutthroat Creek (Northcote and Hartman 1988), only 32 yearling or older fish could be found by trapping and electrofishing (October 1988 to March 1989) and of these only four were sexually mature. Thirdly, environmental conditions in small, headwater streams can often be very severe. Elliott (1987) notes that the "fringe" population of brown trout isolated above a waterfall in Wilfin Beck is subject to frequent high and low stream discharge. He suggests that there may have been selection in this population for genotypes enabling the trout to cope physiologically and behaviourally with extremes in flow. Similarly the trout in the headwaters of Cutthroat

Creek may also show adaptations to low flow and concomitant low levels of dissolved oxygen. That some individuals were able to survive in pools where dissolved oxygen remained for over a month at levels below 2 m L^{-1} is indeed surprising.

These features of headwater stream populations which occupy marginal habitats may confer high adaptive significance to the species as a whole (Scudder 1989). Instead of the conventional view that small, inbred populations develop only trivial differentiation and lead to degeneration if not extinction, more recent work cited by Scudder (*loc. cit.*) contends that the reverse is true. Thus the variation and selection occurring in marginal rather than central populations of a species may be the source of its ongoing evolution and genetic diversity. The specialized adaptive traits of marginal populations need preservation, not elimination either by degradation or removal of their distinctive habitats or by introduction of central populations as frequently has happened. Residency may not be the norm of life history options shown by stream salmonids in many areas of their range, but it is a feature which needs better appreciation, recognition, as well as protection. To promote each of those, further experimental study of residency in stream salmonids should reveal as much new information and insight as has that of migration in the recent decades.

Acknowledgments

I am most grateful for the helpful suggestions and criticisms of this review given by D.T. Crisp, J.M. Elliott, K.D. Fausch, J. Heggenes, K. Hindar, B. Jonsson and E.D. Le Cren. Support for its preparation came in part from an operating grant from the Canadian Natural Sciences and Engineering Research Council (NSERC) and from a Canada - Japan Scientific Exchange Award (NSERC and the Japan Society for the Promotion of Science) which permitted its oral presentation at a stream fish symposium held in conjunction with the International Ecological Congress in Yokohama, August, 1990.

References

- Alm, G. 1949. Influence of heredity and environment on various forms of trout. - Rep. Inst. Freshw. Res., Drottningholm 29: 29-34.
- Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. - Trans. Amer. Fish. Soc. 113: 1-32.
- Baglinière, J.L., G. Maise, P.Y. Lebaill and A. Nihouarn. 1989. Population dynamics of brown trout, *Salmo trutta* L., in a tributary in Brittany (France): spawning and juveniles. - J. Fish Biol. 34: 97-110.
- Berg, O.K. 1985. The formation of non-anadromous populations of Atlantic salmon, *Salmo salar* L., in Europe. - J. Fish Biol. 27: 805-815.
- Birt, T.P., J.M. Green and W.S. Davidson. 1991. Mitochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar*. - Can. J. Fish. Aquat. Sci. 48: 577-582.
- Bjornn, T.C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. - Trans. Amer. Fish. Soc. 100: 423-438.
- Burnet, A.M.R. 1969. Territorial behaviour in brown trout (*Salmo trutta* L.). - New Zealand J. Mar. Freshw. Res. 3: 385-388.
- Cane, A. 1974. Some aspects of the ecology of the Alwen River system, North Wales. - Ph.D. thesis, Univ. of Liverpool.
- Carey, W.E., and D.L.G. Noakes. 1981. Development of photo-behavioural responses in young rainbow trout, *Salmo gairdneri* Richardson. - J. Fish Biol. 19: 285-296.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. - Am. Nat. 100: 345-357.
- Chapman, D.W. and T.C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. p. 153-176. - In: T.G. Northcote (ed.) Symposium on salmon and trout in streams. University of British Columbia, Vancouver, B.C.
- Chisholm, I.M. and W.A. Hubert. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. - Trans. Amer. Fish. Soc. 116: 176-184.
- Clapp, D.F. and R.D. Clark. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. - Trans. Amer. Fish. Soc. 119: 1022-1034.
- Cooper, E.L. 1953. Periodicity of growth and change of condition of brook trout (*Salvelinus fontinalis*) in three Michigan trout streams. - Copeia 1953: 107-114.
- Crisp, D.T. 1989. Use of artificial eggs in studies of washout depth and drift distance for salmonid eggs. - Hydrobiologia 178: 155-163.
- Crisp, D.T. 1991. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L., and salmon, *S. salar* L. III. Effects of developmental stage and day and night upon dispersal. - J. Fish Biol. 39: 371-381.
- Crisp, D.T. and M.A. Hurley. 1991a. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L. and salmon, *S. salar* L. I. Effect of four different water velocity treatments upon dispersal rate. - J. Fish Biol. 39: 347-361.
- Crisp, D.P. and M.A. Hurley. 1991b. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L., and salmon, *S. salar* L. II. Effects of constant and changing velocities and of day and night on dispersal rate. - J. Fish Biol. 39: 363-370.
- Crisp, D.T., R.H.K. Mann and P.R. Cubby. 1984. Effects of impoundment upon fish populations of afferent streams at Cow Green Reservoir. - J. Appl. Ecol. 21: 739-756.
- Crozier, W.W. and A. Ferguson. 1986. Electrophoretic examination of the population structure of brown trout, *Salmo trutta* L., from the Lough Neagh catchment, Northern Ireland. - J. Fish Biol. 28: 459-477.
- Cunjak, R.A. 1988. Physiological consequences of overwintering in streams: the cost of acclimatization? - Can. J. Fish. Aquat. Sci. 45: 443-452.
- Cunjak, R.A., and G. Power. 1986a. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). - Can. J. Fish. Aquat. Sci. 43: 1970-1981.
- Cunjak, R.A., and G. Power. 1986b. Seasonal changes in the physiology of brook trout, *Salvelinus fontinalis* (Mitchill), in a subarctic river system. - J. Fish Biol. 29: 279-288.
- Cunjak, R.A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. - J. Fish Biol. 31: 493-511.
- Dill, L.M. 1969. The sub-gravel behaviour of Pacific salmon larvae. p. 89-99. - In: T.G. Northcote (ed.) Symposium on salmon and trout in streams. University of British Columbia, Vancouver, British Columbia.
- Dill, P.A. 1970. On the development of diel activity rhythms in Atlantic salmon and rainbow trout. - Ph.D. thesis, University of Western Ontario, London.
- Dumas, J. 1976. Dynamique et sédentarité d'une population naturalisée de truites arc-en-ciel (*Salmo gairdneri* Richardson) dans un ruisseau demontagne, l'Estibère (Hautes-Pyrénées). - Ann. Hydrobiol. 7: 115-139.
- Elliott, J.M. 1987. Population regulation in contrasting populations of trout *Salmo trutta* in two Lake District streams. - J. Anim. Ecol. 56: 83-98.
- Elliott, J.M. 1988. Growth, size, biomass and production in contrasting populations of trout *Salmo trutta* in two Lake District streams. - J. Anim. Ecol. 57: 49-60.
- Elliott, J.M. 1989. The natural regulation of numbers and growth in contrasting populations of brown trout, *Salmo trutta*, in two Lake District streams. - Freshw. Biol. 21: 7-19.
- Elliott, J.M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. II. Fish growth and size variation. - J. Anim. Ecol. 59: 171-185.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. - Can. J. Zool. 62: 441-451.
- Fausch, K.D. and R.J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. - Trans. Amer. Fish. Soc. 115: 363-381.
- Fuss, H.J. 1982. Age, growth and instream movement of Olympic Peninsula coastal cutthroat trout (*Salmo clarki clarki*). - M.Sc. thesis, University of Washington, Seattle.

- Godin, J.-G.J. 1982. Migration of salmonid fishes during early life history phases: daily and annual timing. p. 22-50. - In: E.L. Brannon and E.O. Salo (eds.) Proceedings of the salmon and trout migratory behavior symposium, University of Washington, Seattle.
- Grant, J.W.A. 1990. Aggressiveness and the foraging behaviour of young-of-the-year brook charr (*Salvelinus fontinalis*). - Can. J. Fish. Aquat. Sci. 47: 915-920.
- Grant, J.W.A. and D.L. Kramer. 1990. Territory size as a predictor to the upper limit to population density of juvenile salmonids in streams. - Can. J. Fish. Aquat. Sci. 47: 1724-1737.
- Gross, M.R. 1987. Evolution of diadromy in fishes. - American Fisheries Society Symposium 1: 14-25.
- Gross, M.R., R.M. Coleman and R.M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. - Science 239: 1291-1293.
- Halvorsen, M. and O.B. Stabell. 1990. Homing behaviour of displaced stream-dwelling brown trout. - Anim. Behav. 39: 1089-1097.
- Harcup, M.F., R. Williams and D.M. Ellis. 1984. Movements of brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. - J. Fish Biol. 24: 415-426.
- Harden Jones, F.R. 1968. Fish migration. - Arnold, London, 325 p.
- Harden Jones, F.R. 1981. Fish migration: strategy and tactics. - Society for Experimental Biology, Seminar Series, 13: 139-165.
- Hartman, G.F. and T.G. Brown. 1987. Use of small, temporary, floodplain tributaries by juvenile salmonids in a west coast rain-forest drainage basin, Carnation Creek, British Columbia. - Can. J. Fish. Aquat. Sci. 44: 262-270.
- Heggenes, J. 1988a. Physical habitat selection by brown trout (*Salmo trutta*) in riverine systems. - Nordic J. Freshw. Res. 64: 74-90.
- Heggenes, J. 1988b. Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. - Trans. Amer. Fish. Soc. 117: 336-344.
- Heggenes, J. 1988c. Effect of experimentally increased intraspecific competition on sedentary adult brown trout (*Salmo trutta*) movement and stream habitat choice. - Can. J. Fish. Aquat. Sci. 45: 1163-1172.
- Heggenes, J. and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. - J. Fish Biol. 32: 717-727.
- Heggenes, J., T.G. Northcote and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. - Can. J. Fish. Aquat. Sci. 48: 757-762.
- Heland, M. 1980a. La devalaison des alevins de truite commune *Salmo trutta* L. 1. Caractérisation en milieu artificiel. - Ann. Limnol. 16: 233-245.
- Heland, M. 1980b. La devalaison des alevins de truite commune, *Salmo trutta* L. 2. Activité des alevins "devalants" comparés aux sédentaires. - Ann. Limnol. 16: 247-254.
- Hesthagen, T. 1988. Movements of brown trout, *Salmo trutta*, and juvenile Atlantic salmon, *Salmo salar*, in a coastal stream in northern Norway. - J. Fish Biol. 32: 639-653.
- Hindar, K., B. Jonsson, N. Ryman and G. Ståhl. 1991. Genetic relationships among landlocked, resident, and anadromous trout, *Salmo trutta* L. - Heredity. 66: 83-91.
- Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. - J. Fish. Res. Board Can. 26: 1473-1483.
- Hunt, R.L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. - Wisconsin Dept. Nat. Res. Tech. Bull. 82. 28 p.
- Hutchings, J.A. 1985. The adaptive significance of lakeward migrations by juvenile Atlantic salmon, *Salmo salar* L. - M.Sc. thesis, Memorial University, St. Johns, Newfoundland, 133 p.
- Jackson, P.D. 1980. Movement and home range of brown trout, *Salmo trutta* Linnaeus, in the Aberfeldy River, Victoria. - Aust. J. Mar. Freshw. Res. 31: 837-845.
- Jonsson, B. 1982. Diadromous and resident trout *Salmo trutta*: is their difference due to genetics? - Oikos 38: 297-300.
- Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. - Trans. Amer. Fish. Soc. 114: 182-194.
- Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). - Freshw. Biol. 21: 71-86.
- Jonsson, B. and O.T. Sandlund. 1979. Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta m. fario*) in Søre Osa river system, Norway. - Env. Biol. Fish. 4: 43-54.
- Le Cren, E.D. 1973. The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. - Conseil International L'exploration de la Mer, Rapports et Procès-verbaux 164: 241-246.
- Le Cren, E.D. 1984. The biology of the sea trout. p. 1-42. - Atlantic Salmon Trust.
- Leclerc, J. and G. Power. 1980. Lack of movement of brook charr and ouananiche in the Caniapiscou River, northern Quebec. - Env. Biol. Fish. 5: 71-74.
- Maynard Smith, J. 1982. Evolution and the theory of games. - Cambridge University Press, Cambridge. 224 p.
- McDowall, R.M. 1988. Diadromy in fishes. - Croom Helm, London. 308 p.
- McFadden, J.T. 1961. A study of the brook trout (*Salvelinus fontinalis*). - Wildlife Monographs 7.
- Mesick, C.F. 1988. Effects of food and cover on numbers of Apache and brown trout establishing residency in artificial stream channels. - Trans. Amer. Fish. Soc. 117: 421-431.
- Moore, K.M.S., and S.V. Gregory. 1988a. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. - Can. J. Fish. Aquat. Sci. 45: 1921-1930.
- Moore, K.M.S. and S.V. Gregory. 1988b. Response of young-of-the-year cutthroat trout to manipulation of habitat structure in a small stream. - Trans. Amer. Fish. Soc. 117: 162-170.
- Nakano, S. and M. Nagoshi. 1985. Density regulation and growth of a redspot masu-trout, *Oncorhynchus rhodurus*, in a mountain stream. - Physiol. Ecol. Japan 22: 1-16.
- Nikolsky, G.V. 1963. The ecology of fishes. - Academic Press, London. 352 p.

- Nordeng, H. 1983. Solution to the "charr" problem based on Arctic charr (*Salvelinus alpinus*) in Norway. - Can. J. Fish. Aquat. Sci. 40: 1372-1387.
- Northcote, T.G. 1962. Migratory behaviour of juvenile rainbow trout, *Salmo gairdneri*, in outlet and inlet streams of Loon Lake, British Columbia. - J. Fish. Res. Board Can. 19: 201-270.
- Northcote, T.G. 1967. The relation of movements and migrations to production in freshwater fishes. p. 315-344. - In: S.D. Gerking (ed.) The biological basis of freshwater fish production. Blackwell Sci. Publ., Oxford.
- Northcote, T.G. 1969. Patterns and mechanisms in the lakeward migratory behaviour of juvenile trout. p. 183-203. - In: T.G. Northcote (ed.) Symposium on salmon and trout in streams. University of British Columbia, Vancouver.
- Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. p. 326-359. In: S.D. Gerking (ed.) Ecology of freshwater fish production. Blackwell Sci. Publ., Oxford.
- Northcote, T.G. 1981. Juvenile current response, growth and maturity of above and below waterfall stocks of rainbow trout, *Salmo gairdneri*. - J. Fish Biol. 18: 741-751.
- Northcote, T.G. 1984. Mechanisms of fish migration in rivers. p. 317-355. - In: J.D. McCleave, G.P. Arnold, J.J. Dodson and W.E. Neill (eds.) Mechanisms of migration in fishes. Plenum Press, New York.
- Northcote, T.G. and B.W. Kelso. 1981. Differential response to water current by two homozygous LDH phenotypes of young rainbow trout (*Salmo gairdneri*). - Can. J. Fish. Aquat. Sci. 38: 348-352.
- Northcote, T.G. and G.F. Hartman. 1988. The biology and significance of stream trout populations (*Salmo* spp.) living above and below waterfalls. - Pol. Arch. Hydrobiol. 35: 409-442.
- Northcote, T.G., S.N. Williscroft and H. Tsuyuki. 1970. Meristic and lactate dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. - J. Fish. Res. Board Can. 27: 1987-1995.
- Österdahl, L. 1969. The smolt run of a small Swedish river. p. 205-215. - In: T.G. Northcote (ed.) Symposium on salmon and trout in streams. University of British Columbia.
- Ottaway, E.M. and A. Clarke. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to downstream displacement by high water velocities. - J. Fish Biol. 19: 135-145.
- Ottaway, E.M. and D.R. Forrest. 1983. The influence of water velocity on the downstream movement of alevins and fry of brown trout. - J. Fish Biol. 23: 221-227.
- Rounsefell, G.A. 1958. Anadromy in North American Salmonidae. - U.S. Fish. Wildl. Serv. Bull. 58: 171-185.
- Scudder, G.G.E. 1989. The adaptive significance of marginal populations: a general perspective. p. 180-185. - In: C.D. Levings, L.B. Holtby and M.A. Henderson (ed.) Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.
- Shuck, H.A. 1945. Survival, population density, growth and movement of the wild trout in Crystal Creek. - Trans. Amer. Fish. Soc. 73: 209-230.
- Skaala, O. and G. Naevdal. 1989. Genetic differentiation between freshwater resident and anadromous brown trout, *Salmo trutta*, within watercourses. - J. Fish Biol. 34: 597-605.
- Slaney, P.A. and T.G. Northcote. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. - J. Fish. Res. Board Can. 31: 1201-1209.
- Solomon, D.J. 1982. Migration and dispersion of juvenile brown and sea trout. p. 136-145. - In: E.L. Brannon and E.O. Salo (eds.) Salmon and trout migratory behavior symposium. University of Washington, Seattle.
- Solomon, D.J. and R.G. Templeton. 1976. Movements of brown trout, *Salmo trutta* L., in a chalk stream. - J. Fish Biol. 9: 411-423.
- Stefanich, F.A. 1952. The population and movements of fish in Prickly Pear Creek, Montana. - Trans. Amer. Fish. Soc. 81: 260-274.
- Svårdson, G. and N.-A. Nilsson. 1964. Fiskebiologi. - Tema Förlag, Halmstad. 253 p.
- Symons, P.K.E. 1971. Behavior adjustment of population density to available food by juvenile Atlantic salmon. - J. Anim. Ecol. 40: 569-587.
- Trotter, P.C. 1989. Coastal cutthroat trout: a life history compendium. - Trans. Amer. Fish. Soc. 118: 463-473.
- Tsuyuki, H. and S.N. Williscroft. 1973. The pH activity relations of two LDH homotetramers from trout liver and their physiological significance. - J. Fish. Res. Board Can. 30: 1023-1026.
- Tsuyuki, H. and S.N. Williscroft. 1977. Swimming stamina differences between genotypically distinct forms of rainbow trout (*Salmo gairdneri*) and steelhead trout. - J. Fish. Res. Board Can. 34: 996-1003.
- Vuorinen, J. and O.K. Berg. 1989. Genetic divergence of anadromous and nonanadromous Atlantic salmon (*Salmo salar*) in the River Namsen, Norway. - Can. J. Fish. Aquat. Sci. 46: 406-409.
- Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). - Can. J. Fish. Aquat. Sci. 42: 1668-1672.
- Woolland, J.V. 1972. Studies on salmonid fishes in Llyn Tegid and the Welsh Dee. - Ph.D. thesis, University of Liverpool.

Sea Water Migration of Arctic Charr (*Salvelinus alpinus* L.) - Correlation between Freshwater Growth and Seaward Migration, based on Back-calculation from Otoliths

MARTIN-A. SVENNING¹, ASTRID SMITH-NILSEN² and MALCOLM JOBLING¹

¹ The Norwegian College of Fishery Science, University of Tromsø
Dramsveien 201 B, N-9000 Tromsø, Norway

² Helgeland Holding Lmt., P.O.Box 50, N-8614 Ytteren, Norway

Abstract

Arctic charr has a Holarctic distribution of anadromous and resident freshwater forms. The phenotypic plasticity of Arctic charr has given rise to a variety of life history tactics, and migratory behaviour is one aspect of the complex life history of this species. Migration to the sea occurs in spring and the migrant charr reside in coastal waters for a few weeks before returning to freshwater. We have examined the relationship between seawater migration, and freshwater growth in Arctic charr from the Sila river system in Northern Norway. The growth patterns of charr caught at different stages in the migratory cycle were estimated by back-calculation from the otoliths. The results demonstrated that for the examined individuals, aged five and six years, back-calculated size at age was larger for migrating (anadromous) charr than non-migrating (stationary) charr. The results suggest that slow-growing individuals, termed stationary, may "transform" from stationary to anadromous charr, so that most of the charr in the Sila system, eventually, migrate to the sea. We hypothesize that a moderate improvement in growth conditions in "overcrowded" charr populations, might lead to an increase in the proportion of anadromous individuals.

Introduction

The Arctic charr (*Salvelinus alpinus* L.), which has a Holarctic distribution, is found as both anadromous and resident freshwater forms differing in morphology and life history patterns (Johnson 1980, Dempson and Kristoffersen 1987). In Norway the anadromous forms of charr are restricted to northern areas, and in several streams anadromous populations of Arctic charr live sympatrically with resident forms (Nordeng 1983). The phenotypic plasticity of Arctic charr has given rise to a variety of life history tactics, and migratory behaviour is one aspect of the complex life history of this species (Dempson and Kristoffersen 1987). In contrast to Pacific and Atlantic salmon, anadromous charr have an extended, but variable, period of freshwater residence (Randall et al. 1987). The morphological and physiological chang-

es generally associated with the parr-smolt transformation in salmon are not as well defined for charr. Nevertheless, both juvenile and mature fish from anadromous populations of Arctic charr seem to be preadapted for the seaward migration, and they do not depend on acclimation in brackish water before entering full-strength seawater (Finstad et al. 1989, Arnesen et al. 1992). Charr generally do not overwinter at sea and both sexually immature and mature fish stay in the sea only during the summer months (Mathisen and Berg 1968). Migration to the sea occurs in spring and the migrant charr reside in coastal waters for a few weeks before returning to freshwater (Mathisen and Berg 1968, Johnson 1980, Berg and Jonsson 1989).

In the majority of salmonids, freshwater growth rate varies greatly both within and between stocks (Saunders 1981, Thorpe 1989). Within stocks, this

variation in growth results in a range of ages at which the juvenile salmonids undergo the parr-smolt transformation and migrate to sea (Egglishaw and Shackley 1980, Thorpe 1989). For populations of some species of salmonids reared in tanks, length frequency distributions become clearly bimodal with time, with fish of the upper modal group undergoing the parr-smolt transformation, and fish of the lower mode requiring a further year in freshwater (Thorpe 1987, Hirata et al. 1988).

Although bimodality has not been demonstrated for juvenile charr, reared in tanks, it does not seem unreasonable to hypothesize that growth rate differences could affect the age of initial seawater migration in charr.

Thus, the primary aim of the present study was to examine the relationship between fish growth and sea water migration of Arctic charr. We hypothesized that in the period of freshwater growth prior to the initial seaward migration there would be growth differences between juvenile charr that migrate, and those that did not. The growth patterns of charr caught at different stages in the migratory cycle were estimated by back-calculation from the otoliths.

Methods

Study site

The Sila river (66°21'N, 13°10'E) is 1.5 km long, and runs from Lake Silavatn to the sea (Fig. 1). The fluvial basin is only 12.5 km², but very heavy flooding may occur during the spring and summer thaw. Lake Silavatn is 2.5 km² and is sited 26 m a.s.l. The trap used to catch descending and ascending fish was located 100 m upstream from the sea.

Collection of fish

During the period from late April 1988 to mid August 1989, all migrating charr caught in the fish trap were tagged individually using TBA-2 (standard anchor t-bar) tags. Fish were caught either when descending or ascending the river. About 1,500 migrating charr, with lengths from 18 to 44 cm, were tagged each year. The charr migrated to the sea in spring and returned to the Sila river after 5-8 weeks in the sea.

In 1988, a subsample of 69 charr was removed from the downstream migrating population in May and sacrificed (group 1). In July 39 charr were

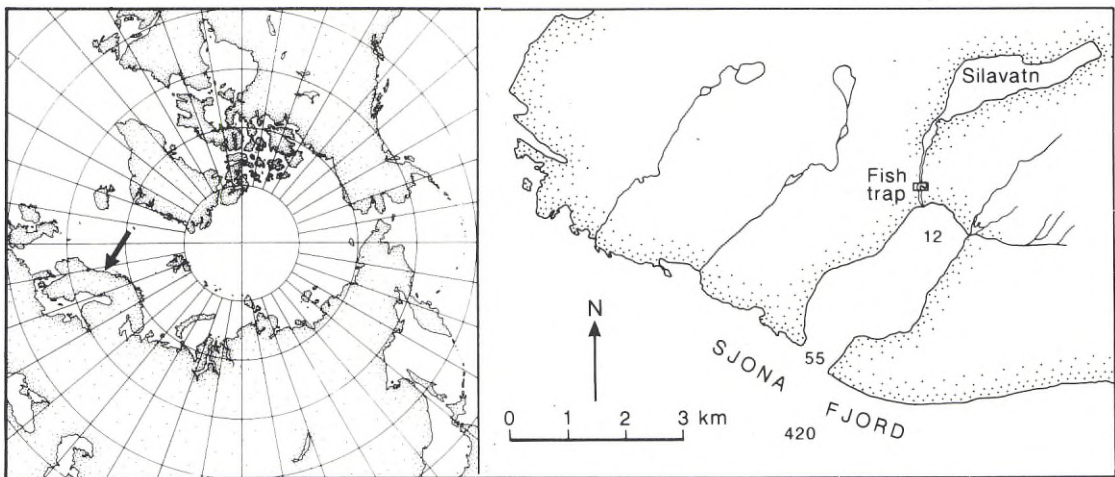


Fig. 1. Illustration of the Sila river study area, with the location of the fish trap shown.

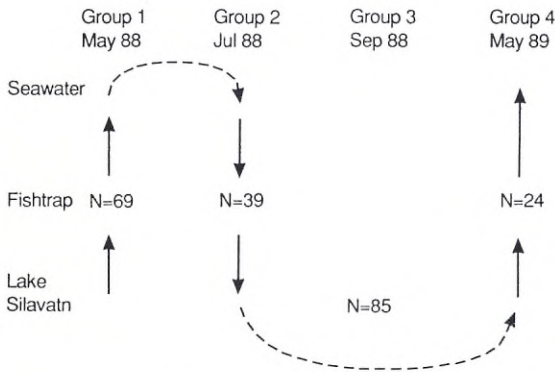


Fig. 2. The numbers of Arctic charr collected in the Sila river system and used for back-calculation purposes. Group 1: Fish sampled whilst migrating downstream in May 1988. Group 2: Fish sampled whilst migrating upstream in July 1988. Group 3: Untagged fish caught in the lake in September 1988. Group 4: Fish sampled in May 1989. The fish had been tagged in 1988 whilst migrating downstream.

sampled and sacrificed from the upstream migrating population (group 2). In May 1989, 24 downstream migrating charr that had been tagged migrating downstream in the previous year, and had therefore previously migrated to the sea, were sampled (group 4). Groups 1, 2 and 4 are termed "anadromous" charr. In addition 85 "non-anadromous" (untagged) individuals, referred to as stationary charr (group 3), were caught by gillnetting in Lake Silavatn in September 1988 (Fig. 2). The mesh size of the gillnets used ranged from 12 to 45 mm. Eight bottom nets (12 to 45 mm) were fished for one night in the littoral zone (1-10 m depth) and fishing was undertaken for one night with four nets (16 to 45 mm) in the pelagic zone (0-6 m depth). All fish sampled were measured (fork length) to the nearest mm, weighed and classified with respect to sex and maturity.

Otolith preparation and reading

Sagittal otoliths were removed from the fish. Otoliths were preserved in 96% ethanol to which a small amount of glycerol had been added. In the

laboratory the otoliths were placed in a black dish, immersed in glycerol, and illuminated using reflected light. Otoliths were viewed at magnification 16X using a binocular microscope. Against the dark background, the opaque zones appeared as white or light-coloured rings, and the hyaline zones as dark rings. The rostral radius of the otolith was measured from the nucleus mid point to the otolith margin, using a camera lucida mounted on the binocular microscope. Distances to successive hyaline annuli were measured along this radius.

We found it easiest to identify the zones along the rostrum, and in old fish rostrum counts have been shown to give the highest age estimates (Nordeng 1961, Kristoffersen 1982). Consequently, we used the rostrum for both age determination and otolith measurements.

Correlation between otolith size and fish length

Relationships between fish fork length and otolith radius were investigated. The regression lines were fitted by least squares using standard procedures (Snedecor and Cochran 1967). Fish length:otolith radius (F:O) relationships for all 4 groups of fish were linear, but the plotted regression lines did not pass through the origin. The regression equations used to estimate fish lengths from otolith radii, were computed as:

$$F = a + bO \quad (1)$$

where F is fish fork length, a is the intercept, b is the regression coefficient (slope of the line) and O is the otolith radius. Regression lines obtained for the individual groups were compared statistically using analysis of covariance.

The relationship described by the regression lines (1) can be represented as a modification of the direct proportion formula (Fraser 1916, Lee 1920). Hence:

$$Fn = a + (F - a)(On/O) \quad (2)$$

where Fn is length of fish when annulus "n" was formed, a is intercept from (1), F is length of fish

when otolith was sampled, On is radius of annulus "n" (at fish length F_n) and O is otolith radius.

Thus, this expression can be used to estimate fish fork lengths at the times of formation of each of the annuli (hyaline zones).

Results

Age, size and sex distribution

The length distribution of the stationary charr (group 3) caught in Lake Silavatn is shown in Fig. 3. The length groups 20-26 cm comprised 64% of the catch, and only five charr (4%) were larger than 26 cm. The lengths of the twelve anadromous (tagged) charr caught during gillnetting in Lake Silavatn ranged between 25 and 39 cm.

The length ranges of all down- and upstream migrating charr captured in 1988 were from 18 to 40 cm and from 22 to 44 cm, respectively (Fig. 4). The differences in length frequencies between down- and upstream migrating charr (chi-square test, $p < 0.001$) are probably due to a combination of marked growth during summer, and higher mortality of young fish during the sea residence. The length distributions of the anadromous charr

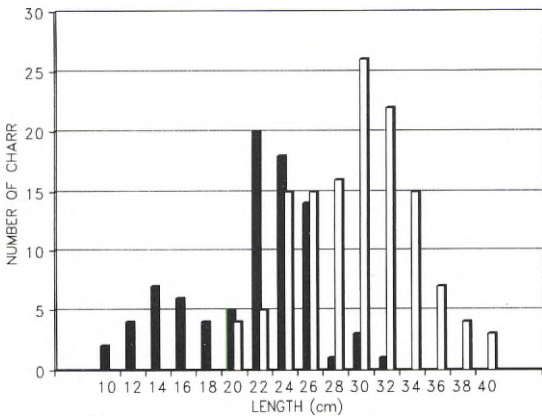


Fig. 3. Length distributions of Arctic charr (*Salvelinus alpinus* L.) sampled from the fish trap in the Sila river (anadromous fish) and by gillnetting in Lake Silavatn (stationary fish). Black columns represent stationary charr (N=85) and open anadromous charr (N=132).

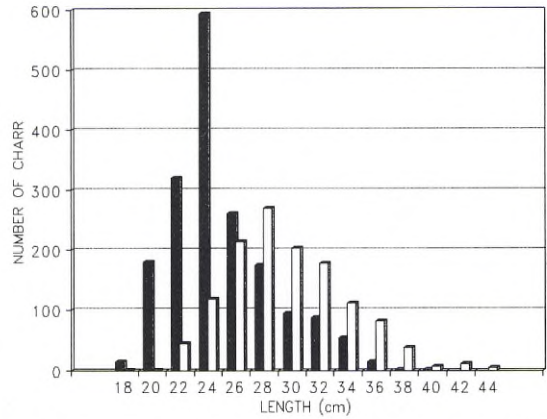


Fig. 4. Length distributions of descending and ascending Arctic charr (*Salvelinus alpinus* L.) caught in the fish trap in the Sila river in 1988. Black columns represent descending charr (N=1797) and open ascending charr (N=1295).

sampled for otolith analyses in 1988 and 1989 are given in Fig. 3 and 5.

The age distributions of the sampled charr are shown in Fig. 6. Ages of the anadromous charr varied between 4 and 13 years and more than 50% of the fish examined were 7 years or older. This suggests that the majority of fish are 4-6 years old when they undertake their first migration, at a time

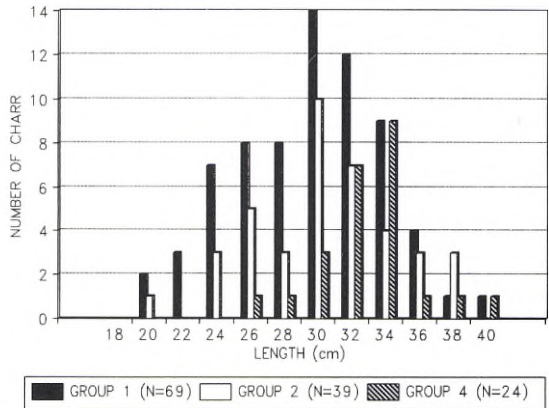


Fig. 5. Length distributions of Arctic charr (*Salvelinus alpinus* L.) sampled during the downstream migration in May 1988 (Group 1) and May 1989 (Group 4), and during the upstream migration in July 1988 (Group 2).

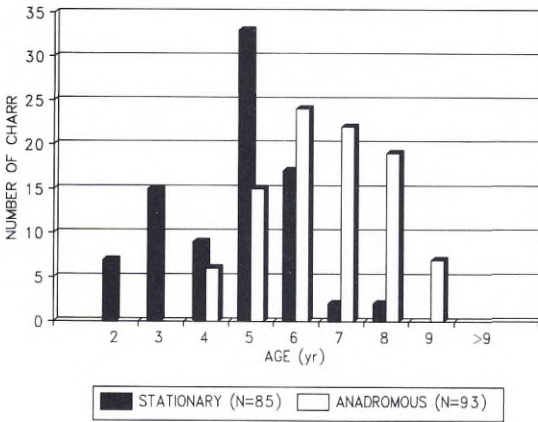


Fig. 6. Age distributions of collected Arctic charr (*Salvelinus alpinus* L.) sampled from the fish trap in the Sila river (anadromous fish) and by gillnetting in Lake Silavatn (stationary fish). Black columns represent stationary charr (N=85) and open anadromous charr (group 1 and 4, N=93).

when body size is at least 18 cm (Fig. 3 and 4). The age distribution of the anadromous fish differed from the age distribution of the stationary charr in which only 4 of the fish sampled were older than 6 years (chi-square = 41.55, df=3, $p < 0.001$).

Sex distributions of the charr are shown in Tables 1 and 2. The sex ratio for the catch of stationary charr was close to 1, but a predominance of mature males over mature females was found among age groups 5 or older. For anadromous charr older than age 6, there was a strong predominance of females (chi-square test, $p < 0.01$). For charr of ages 4-6, there were no significant differences in average lengths between sexes and stage of maturity (t-test, $p >> 0.05$). Mature females age 7-8 were significantly larger than immature females of similar age (t-test, $p < 0.05$).

Otolith radius (O) and fish length (F)

Analysis of covariance of relationships between otolith radii (O) and fish length (F) revealed no significant within groups differences between fish differing in either sex or maturity status ($p > 0.75$). Data for fish of different sex and maturity were

Table 1. Sexually immature and mature charr, *Salvelinus alpinus* (L.), caught in Lake Silavatn, September 1988 (data for 12 tagged "anadromous" charr caught in the lake are excluded).

Age	Males		Females		Tot
	Immature	Mature	Immature	Mature	
1					
2	3		4		7
3	8		7		15
4	3	1	5		9
5	11	5	16	1	33
6	5	5	7		17
7		1	1		2
8		2			2
>8					
Total	30	14	40	1	8

Table 2. Sexually immature and mature charr, *Salvelinus alpinus* (L.), caught migrating downstream in Sila river, from May to July, in 1988 and 1989.

Age	Males		Females		Tot
	Immature	Mature	Immature	Mature	
1					
2					
3					
4	2		5		7
5	11		4		15
6	11		10	3	24
7	6		8	8	22
8	3		11	5	19
>8			2	4	6
Total	33		40	20	93

therefore pooled before between group analyses were conducted. For each group of charr O:F regressions indicated a strong positive correlation between these two parameters (Table 3). Analysis of covariance showed that slopes of regression were significantly different ($F_{[3,208]} = 5.38$; $p = 0.001$). However, when group 2 was excluded the slopes of the regressions no longer differed significantly from each other ($F_{[2,172]} = 0.063$; $p = 0.939$). Data for groups 1, 3 and 4 were pooled and a common regression plotted (Table 3). In accordance with Lee (1920) the common regres-

sion for group 1, 3 and 4 was described by the formula (Fig. 7):

$$Fn = 3.0 + (F-3.0)(On/O) \quad (3)$$

Equation (3) was used to back-calculate the fork lengths of anadromous and stationary charr. Analyses of back-calculated length-at-age were carried out for charr aged 4-6 when sampled, since fish in this age-range were the most numerous (Table 4). The back-calculated average lengths of anadromous charr exceeded those of the stationary charr and differences were highly significant for fish caught at ages 5 and 6 ($p < 0.01$). Few anadromous charr of age 4 were sampled and the observed differences in back-calculated length-at-age for anadromous and stationary charr did not reach a level of significance ($p = 0.11$).

Discussion

In order to examine whether anadromous behaviour, in terms of seawater migration, could be

Table 3. Regressions describing fish length (F) : otolith radius (O) relationships for different groups of charr (*Salvelinus alpinus* L.) from the Lake Sila river system.

Groups	N	Intercept (a)	Slope (b)	r	p
Group 1	69	7.6	133.8	0.82	<0.01
Group 2	39	-104.0	205.1	0.88	<0.01
Group 3	85	7.9	129.7	0.93	<0.01
Group 4	24	7.5	131.1	0.86	<0.01
Group 1+3+4	178	3.0	134.3	0.93	<0.01

related to freshwater growth, the lengths-at-age of anadromous and stationary charr from the Sila river system were back-calculated. The results demonstrated that migrating charr age 4-6, had significantly better growth as juveniles than non-migrating individuals of the same age.

Estimated lengths of juvenile charr were based on back-calculation of the growth patterns of individual fish from their otoliths. The relationship O:F for the subsample of ascending charr (group 2) was significantly different from the

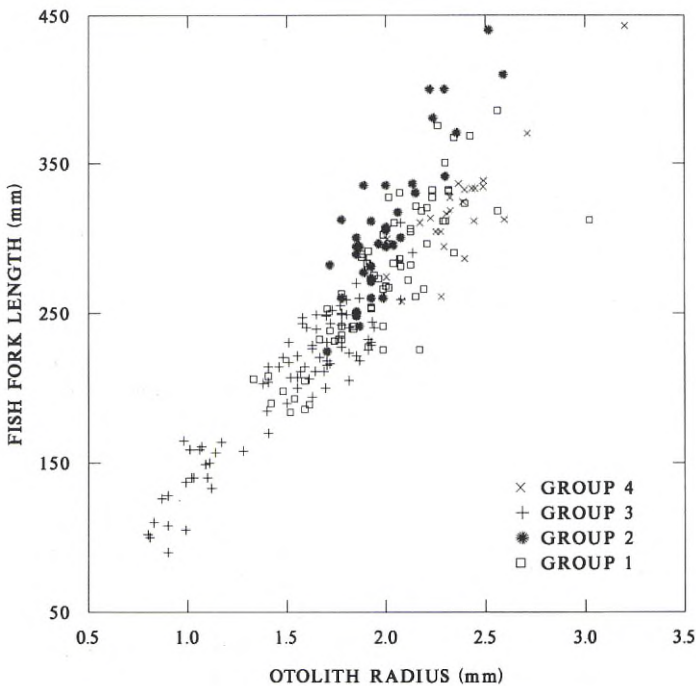


Fig. 7. The relationships between otolith radius and fish fork length of the four groups of Arctic charr (*Salvelinus alpinus* L.) from the Sila river system.

Table 4. Back-calculated lengths (mm) of anadromous (A) and stationary (S) charr (*Salvelinus alpinus* L.) from Lake Sila river system. Standard errors are given in brackets, N = number in sample.

Age	Charr population	N	Annulus					
			1	2	3	4	5	6
4	A	6	53(7)	95(8)	146(11)	190(7)		
	S	9	49(6)	88(14)	132(24)	175(20)		
5	A	15	54(6)	92(10)	135(15)	194(26)	212(29)	
	S	33	48(8)	84(11)	127(14)	172(16)	199(19)	
6	A	24	53(8)	102(9)	150(14)	198(25)	232(29)	256(29)
	S	17	49(9)	87(15)	130(22)	170(21)	200(26)	225(30)

regressions for other groups of fish. The growth rates of anadromous charr are different during the period in freshwater than during the foraging period in the sea. During a summer sea residence period of approximately 43 days, the anadromous charr from the Sila river system, increase in length by 3-4 cm and increase in weight by almost 80% (Svenning unpubl.). It seems reasonable to suggest that the rapid growth in body length during the early summer occurs without a marked increase in the size of the otolith. Uncoupling of body and otolith growth was reported by Reay (1972) who found that 50% of the body growth increment in sandeels (*Ammodytes tobianus* L.) was achieved 3-4 weeks earlier than that of the otoliths. Casselman (1990) found that for northern pike (*Esox lucius*) otoliths grew relatively slower than the body during rapid growth and relatively faster than the body during slow growth. This may indicate that the relationship O:F depends both upon fish growth rates and metabolic modifiers (Mosegaard 1986, Mosegaard et al. 1988, Wright et al. 1990) and caution should be exercised when back-calculating fish lengths from otolith size (Kristoffersen and Klemetsen 1991). In the present study with charr, however, there were no differences in the O:F length relationships between stationary charr (group 3) and downstream migrating charr which had been tagged the year before (group 4), and had previously migrated to the sea. This suggests that the growth of the otoliths of repeat migrants in freshwater, exceeds the overall growth of the

body, to such an extent that the relationship O:F for repeat migrants, in spring, is not distinct from the O:F relationship of stationary charr and first time migrants.

Since the smallest size of first-time migrants of Arctic charr from Norwegian charr lakes is about 20 cm, irrespective of the age of the migrant, it is conceivable that an individual fish must reach a threshold size before it can migrate to sea. Thus, it is the most rapidly growing individuals within the population that migrate to the sea at the youngest age (Table 4, see also Strand 1991). Size-dependent salinity tolerance may be due to a more favorable surface-to-volume ratio for larger fish, or to a progressive development of hypoosmoregulatory mechanisms with size, or both (McCormick and Saunders 1987). In the Sila river system many of the first time migrants appear to be 5 or even 6 years old with an average fork length of about 23 cm. Consequently fish may recruit to the anadromous proportion of the population within a critical size range of 19-23 cm fork length.

The age distribution of the stationary charr caught in lake Silavatn indicated a marked decline in fish older than 6 years. In contrast, charr older than 5-6 years dominated among the anadromous individuals, both in the trap and the gillnet catches. The 12 tagged anadromous charr caught in the gillnets in the lake were the largest and oldest fish taken in the nets. Thus, despite the fact that sampling was conducted with only one night netting in the lake, the recapture of large anadromous

charr suggests that if large old stationary resident individuals were present in the lake, some would have been caught. A possible explanation for the lack of old stationary charr in the catches may be as follows: the slow-growing fish which have been termed stationary, will, before they reach the age of 7, achieve the critical size for migration and "transform" from stationary to anadromous charr. This means that most of the charr in the Sila river system - sooner or later - migrate to the sea.

Anadromy is more frequent in cold rather than warm temperate latitudes (McDowall 1987, Baker 1978), and this trend is displayed by a number of salmonid species (Thorpe 1989). If conditions for feeding and growth in freshwater are very good, then the growth advantage to be gained by undertaking a seaward migration is minimized. Thus under conditions of high productivity and abundant food supply in the freshwater system the proportion of anadromous individuals within a population would be expected to be reduced, leading to increased incidence of "non-migrating" populations at the southern end of the range, where "growth opportunity" (*sensu* Metcalfe and Thorpe 1990) is greatest. Within the geographic range where "anadromous populations" of salmonids are found, feeding conditions and growth opportunity within freshwater systems may influence both the age at which the fish undertake initial seaward migration and the proportion of the population that becomes anadromous (L'Abée-Lund et al. 1989, Thorpe 1989, Metcalfe and Thorpe 1990, Taylor 1990). When conditions for growth in freshwater are reasonably good a large proportion of the population may remain "resident", but fish which do become anadromous, migrate to sea at a comparatively young age. Under poorer feeding conditions the proportion of anadromous fish in the population may increase and the age at which seaward migration is undertaken also increases. Nordeng (1983) has provided experimental evidence relating to the influence of feeding conditions on anadromy in Arctic charr. In his experiments high levels of food supply significantly increased the proportion of charr of the resident form at the expense of anadromous fish.

Gross (1987) suggested that alterations of natural habitats, which lead to enhanced growth rates of juvenile fish, may select for resident populations, and evidence favouring this hypothesis exist for some species of salmonids (Thorpe 1977, 1986). It is conceivable, however, that habitat alteration which leads to increased growth will not always result in an increased proportion of resident fish in the population. Whether or not habitat alterations will result in increased proportions of "resident" or "anadromous" fish in the population would be expected to depend upon where on the "growth opportunity" continuum the habitat lies. If the habitat provides reasonable "growth opportunity" then habitat improvement would be expected to result in increased proportion of resident fish, but if the habitat originally provided very poor conditions for growth and development, an improvement in available food resources might lead to increased anadromy within the population.

In northern Norway there are many lakes that contain large populations of charr dominated by small slow-growing, old, mature individuals. The proportion of anadromous individuals is small in these populations. Were growth conditions for these charr populations to improve, either via an increase in the food resources or via a decrease in the population density, a greater proportion of the fish would be expected to reach the minimum threshold (critical) size required for seaward migration and survival in seawater. Thus, for these "overcrowded" populations, one could hypothesize that a moderate improvement in growth conditions could lead to an increase in the proportion of anadromous individuals within the population. Conducting extensive fishing operations aimed at reducing population densities, and improving the food and growth base for the remaining fish, could create the conditions required for testing this hypothesis.

Acknowledgment

Thanks are due to Rolf Pedersen, Kristen Nilsen and John Pedersen for field work assistance and for help and hospitality in Silavågen.

References

- Arnesen, A.M., M. Halvorsen and K. J. Nilssen. 1992. Development of hypoosmoregulatory capacity in Arctic charr (*Salvelinus alpinus* L.) reared under either continuous light or natural photoperiod. - *Can. J. Fish. Aquat. Sci.* 49: 229-237.
- Berg, O.K. and B. Jonsson. 1989. Migratory patterns of anadromous Atlantic salmon, brown trout and Arctic charr from the Vardnes river in northern Norway. p. 106-115. - In: Brannon, E. and B. Jonsson (eds.) Proceedings of the salmonid migration and distribution symposium. Contribution 793, School of Fish., Seattle.
- Baker, R.R. 1978. The evolutionary ecology of animal migration. - Hodden and Stoughton, London. 1012 p.
- Dempson, J.B. and A.H. Kristoffersen. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. - *Amer. Fish. Soc. Symp.* 1: 340-25.
- Casselmann, J.M. 1990. Growth and relative size of calcified structure of fish. - *Trans. Amer. Fish. Soc.* 119: 673-688.
- Egglisshaw, H.J. and P.E. Shackley. 1980. Survival and growth of salmon, *Salmo salar* (L.), planted in a Scottish stream. - *J. Fish Biol.* 16: 565-584.
- Finstad, B., K.J. Nilssen and A.M. Arnesen. 1989. Seasonal changes in seawater tolerance of Arctic charr (*Salvelinus alpinus*). - *J. Comp. Physiol.* B159: 371-378.
- Fraser, C.McL. 1916. Growth of the spring salmon. - *Trans. Pacif. Soc. Seattle*, for 1915: 29-39.
- Gross, M. 1987. Evolution of diadromy in fishes. - *Amer. Fish. Soc. Symp.* 1: 14-25
- Hirata, T., A. Goto and F. Yamazaki. 1988. Individual growth and smoltification of juvenile masu salmon, *Oncorhynchus masou* Brevoort, under rearing conditions. - *J. Fish. Biol.* 32: 77-84.
- Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. p. 1-98 - In: Balon, E. (ed.) Charrs. Junk, The Hague. 919 p.
- Kristoffersen, K. 1982. Aldersbestemmelse av røye, *Salvelinus alpinus* (L.) fra Ellasjøen, Bjørnøya. Et detaljstudium av soner og vekst i otolithene. - *Cand. real. Thesis, Univ. Tromsø*. 130 p. (In Norwegian.)
- Kristoffersen, K. and A. Klemetsen. 1991. Age determination of Arctic charr (*Salvelinus alpinus*) from surface and cross section of otoliths related to otolith growth. - *Nordic J. Freshw. Res.* 66: 98-107.
- L'Abée-Lund, J.H., B. Jonsson, A.J. Jensen, L.M.Sættem, T.G. Heggberget, B.O. Johnson and T. Næsje. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout, *Salmo trutta*. - *J. Anim. Ecol.* 58: 525-542.
- Lee, R.M. 1920. A review of the methods of age and growth determination by means of scales. - *Fishery Invest. Lond.* Ser. II, 4(2) 32 p.
- Mathisen, O.A. and M. Berg. 1968. Growth rates of the char, *Salvelinus alpinus* (L.), in the Vardnes river, Troms, Northern Norway. - *Rep. Inst. Freshw. Res., Drottningholm* 48: 177-186
- McDowall, R.M. 1987. The occurrence and distribution of diadromy among fishes. - *Amer. Fish. Soc. Symp.* 1: 1-13.
- McCormick, S.D. and R.L. Saunders. 1987. Preparatory physiological adaptations for marine life of salmonids: Osmoregulation, growth and metabolism. - *Amer. Fish. Soc. Symp.* 1: 211-229.
- Metcalf, N.B. and J.E. Thorpe. 1990. Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. - *J. Anim. Ecol.* 59: 135-145.
- Mosegaard, H. 1986. Growth in salmonid otoliths. - *Acta Univ. Uppsala. Fac. Sci.* 52: 1-18.
- Mosegaard, H., H. Svedeng and K. Tabermann. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. - *Can. J. Fish. Aquat. Sci.* 45: 1514-1524.
- Nordeng, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North-Norway. 1. Age and spawning frequency determined from scales and otoliths. - *Nytt. Mag. Zool.* 10: 67-123.
- Nordeng, H. 1983. Solution of the "char problem" based on char, *Salvelinus alpinus*, in Norway. - *Can. J. Fish. Aquat. Sci.* 40: 1372-1387.
- Randall G.R., M.C. Healy and J.B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout and char. - *Amer. Fish. Soc. Symp.* 1: 27-41.
- Reay, P.J. 1972. The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. - *J. Cons. int. Explor. Mer* 34: 485-504
- Saunders, R.L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic provinces and New England, USA. - *Can. J. Fish. Aquat. Sci.* 38: 1612-1625.
- Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. Sixth edition. - Iowa State University Press, Ames, Iowa. 593 p.
- Strand, R. 1991. Alder, størrelse og smoltutvandring hos røye (*Salvelinus alpinus* L.) i Halselva, Finnmark. - Thesis, Univ. Trondheim. 53 p. (In Norwegian.)
- Taylor, E.B. 1990. Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). - *J. Fish Biol.* 37: 1-17.
- Thorpe, J.E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. - *J. Fish Biol.* 11: 175-184.
- Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. - *Can. Spec. Publ. Fish. Aquat. Sci.* 89: 7-14.
- Thorpe, J.E. 1987. Environmental regulation of growth patterns in juvenile Atlantic salmon. p. 463-474. - In Summerfelt, R.C. and G.E. Hall (eds.) The age and growth of fish. Iowa State Univ. Press, Ames, Iowa. 544 p.
- Thorpe, J.E. 1989. Developmental variation in salmonid populations. - *J. Fish. Biol.* 35 (Suppl. A): 295-303
- Wright, P.J., N.B. Metcalfe and J.E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. - *J. Fish Biol.* 36: 241-249.

Stream Grazer Responses to Predator Odour - an Experimental Study

BJÖRN MALMQVIST

Department of Animal Ecology, University of Umeå, S-901 87 Umeå, Sweden

Abstract

The behavioural changes of grazing stream invertebrates were studied during exposure to the odour of potential predators in the laboratory. The technique used involved the recording (time lapse VCR) of crawling and drift rates of five species of grazing invertebrates in an experimental arena. Tests were carried out by alternately exposing feeding grazers to water that had been/not been in contact with predators. The caseless caddisfly larva *Rhyacophila nubila*, did not generally produce any obvious responses among the potential prey species, which included the snail *Ancylus fluviatilis*, the mayfly nymphs *Baetis rhodani* and *Rhithrogena germanica*, the cased caddisfly larvae *Agapetus ochripes* and *Silo pallipes*, and nymphs of the taeniopterygid stonefly *Brachyptera risi*. In contrast, nymphs of the predatory stonefly *Dinocras cephalotes* elicited responses in several of the grazers. *Silo pallipes* crawled faster in the presence of *Dinocras* odour, and significantly more larvae of this caddisfly moved away in a downstream direction than in the control. Downstream movement suggests an avoidance response, although the animals kept foraging while retreating. *A. ochripes* and *B. rhodani* slowed down their rate of movement in the presence of *Dinocras*. The former species and *A. fluviatilis* spent more time stationary in the presence of *Dinocras* odour than in controls. *A. ochripes* also reduced movement rates in the presence of sculpin odour. The reduced movement rates are likely to be adaptations that minimize the risk of direct confrontations with the predators, and suggest that predator presence might reduce the rate of food intake.

Introduction

There are many ways in which invertebrate prey inhabiting lotic environments are influenced by vertebrate and invertebrate predators. Beside the direct risk of predation indirect effects are often present. The indirect effects are associated with the importance of balancing the risk of predation with necessary functions such as feeding (cf. Sih 1980), or are the consequences of inefficient predation (cf. Vermeij 1982). In the latter case, stonefly nymphs may serve as an example of predators causing substantial drift of mayfly nymphs and other benthic insects. This is not only the result of escape from unsuccessful attacks (cf. Molles and Pietruszka 1983, Sjöström 1985, Allan et al. 1987a), but also of evasion from moving, hunting or non-hunting predators (Malmqvist and Sjöström 1987). Such evasive behaviour must follow the detection of the predator, and cues can be visual, tactile,

olfactory etc. (e.g. Peckarsky 1980, Bengtsson 1982, Williams and Moore 1985, Andersson et al. 1986, Malmqvist and Sjöström 1987, Petranks et al. 1987, Williams 1987, Malmqvist 1988, Peckarsky and Penton 1989).

Thus, several benthic freshwater invertebrates can detect a predator before an encounter has taken place, and are thereby also able to adjust their behaviour in order to minimize the predation risk. The adaptive behaviour may vary with the extent of the risk that the potential prey animal is exposed to and with morphological, physiological or behavioural constraints of a particular prey type. If the predator is very close and poses an immediate threat to the prey one might expect it either to flee or feign death. On the other hand, if the danger is not too acute it would be more opportune to just diminish the risk of encountering the predator. This could be accomplished by decreasing the movement rate (Sih 1984, Allan et al. 1987b).

Movements per se also attract predators (e.g. Ware 1973) and should be kept to a minimum when the risk of encounter is great.

In streams, a common mechanism of escaping invertebrate predators is to enter the water current, and become a part of the "drift". This is a typical behaviour in, e.g. baetid mayfly nymphs encountering a stonefly nymph (Peckarsky 1980, Malmqvist and Sjöström 1987). However, when leaving the substrate the prey may then be at risk from drift-feeding predators, such as fish (e.g. trout) and net-spinning caddis larvae. In fact, in addition to, or instead of drifting for flight other behaviours are found among lotic insects, including running away (heptageniid mayflies, Peckarsky 1980), 'freezing' (veliid bugs, Brönmark et al. 1984, stoneflies, Otto and Sjöström 1983), and increasing apparent size (ephemerellid mayflies, Peckarsky 1980). Animals grazing algae on the top surfaces of stones are perhaps more exposed to predators than representatives of other functional feeding groups. Therefore, their anti-predator behaviours might be particularly interesting to study in detail.

A good deal of work has been directed at various aspects of the optimality of behaviour, in particular patch use, of grazing invertebrates in streams (e.g. Hart 1981, 1987, Lamberti and Resh 1983, McAuliffe 1984, Kohler 1984). Drift is a mechanism by which, for example, mayfly nymphs are thought to reach better food patches (e.g. Bohle 1978, Kohler 1985). Both locomotion during grazing and drift behaviour would be expected to change through the presence of predators.

In this study I analyse responses expressed as changes in movement rates, or related changes, of several grazers when exposed to the odour of three of their potential predators. To observe such responses two conditions must be fulfilled, 1) the prey animal must have the ability to identify the odour of the predator, and 2) it must respond to the odour by an observable change in behaviour.

Materials and methods

The following grazing species were tested: the mayflies *Baetis rhodani* Pictet and *Rhithrogena germanica* Eaton, the caddisflies *Agapetus ochripes* Curtis and *Silo pallipes* Fabr., the stonefly *Brach-*

yptera risi Mort., and the gastropod *Ancylus fluviatilis* Müller. The predators used were nymphs of the large perlid stonefly *Dinocras cephalotes* (Curtis) (length 2.0-2.5 cm) and caseless caddis larvae, *Rhyacophila nubila* Zett. (fifth instar), and a fish, the sculpin *Cottus gobio* L. (length 6 cm). Grazer body lengths (excluding cerci and antennae) ranged between 0.2-0.7 cm (*Ancylus*), 0.5-1.3 cm (*Rhithrogena*), 0.4-0.9 cm (*Baetis*), 0.15-0.30 cm (*Agapetus*), and 0.5-0.9 cm (*Silo* and *Brachyptera*). The stonefly *Brachyptera risi* was not tested with predators other than fish. All prey species (except *R. germanica*) used in this study are widely distributed and probably the most common non-chironomid grazers found in forest streams in southern Sweden. Of the predators, larvae of *R. nubila* are found in more or less every stream, except for the smallest ones, whereas *D. cephalotes* and sculpins have a more limited distribution, although completely overlapping that of the six grazers.

Ten similar-sized individuals of a single prey species were allowed to feed on benthic algae (mainly small green algae) grown on the top surface of unglazed ceramic tiles (10x10x0.75 cm) in an observation aquarium (15x18 cm, depth 2.0 cm) with three parallel inflows and outflows to make the water flow in a near-laminar way over the tile and animals (Fig. 1). Ordinary tap water (10.5 ± 1.5 °C, 800 ml min⁻¹), was passed either through a glass tube containing predator(s) (one sculpin or five insect predators) or another identical tube without predator(s) before entering the observation aquarium. Flow was diverted through either the predator or predator-free tube by means of a manually operated valve. A wall of corrugated cardboard prevented visual contact between the prey aquarium on the one hand, and the experimenter and the predators on the other. Prey animals were kept in running tap water on natural substratum, but without food, for 24 hours and were acclimatized in the observation aquarium for approximately one hour prior to the start of each experiment. Although analyses would have been simpler if single grazers had been used in each experiment, it was thought to be more realistic to keep several individuals together to allow the kinds of interactions which are natural in the

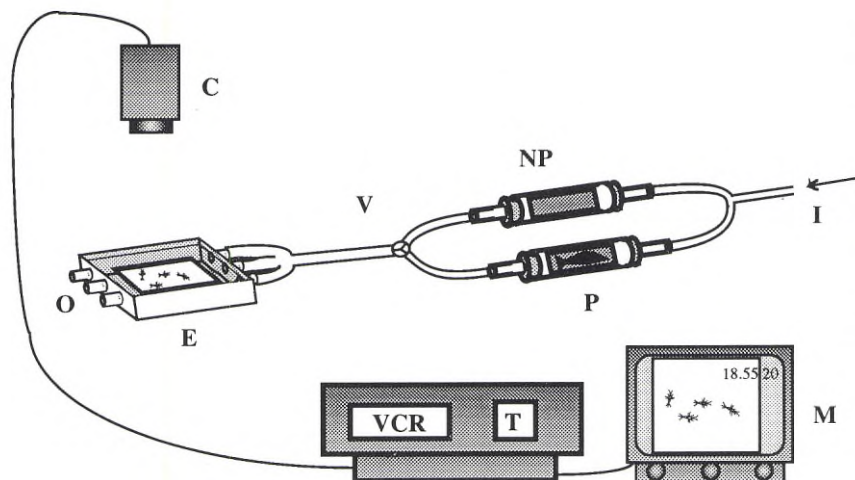


Fig. 1. Experimental setup showing water entering (I) either through the tube P (with predator) or NP (without predator) depending on the setting of valve (V), proceeding over the animals in the experimental chamber (E), and leaving through three outlet tubes (O). The behaviour of individual animals is recorded via the video camera (C) by the time lapse VCR with built in time display (T). On replay, distances moved by the animals are measured on the screen of the monitor (M).

grazers' natural environments. Grazers were exposed to water with or without predator odour for six to nine alternating 30 min periods in each experiment. The experiment was replicated three times for each predator-prey combination using new animals. In total, individual movement patterns over 146 h of recordings were analyzed.

Some mayflies, like heptageniids, are extremely sensitive to moving shadows (vision being an example of an alternative predator detection mechanism). Therefore, in order to avoid visual disturbance when switching the valve, experiments were conducted in darkness using an infrared light source. Rates of movement and events of immigration and emigration on and off the tile were recorded with infrared light sensitive video equipment. On playback, the tracks of individual animals were transferred to transparent film and the track lengths measured using a map wheel.

Consistencies among trials concerning the movement rates in the presence and absence of predator odour, respectively, were considered as was the magnitude of differences in consistent cases. Algal densities varied between experiments and caused differences in the absolute distances moved.

Results

In over sixty per cent of the trials locomotory activity of the prey species tended to decrease in the presence of predator contaminated water. The strongest responses were shown by *Baetis rhodani* and *Agapetus ochripes* encountering *Dinocras* odour (Fig. 2). The response shown by *B. rhodani* encountering *Dinocras* contaminated water resulted in a reduction to less than a third of the control rate (Fig. 2 and 3; 25.2% in the first experiment, 35.1% in the second, and 29.6% in the third experiment). Nymphs of the other mayfly species, *Rhithrogena germanica*, did not show any evidence of changed behaviour in the presence of predator odour (Fig. 2).

The caddis larvae *A. ochripes* and *Silo pallipes* both responded consistently to *Dinocras* odour, although in opposite directions: *Agapetus* larvae by decreasing their total locomotory activity to 15.2%, 13.1%, and 55.7% of the control rates, in the three experiments, respectively, and *Silo* larvae by increasing their rates with 12.9%, 115.7%, and 32.6%. In the presence of sculpin odour, *Agapetus* reduced its total locomotion (to 45.3%, 47.3%, and 72.4%, respectively, of the controls).

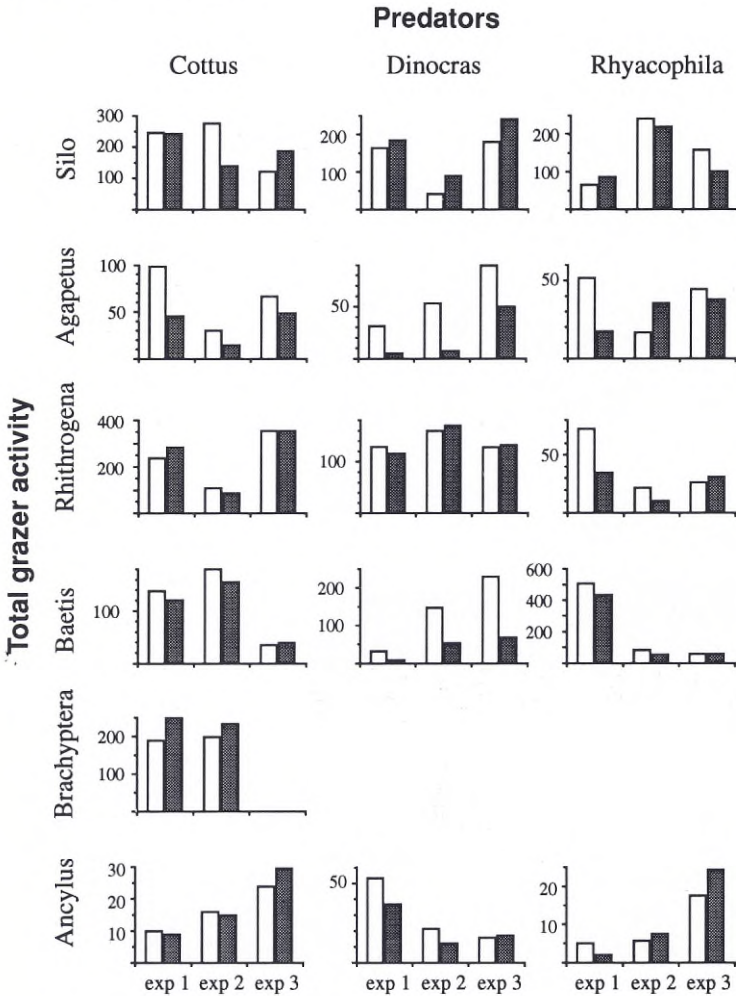


Fig. 2. Total movement distances (combined for the three experiments) for each grazer species in absence and presence of odour from three predator species. Note that consistently reduced rates were recorded for *Agapetus* in response to *Cottus* and *Dinocras*, and for *Baetis* in response to *Dinocras*. Consistently increased rates were present in *Silo* in response to *Dinocras* and *Brachyptera* in response to *Cottus*. Shaded bars denote predator odour treatment and open bars denote controls.

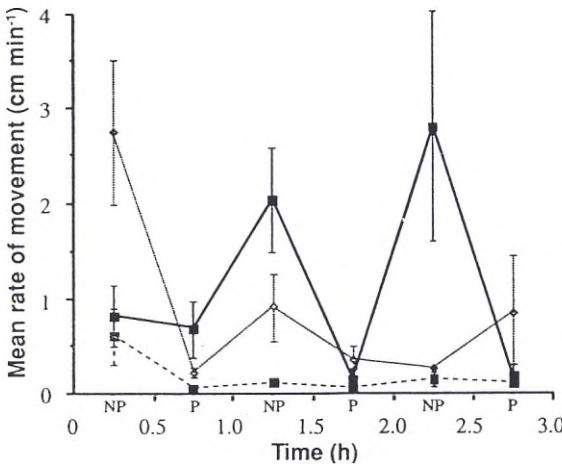


Fig. 3. The movement rate of *Baetis rhodani* exposed to odour from *Dinocras cephalotes* in three separate experiments. Each point represents the mean rate of five to ten individual *Baetis* nymphs. Although the levels of movement rates differ among experiments, in all but one case movement rate dropped when exposure to predator odour followed. Vertical bars denote ± 1 standard error. NP = no predator odour present, P = predator odour present.

Table 1. The number of larval *Silo pallipes* exposed to odour from *Dinocras cephalotes* moving away from, toward the predator, or neither. The values represent net direction, i.e. position of individual larvae at the end of the first 30 min exposure period of each of three experiments compared to that at the beginning of each experiment and the same in 30 min control exposures without *Dinocras* odour.

Treatment	Direction of movement			
	N	Downstream	Upstream	Perpendicular
Predator present	18	12	4	2
Control	15	1	14	0

The increased crawling rate of *Silo* suggests that the observed response could be one of avoidance. Therefore, I analysed the data in order to estimate the net direction of *Silo* larvae movements. I found that significantly more larvae moved downstream in *Dinocras* treatments than in controls (Table 1; χ^2 -test, $P < 0.001$). Yet, more than 28% of *Silo* larvae exposed to *Dinocras* showed a net upstream movement. Movements were not straight but showed typical grazing tracks, i.e. sweeping zigzag patterns (cf. Wiley and Kohler 1984).

Ancylus fluviatilis and *Rhithrogena germanica* showed no clear changes in movement rates in response to any predator odour treatment (Fig. 2).

Whilst the effects of odour from sculpins and *Rhyacophila* were hard to detect, those of *Dinocras* were the more obvious. This was established not only through differences in movement rates but also in the number of prey that showed no detectable movement during the first 30 min exposure to predator odour following upon the first control treatment. The number of such stationary individuals increased significantly when exposed to *Dinocras* odour in *Ancylus* ($\bar{x} = 4.92$, $P < 0.01$) and *Agapetus* ($\bar{x} = 4.40$, $P < 0.05$), but not for the other species.

Also the frequency of drift events of *Baetis rhodani* was depressed as a response to odour from *Dinocras* (Table 2). There were, however, no significant changes in drift behaviour of this mayfly in response to odour from *Rhyacophila* or sculpin. In the latter case there was indeed a

Table 2. Total number of drift events per 30 min exposure of *Baetis rhodani* to the odour of different predators. Ns = not significant.

Predator species	Without predator	With predator	χ^2	Significance
<i>Cottus</i>	9	4	0.96	Ns
<i>Dinocras</i>	43	14	7.38	$P < 0.01$
<i>Rhyacophila</i>	52	56	0.07	Ns

tendency of reduced drift, but the number of observations was too low to support this conclusion as well as accepting the null hypothesis that sculpin odour did not influence the drift of *Baetis*.

Discussion

This study suggests that indirect effects of predator presence may pose constraints on optimal feeding behaviour in some grazing stream invertebrates. Changed movement rates within food patches and reduced drift, a behaviour used for travel between food patches, are likely to lead to a reduced food intake. In other studies, the perception of predator presence was observed to restrict drift in large mayfly nymphs and crustaceans, inhibit larval odonate movements, and was thought to lower the efficiency of feeding (Heads 1985, Allan et al. 1986, Andersson et al. 1986 - but see Allan and Malmqvist 1989, Malmqvist 1988, Martínez and Malmqvist unpubl.), thus subsequently reducing fitness. Feltmate and Williams (1989) in fact showed that the presence of rainbow trout reduced the feeding rate of the predacious stonefly *Paragnetina media*. The mechanism for predator detection was not made clear in all these studies, although Andersson et al. (op. cit.) and Martínez and Malmqvist (unpubl.) have experimental evidence for effects via chemical cues. Recently, also Kohler and McPeck (1989), in laboratory experiments, demonstrated that nymphs of *Baetis tricaudatus* Dodds were able to detect sculpin odour and respond by a set of adaptive behavioural adjustments including the use of top surfaces of the substrate, movement rates within and between food patches, and in drift.

Baetis rhodani is obviously a vigilant species, responding sensitively to its environment with respect to predators (Malmqvist 1986, 1988, Malmqvist and Sjöström 1987, Martínez and Malmqvist unpubl.). It is interesting to note that nymphs of this species slowed down their activity, but did not stop it entirely. This suggests that they continued feeding, supported by the typical zigzag movements used by grazers (see above), thereby balancing the conflicting demands of food intake and predator avoidance (cf. Sih 1980). In contrast, findings support a different strategy in *Ancylus fluviatilis* and *Agapetus ochripes*, both of which significantly increased their habit of "freezing" their movements over periods as long as 30 minutes. This habit explains, at least partly, the reduced total activity of the latter species (Fig. 2).

While all the species tested occur in flowing water, the current speed provided in the experiment probably was considerably lower for some of the species than in their natural environments. This applies in particular to *Baetis* and *Rhithrogena* and this might have influenced the results, especially of drift rates (making them comparatively higher than natural in *Baetis*). However, since all results of treatments were related to controls, behavioural changes, where observed, were qualitatively considered to be realistic.

Williams (1987) carried out experiments in which he registered the behaviour of mayfly nymphs being touched with stonefly antennae. He demonstrated that the presence of stonefly predators, or water from a tank with such, influenced the responses of various mayfly nymphs, including *Baetis rhodani*, on tactile stimulation. In *B. rhodani*, for example, drift behaviour increased in contacts with predator antennae (see also Malmqvist and Sjöström 1987 and Peckarsky and Penton 1989 for similar results), whereas "freezing" behaviour increased (compared with predator-free controls) in intraspecific contacts. Other workers have also observed that baetids react at a very short range from stonefly predators (Peckarsky 1980, Malmqvist and Sjöström 1987, Peckarsky and Penton 1989). These non-contact responses were however interpreted differently by the authors as resulting from chemical (Peckarsky 1980), visual

(Malmqvist and Sjöström 1987), and hydrodynamic stimuli (Peckarsky and Penton 1989). In the experiments reported here, in which the predator was invisible to the prey, reductions in movement rates were obvious only after analysing a large number of 1-30 min videotape sequences focussing on individual animals. The observed behavioural patterns were different from, and more subtle, than those observed directly. Apparently baetids possess a complex repertoire of predator detection capacities. There is an increasing body of literature on freshwater invertebrates that show multiple behavioural defenses, e.g. in Hemiptera (Brönmark et al. 1984), Gastropoda (Brönmark and Malmqvist 1986), and Plecoptera (Moore and Williams 1990).

The observed increased mobility of *Silo* in the presence of *Dinocras* odour was unexpected. These caddis larvae appear well protected and withdrawal into their cases should render them invulnerable to attacks from *Dinocras*. Withdrawal may, however, cause them to lose their hold and be displaced by the current into suboptimal habitats. Cased caddis of the *Silo* type, considering their own body mass, carry a heavy load which could be energetically costly to return to the stone surfaces. In such a perspective, a controlled movement away from an enemy might reduce the risk of an encounter. In fact, *Silo* larvae did show a significant tendency to move away (downstream) from the source of *Dinocras* odour. From track analyses it was obvious that they did not stop feeding while retreating. Since food intake was not measured, it is not known whether downstream movement led to reduced energy intake in *Silo*. Further studies may reveal whether *Silo*, with their continued feeding behaviour while avoiding *Dinocras*, do reduce their food intake, and thus balance conflicting demands, or if they can keep the same efficiency in terms of costs and benefits while retreating. Because of their smaller size and slower crawling speed, *Agapetus* could not be expected to have the possibility of a similar rapid avoidance as *Silo*, and hence may benefit more from the reduced or stopped movement observed.

The weak responses of prey animals to sculpin odour in this experiment may be due to the fact that

this predator was not found at the sites from where the prey animals were collected. Thus the test animals were naive to this fish, and it may not have been identified as a threat. Normally, *Cottus gobio* include members of the taxonomic groups studied here in their diet (Andreasson 1971). Soluk and Collins (1988) observed that *Baetis tricaudatus* and *Ephemerella subvaria* McDunnough responded to the presence of a stonefly predator by changing positions on stones. When exposed to sculpins (*Cottus bairdi* Girard), however, no effects were discovered. With regard to differential responses of *Baetis* nymphs to predacious stonefly nymphs and sculpins, my results are similar to those reported by Soluk and Collins (op.cit.).

The lack of reaction to *Rhyacophila* odour must have other explanations since *Rhyacophila nubila* are widespread free-living caddis larvae, that were also found at the sites where the grazers were collected for this study. They seem to have an opportunistic mode of feeding and switch between grazing, ambush, and, more rarely, active hunting behaviour (Malmqvist unpubl.). Although they appear to be sluggish and poorly equipped for prey capture, they obviously manage to catch or damage mayfly nymphs (e.g. Nilsson 1986). *Agapetus* was thought to be the main prey for *R. nubila* in a study by Malmqvist and Sjöström (1984). The less active mode of foraging in *Rhyacophila* perhaps make them only a minor threat to members of the grazing guild, or maybe they simply excrete insufficient amounts of chemicals to be detected.

Inappropriate responses can also occur when the concentrations of odour are too small or too high. This has been the case in experiments using extracts of predators (Martínez pers. comm.). In this study, however, predators produced their own exudates in concentrations presumably representative of what prey might perceive in the wild. Also, the experiments were conducted in darkness. In natural situations, low light levels would considerably reduce the risk of being eaten by visually hunting predators. Thereby it is possible that behavioural responses to the presence of sculpins were relaxed (cf. Kohler and McPeck 1989).

In conclusion, this study demonstrated that the presence of odour alone can cause some grazing invertebrates to alter their movement patterns.

Independent of the type of response, the changed behaviour is likely to influence food intake and thereby, if frequently exposed, ultimately the fitness of the animals. A second consequence of these observations is that lotic predators should avoid "advertising" their presence by hunting in an upstream direction (Peckarsky 1980).

Acknowledgments

I thank Drs Carin Magnhagen, Lee Anne Martínez, Christian Otto, Bobbi Peckarsky, Simon Rundle and Bernhard Statzner for constructive comments on this work, and Mattias Alfredsson and Ann Erlandsson for technical assistance. The Swedish Natural Science Research Council and the Crafoord Foundation provided financial support.

References

- Allan, J.D., A.S. Flecker and N.L. McClintock. 1986. Diel epibenthic activity of mayfly nymphs, and its nonconcordance with behavioral drift. - *Limnol. & Oceanogr.* 31: 1057-1065.
- Allan, J.D., A.S. Flecker and N.L. McClintock. 1987a. Prey size selection by carnivorous stoneflies. - *Limnol. & Oceanogr.* 32: 864-872.
- Allan, J.D., A.S. Flecker and N.L. McClintock. 1987b. Prey preference of stoneflies: sedentary vs mobile prey. - *Oikos* 49: 323-331.
- Allan, J.D. and B. Malmqvist. 1989. Diel activity of *Gammarus pulex* (Crustacea) in a south Swedish stream: comparison of drift catches vs baited traps. - *Hydrobiologia* 179: 73-80.
- Andersson, K., C. Brönmark, J. Herrmann, B. Malmqvist, C. Otto and P. Sjöström. 1986. Presence of sculpins (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). - *Hydrobiologia* 133: 209-215.
- Andreasson, S. 1971. Feeding habits of a sculpin (*Cottus gobio* L. Pisces) population. - *Rep. Inst. Fresw. Res., Drottningholm* 51: 5-30.
- Bengtsson, G. 1982. Energetic costs of amino acids exudation in the interaction between the predator *Gammarus pulex* L. and the prey *Asellus aquaticus* L. - *J. Chem. Ecol.* 8: 1271-1281.
- Bohle, H.W. 1978. Beziehungen zwischen dem Nahrungsangebot, der Drift und der räumlichen Verteilung bei Larven von *Baetis rhodani* (Pictet) (Ephemeroptera: Baetidae). - *Arch. Hydrobiol.* 84: 500-525.
- Brönmark, C., B. Malmqvist and C. Otto. 1984. Anti-predator adaptations in a neustonic insect (*Velia caprai*). - *Oecologia* 61: 189-191.

- Brönmark, C. and B. Malmqvist. 1986. Interactions between the leech *Glossiphonia complanata* and its gastropod prey. - *Oecologia* 69: 268-276.
- Feltmate, B.W. and D.D. Williams. 1989. Influence of rainbow trout (*Oncorhynchus mykiss*) on density and feeding behaviour of a perlid stonefly. - *Can. J. Fish. Aquat. Sci.* 46: 1575-1580.
- Hart, D.D. 1981. Foraging and resource patchiness: field experiments with a grazing stream insect. - *Oikos* 37: 46-52.
- Hart, D.D. 1987. Experimental studies of exploitative competition in a grazing stream insect. *Oecologia* - 73: 41-47.
- Heads, P.A. 1985. The effect of invertebrate and vertebrate predators on the foraging movements of *Ischnura elegans* larvae (Odonata: Zygoptera). - *Freshw. Biol.* 15: 559-571.
- Kohler, S.L. 1984. Search mechanism of a stream grazer in patchy environments: the role of food abundance. - *Oecologia* 62: 209-218.
- Kohler, S.L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. - *Ecology* 66: 1749-1761.
- Kohler, S.L. and M.A. McPeck. 1989. Predation risk and the foraging behavior of competing stream insects. - *Ecology* 70: 1811-1825.
- Lamberti, G.A. and V.H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. - *Ecology* 64: 1124-1135.
- Malmqvist, B. 1986. Drift of mayflies in response to disturbance by predacious stonefly nymphs. - *Proc. 3rd Europ. Congr. Entomol., Nederlandse Entomologische Vereniging, Amsterdam.* p. 107-110.
- Malmqvist, B. 1988. Downstream drift in Madeiran levdas: tests of hypotheses relating to the influence of predators on the drift of insects. - *Aquatic Insects* 10: 141-152.
- Malmqvist, B. and P. Sjöström. 1984. The microdistribution of some lotic insect predators in relation to their prey and to abiotic factors. - *Freshw. Biol.* 14: 649-656.
- Malmqvist, B. and P. Sjöström. 1987. Stream drift as a consequence of disturbance by invertebrate predators. - *Oecologia* 74: 396-403.
- McAuliffe, J.R. 1984. Resource depression by a stream herbivore: effects on distribution and abundances of other grazers. - *Oikos* 42: 327-333.
- Molles, M.C. and R.D. Pietruszka. 1983. Mechanisms of prey selection by predaceous stoneflies: roles of prey morphology, behavior and predator hunger. - *Oecologia* 57: 25-31.
- Moore, K.A. and D.D. Williams. 1990. Novel strategies in the complex defense repertoire of a stonefly (*Pteronarcys dorsata*) nymph. - *Oikos* 57: 49-56.
- Nilsson, C. 1986. The occurrence of lost and malformed legs in mayfly nymphs as a result of predator attacks. - *Ann. Zool. Fenn.* 23: 57-60.
- Otto C. and P. Sjöström. 1983. Cerci as antipredatory attributes in stonefly nymphs. - *Oikos* 41: 200-204.
- Peckarsky, B.L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. - *Ecology* 61: 932-943.
- Peckarsky, B.L. and M.A. Penton. 1989. Early warning lowers risk of stonefly predation for a vulnerable mayfly. - *Oikos* 54: 301-309.
- Petranka, J.W., L.B. Kats and A. Sih. 1987. Predator-prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. - *Anim. Behav.* 35: 420-425.
- Sih, A., 1980. Optimal behavior: can foragers balance two conflicting demands. - *Science* 210: 1041-1043.
- Sih, A. 1984. The behavioral response race between predator and prey. - *Am. Nat.* 123: 143-150.
- Sjöström, P. 1985. Hunting behaviour of the perlid stonefly nymph *Dinocras cephalotes* (Plecoptera) under different light conditions. - *Anim. Behav.* 33: 534-540.
- Soluk, D.A. and N.C. Collins. 1988. Balancing risks? Responses and non-responses of mayfly larvae to fish and stonefly predators. - *Oecologia* 77: 370-374.
- Vermeij, G.A. 1982. Unsuccessful predation and evolution. - *Am. Nat.* 120: 701-720.
- Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). - *J. Fish. Res. Board Can.* 30: 787-797.
- Wiley, M.J. and S.L. Kohler. 1984. Behavioral adaptations of aquatic insects. p. 101-133. - In: Resh, V.H. and D.M. Rosenberg (eds.) *The ecology of aquatic insects*. Praeger, New York.
- Williams, D.D. 1987. A laboratory study of predator-prey interactions of stoneflies and mayflies. - *Freshw. Biol.* 17: 471-490.
- Williams, D.D. and K.A. Moore. 1985. The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: a laboratory analysis. - *Oikos* 44: 280-286.

Diet and Food Consumption of Young, Profundal Arctic Charr (*Salvelinus alpinus*) in Lake Takvatn

ANDERS KLEMETSEN¹, HARALD MULADAL² and PER-ARNE AMUNDSEN¹

¹ University of Tromsø, The Norwegian College of Fishery Science, Breivika, N-9001 Tromsø, Norway

² Akvaplan-NIVA, S.Tollbugt.3, N-9000 Tromsø, Norway

Abstract

Gillnet sampling in July-November 1985 revealed that a large part of the young charr in Lake Takvatn, North Norway, inhabits the profundal zone of the lake (>20 m) in the ice-free season. The fish ranged from 6-16 cm (12 cm modal) in length and from 1-4 years of age. In July 3+ charr dominated but most had left the profundal by August, when 2+ took over as the dominating year class. The chironomid *Heterotrissocladius subpilosus* made up 93% of the profundal benthos, and also dominated the stomach contents of the charr parr in the early part of the season. The pupae were selected positively, and the larvae negatively. Food diversity increased with the season. Crustacean plankton became important in the autumn, with *Bosmina longispina* as the major prey. At this time, some fishes also had littoral prey species in their stomachs, indicating that feeding migrations from the profundal to the littoral zone had taken place. Daily food rations of 3+ charr were nearly identical to previous estimates for littoral charr. In contrast, the food consumption of the 2+ fish were three times higher in July and August. It is concluded that the profundal habitat is only suitable for the smallest charr.

Introduction

The Arctic charr, *Salvelinus alpinus*, is the most common freshwater fish in North Norway. Along the coast, anadromous life histories prevail, most commonly along with resident segments of the same populations (Nordeng 1983). Lacustrine, landlocked populations are widespread in inland areas. Many of these populations have high densities, small fish sizes, stunted growth and high parasite loads. This was the situation in the oligotrophic Lake Takvatn in the early nineteneighties (Kristoffersen 1987, Amundsen and Klemetsen 1988, Amundsen 1989, Svenning and Grotnes 1991). During this state of high density, Klemetsen et al. (1989) recognized three life cycle stages in the population, which resembled the stages of parr, smolt and adult in anadromous charr. In the ice-free season, the adults dominated in the littoral zone, the smolts in the pelagic zone and the parr in the profundal zone of the lake.

The present contribution considers the diet and quantitative food intake of parr from the profundal

zone of Lake Takvatn. The profundal zone is the most uniform region of any oligotrophic lake. Temperature, light and chemical conditions vary little through the year, and the bottom is flat and without vegetation. The diversity, and also the density of the benthos is low. Oligochaetes, sphaeriid mussels and chironomids make up the communities. In the Scandinavian subarctic region, the orthocladid chironomid *Heterotrissocladius subpilosus* often dominates (Brundin 1949). In Lake Takvatn, we expected to find a simple, low density, profundal benthos, possibly with *H. subpilosus* as the dominant species. Very little is known on the food and feeding habits of young, lacustrine charr. We expected the parr in Lake Takvatn to feed extensively on the profundal benthos, especially the chironomids. Hypolimnetic zooplankton seemed to be the only other prey community available in the habitat.

The growth stagnation of the charr in Lake Takvatn occurred at around 20 cm fork length, and at 5-6 years of age (Amundsen 1989, Svenning and Grotnes 1991). These were adult fish living in the

littoral region of the lake. By estimating their daily food consumptions, Amundsen and Klemetsen (1988) found that growth was food limited. Extrapolation of age readings by Svenning (1985) indicated that the growth of the Takvatn charr was best during the first three years of life. If this could be verified, we expected the food consumption of the profundal parr to be higher than that estimated for the littoral adult fish.

Methods

Study area

Lake Takvatn is an oligotrophic, dimictic lake situated in a birch wood landscape at 214 m a.s.l. in Troms county, North Norway (69°07'N, 19°05'E). The area of the lake is 14.2 km², and there are two main basins, both with a maximum depth of nearly 80 m (Fig. 1). The ice-free period is 24 ± 4 weeks, and epilimnic temperatures are about 12 °C. In 1985, the profundal temperatures were 5–6 °C in the period July–October. By the first week of November it was 3 °C at 30 m. There are two months of midnight sun at this latitude. In addition to the charr, Lake Takvatn holds a substantial population of three-spined stickleback *Gasterosteus aculeatus* and a small population of brown trout *Salmo trutta*. A detailed description of the lake and its biota is given by Klemetsen et al. (1989).

Samples and treatment: charr

The sampling of profundal charr was performed at one fixed station at 30 m depth (Fig. 1), in the first week of every month from July to November 1985. Fleets of 1.5 m deep gillnets with bar mesh sizes 4, 6, 8, 10, 12.5 and 16 mm were used. Three separate fleets with the mesh sizes placed at random were used. When necessary, this effort was repeated for one or two consecutive nights. This is a narrow range of mesh, but test fishing in 1984 had demonstrated that coarser nets caught very few fish. In 1985, the 16 mm nets caught only 4% of the total catch and the 4 mm net caught no fish. We are confident that the range of nets took

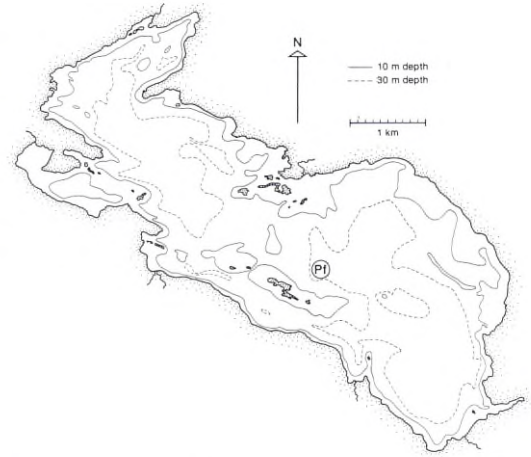


Fig. 1. Map of Lake Takvatn. Pf marks the sampling station.

representative samples of the profundal charr in Lake Takvatn in 1985 (for further detail, see Klemetsen et al. 1989). The nets were left fishing for 12 h at night. Routine sampling of the charr was performed in the field. Stomachs and otoliths were stored individually in ethanol. The total sample included 17 sticklebacks which were not treated further. No brown trout were caught.

All charr were aged by surface reading of the otoliths immersed in glycerol. Each stomach was opened and its degree of filling with food estimated. The majority of the prey were identified to species, except for some chironomids where larvae and pupae are described only for genera. A few rare chironomids were not identified below the family level. After identification, the relative contribution of each prey item to the stomach filling was estimated. This is essentially the points method of Hynes (1950), but employing a percentage scale. The importance of each prey item to the diet is documented as frequency of occurrence and per cent volume. The relative volume expresses the average contribution of the prey as a percentage of the average degree of filling in the sample. Dry weights (65 °C for >48 h) and ash weights (540 °C for >16 h) for individual stomach contents were then determined. The stomach content weights were expressed as mg ash-free dry weight (AFDW) g⁻¹ fish fresh weight.

All benthos prey were counted after identification. For disintegrated prey, the most durable part of the body, e.g. chironomid larva head capsules, were counted. These counts were combined with the benthos grab counts to estimate prey election indices, after Strauss (1979). This linear index L is given by

$$L = r - p$$

where r is the proportion of the prey in the stomach contents and p the proportion in the environment. The index varies between +1 and -1.

Daily food consumption was estimated by the Bajkov/Eggers method (Bajkov 1935, Eggers 1979), as described by Amundsen and Klemetsen (1988). With large intra-sample variabilities, this method gives more robust estimates than the Elliott and Persson (1978) method (Amundsen and Klemetsen 1986). The daily food consumption C_{24} is estimated by the equation

$$C_{24} = 24 SR$$

where S is the mean stomach content over the 24 h period and R the gastric evacuation rate. 12 h sampling periods were used because Amundsen and Klemetsen (1986) in general could not demonstrate diel variations in the stomach content weights of Takvatn charr taken at 3 h sampling intervals around the clock. Moreover, at 30 m depth, the light differences between day and night are considerably damped out. Geometric means of the stomach contents were used in the present study (Amundsen and Klemetsen 1986). The estimation of R for charr is given by Amundsen and Klemetsen (1988).

Samples and treatment: benthos

Benthos samples were taken at monthly intervals at the fish sampling station, and at the same time as the fish sampling. Thirty samples were taken every month with a 225 cm² Ekman grab. Each grab sample was sieved through 250 µm square mesh, and the animals were picked out and stored in ethanol.

In the laboratory, the animals were identified and counted. With the exception of three larvae,

the identification of chironomid larvae and pupae was taken as far as possible, i.e. to species, subgenus or genus. The procedures and tables in Wiederholm (1983, 1986) were employed for the identification work. The three unidentified larvae probably belonged to two different species. Oligochaetes were not identified further. Benthos densities are based on mean values per sample, although variance to mean ratios for the dominating animal *H. subpilosus* always showed contagious distributions (Elliott 1977).

Results

A total of 560 charr were caught during 1985. Four specimens were markedly larger than the rest. They ranged from 25 to 29 cm in length. All were maturing males, and all had small charr in their stomachs (1-2 specimens, 4-8 cm). They will not be treated further in this paper. The length range of the remaining catch was 6.3-19.8 cm, the majority within the 6-16 cm length classes, and with a modal length class of 12 cm. The range of weights was 1.5-53 g. The majority was below 20 g and the mean weight was 13.3 g.

There was a significant drop (t -test, $p < 0.05$) in the mean length of the charr samples from July to August (Fig. 2). This was followed by a steadily increasing mean length until the last sample in November (significant, $p < 0.05$, between August and November, and October and November). A correspondent change was found for the age distribution and the CPUE (Fig. 3). In July, the catch was very high and strongly dominated by 3+ charr. From July to August the CPUE dropped sharply, followed by a steady increase until October. During the same period, 2+ took over as the dominating age class. Klemetsen et al. (1989) demonstrated that the disappearance of 3+ fish from the profundal coincided with an increase of 3+ and also 4+ fish in the pelagic zone. They proposed that this habitat shift was coupled to a life stage shift from parr to smolt.

The growth of the charr in the profundal samples corresponded fairly closely to the growth found in 1980 by Svenning (1985) and M.-A. Svenning (pers. comm.) for 3+ and older fish

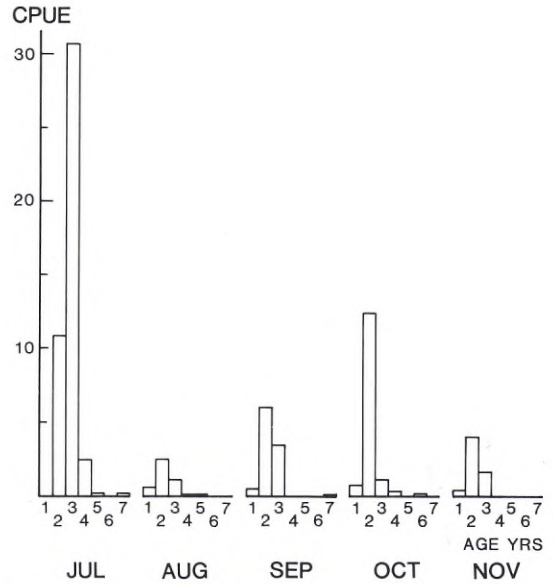
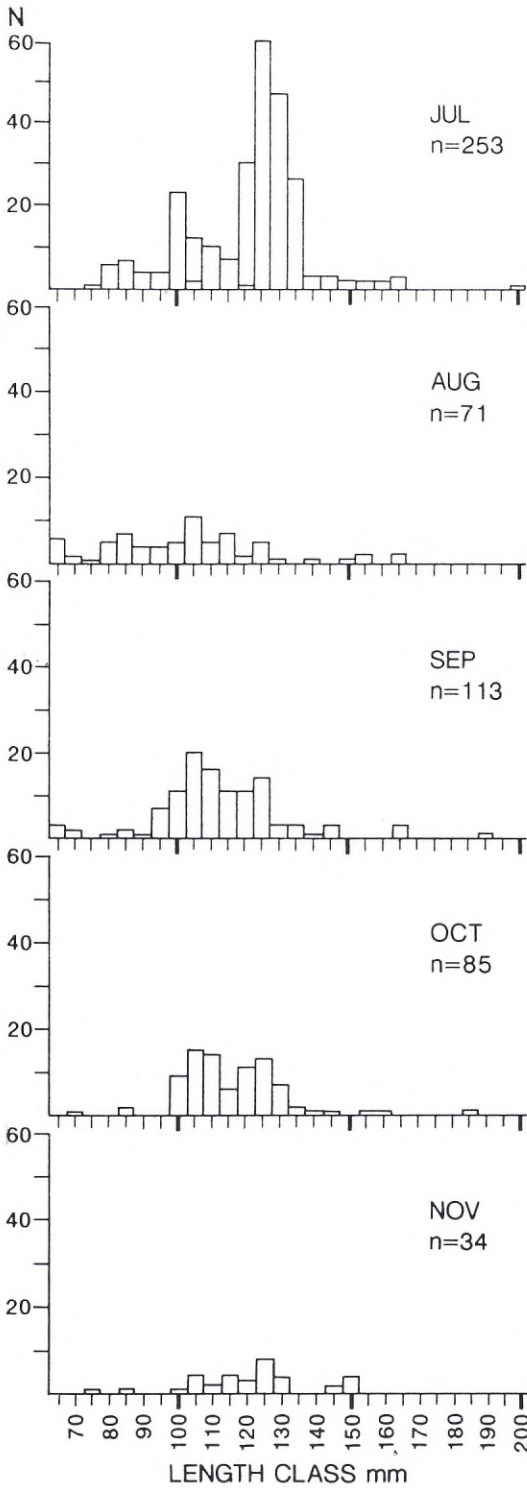


Fig. 3. Catch per unit effort (CPUE) of the different age groups of profundal charr July-November 1985. After Klemetsen et al. (1989).

(Fig. 4). By implication, this indicates that charr below three years of age had the fastest growth in the lake. The present length by age readings confirmed this for 1+ and 2+; although it cannot be ruled out that fastgrowing specimens were over-represented in the samples of these year classes. The smallest mesh sizes may select more on body circumference, expressed indirectly for instance in the condition factor, than on body length but such detailed analysis is outside the scope of the present contribution.

The profundal macrobenthos samples showed a community of very simple structure. Apart from a single specimen of the amphipod *Gammarus lacustris* (probably strayed from the littoral zone); only Oligochaeta and Chironomidae were present. The orthocladiid chironomid *H. subpilosus* dominated completely (Fig. 5, Table 1). This single species made up 93% of the total material (Table 1).

Fig. 2. Length class distributions of samples of profundal Takvatn charr July-November 1985.

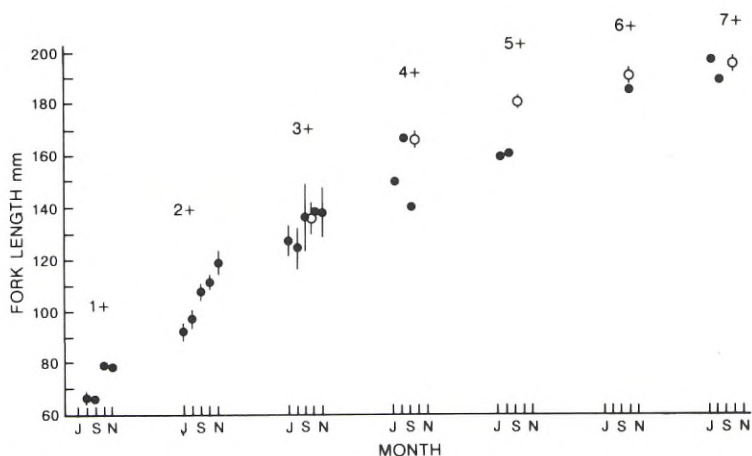


Fig. 4. Seasonal development of the mean lengths of age group samples of profundal charr July (J) to November (N) 1985. Age by length readings after Svenning (1985) are inserted for comparison (open circles). 95% confidence limits given.

Oligochaeta made up 4%, the remaining 2% consisted of three identified and two unidentified chironomids. Two additional chironomids, *H. maeri* and *Abiskomyia* sp. were found in the charr stomachs. Following Sæther (1979), Lake Takvatn may be classified as a beta-oligotrophic lake. The strong dominance of *H. subpilosus* in the profundal of Scandinavian subarctic lakes was established

already by Brundin (1949). The density of the Lake Takvatn profundal benthos decreased by about one half, from about 600 to about 300 ind. m⁻², from July to September. This was a direct consequence of *H. subpilosus* emergence (Fig. 5). Pupae of the species were found only during the first part of the sampling period, mainly in July.

The diet of the profundal charr showed several strong seasonal trends (Fig. 6). The diversity developed from just one prey species, *H. subpilosus*, in July to 10 different prey species in November. The dominance of *H. subpilosus* had already disappeared by August, and pupae were not found in charr stomachs after September. Larvae were

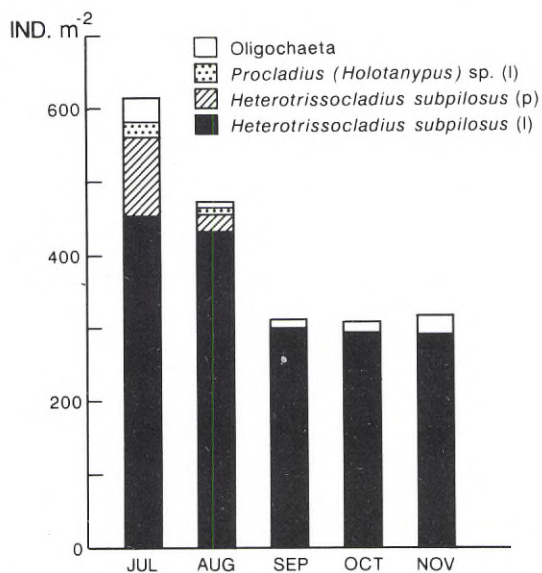


Fig. 5. Mean number of animals in macrobenthos samples from the profundal zone of Lake Takvatn 1985.

Table 1. Profundal benthos (N) from Ekman grab samples in Lake Takvatn 1985. Sampling site (30 m depth) is shown in Fig. 1. l = larvae, p = pupae.

TAXON	N	%
Oligochaeta, indet.	57	4.2
<i>Gammarus lacustris</i>	1	0.1
<i>Procladius (Holotanypus) sp. l</i>	20	1.5
<i>Procladius (Holotanypus) sp. p</i>	1	0.1
<i>Protanypus sp. l</i>	3	0.2
<i>Corynoneura sp. l</i>	6	0.4
<i>Heterotrissocladus subpilosus l</i>	1,198	87.2
<i>Heterotrissocladus subpilosus p</i>	83	6.0
Chironomidae, indet. l (two spp.)	3	0.3
Total	1,372	100.0

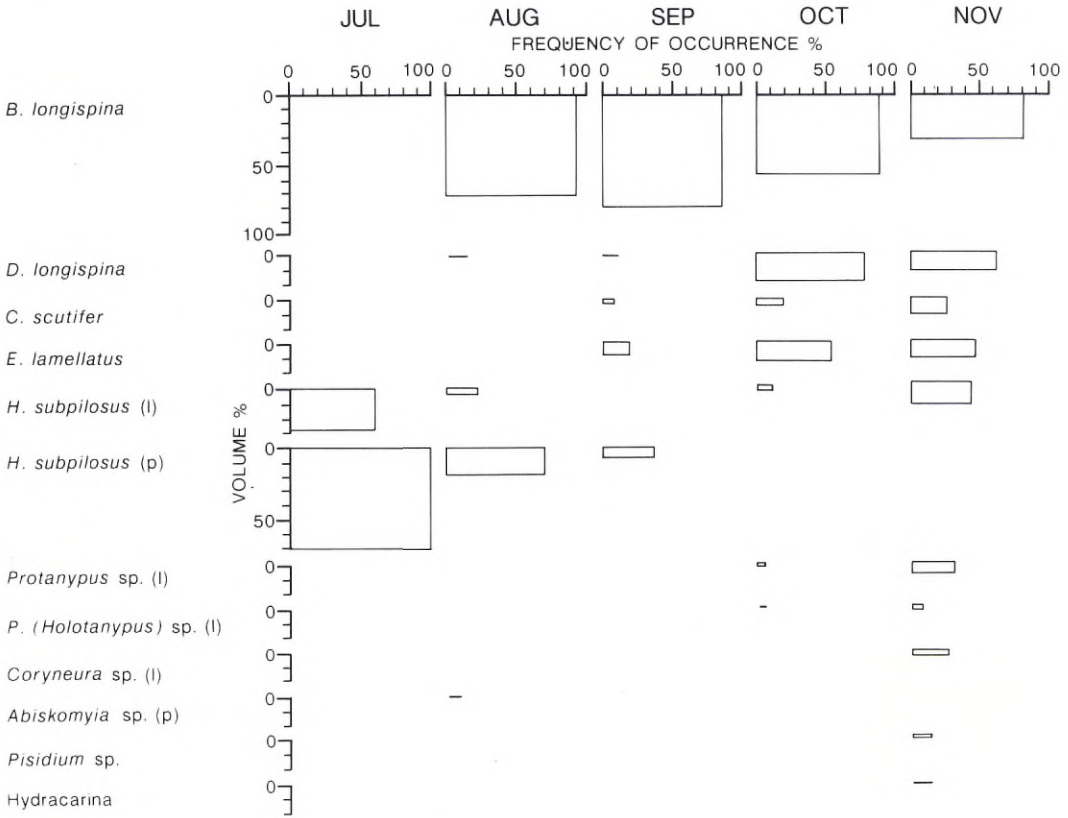


Fig. 6. The diet of profundal Takvatn charr 1985.

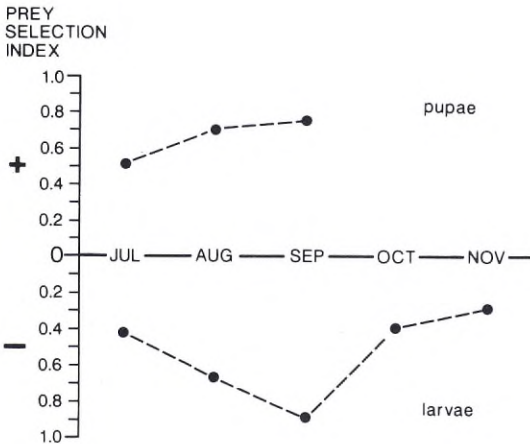


Fig. 7. Prey selection indices for pupae of *Heterotrissocladius subpilosus* in profundal Takvatn charr 1985.

important in the first, and again in the last monthly sample. The other chironomid larvae also occurred in November. Crustacean zooplankton became dominant from August, in association with the decrease of the *H. subpilosus* pupae. *Bosmina longispina* was the chief prey in August and September, and was still dominant in October and November when the other cladoceran, *Daphnia longispina*, also became a significant part of the diet. The copepod *Cyclops scutifer* was never important.

The chydroid cladoceran *Eurycercus lamellatus* was a regular element of the diet from September to November, and in November water mites Hydracarina were also found in the stomachs. This is intriguing because both these prey are littoral animals. This may be the case also for pea mussels *Pisidium* sp.

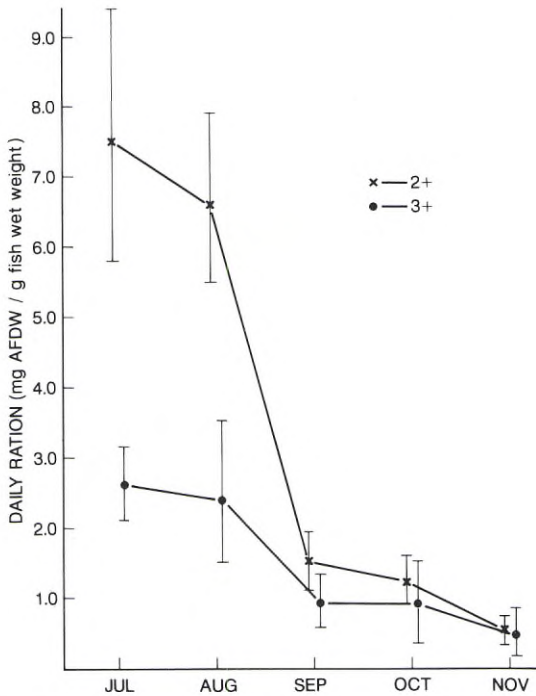


Fig. 8. Daily ration of 2+ and 3+ profundal Takvatn charr July-November 1985. 95% confidence limits are given for the ash-free dry weight AFDW estimates.

There was a weak tendency in the material for the younger year-classes to eat more plankton and less benthos than the older charr, but the variance was too great to conclude validly on this point.

The prey selection indices for *H. subpilosus* always deviated considerably from zero values (Fig. 7). The pupae were present in the diet from July to September. In this period they were always positively selected, with index values between +0.5 and +0.8. In contrast, the larvae were always negatively selected, with indices between -0.3 and -0.9. The profundal benthos of low importance in the diet (see Fig. 6) were taken at random by the young charr (index values close to zero).

In the summer (July and August), the daily ration was found to be very much higher in 2+ than in 3+ fish (Fig. 8); $p < 0.001$, Mann-Whitney U-test. The consumption rates fell markedly in both age groups from September. In the autumn (September-November) the daily food rations were never significantly different between the two age

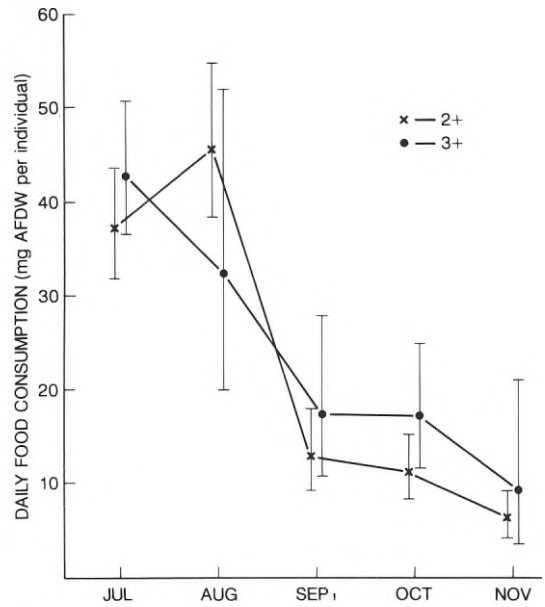


Fig. 9. Daily food consumption per individual fish of 2+ and 3+ profundal Takvatn charr July-November 1985. 95% confidence limits given.

groups ($p > 0.05$). Considering individual fish, it appeared that the smaller (9-12 cm) two-year-old fish ate the same amount of food as the larger (13-14 cm) three-year-old fish (Fig. 9). The differences in daily food consumption between the samples of 2+ and 3+ fish were not significant at any time ($p > 0.05$).

Discussion

In arctic lakes, young charr have repeatedly been sampled in shallow water close to the shores, usually with beach seine or electroshocking (Johnson 1983, Sparholt 1985, Riget et al. 1986, M.-A. Svenning pers. comm., for Svalbard). The observations from more temperate lakes tend to show that the young charr leave the shore regions in early life, probably during the first summer (Lindström 1955, and pers. comm., Kircheis 1976, and pers. comm., Hindar and Jonsson 1982). In Lake

Thingvallavatn, Iceland, Sandlund et al. (1988) found 0+ charr in the surf zone during the summer. Apparently, several of these fish left the littoral for the pelagic zone in the autumn, and some fish possibly also migrated to deeper benthic areas.

The present material had no 0+ and very few 1+ fish. No fish were caught in the 4 mm nets. This may be due to one of two reasons. Because of low weight (6 cm charr weighed 1.5-2 g) and low swimming velocity such small fish may lack sufficient momentum to become captured in the nets, even with a net thread thickness of only 0.09 mm as in our smallest mesh sizes. In other words, the two youngest year classes might have been there but the nets did not catch them. The alternative is that the 0-group and most of the 1-group had not moved into deep water. Because the spawning areas in Lake Takvatn are in shallow water, the fry also have to start out in shallow water. Observations from 1989 indicate that they are still there in early summer. In early June, shortly after ice-break, three charr fry were caught; one in an airlift-operated sampling device for benthos and two in stickleback traps. At this time, the fish are small enough to hide from predators among the stones in the shore region. Interestingly, Fürst and Hammar (1984, see also Fürst et al. 1978, 1981), in a tank experiment, observed that two weeks old alevins congregated close to the shoreline and sometimes hid under stones. As they become larger, 0+ Takvatn charr face heavy predation risks in the littoral zone. Potential predators are larger charr, brown trout and diving birds, above all redbreasted mergansers *Mergus serrator* which have 15-20 broods on the lake annually. They also face heavy competition for food and space, both from their own kind and from the dense stickleback population. Most probably the charr in Lake Takvatn move into deeper water during their first summer. If so, the main reason for not catching them is that gillnets are unsuitable gear for such small charr.

The expectation of a strong dominance of profundal benthos in the diet of the young charr was fulfilled only in the early part of the season. From August, planktonic crustaceans became important prey. Kildemo (1982) found that the plankton density was much lower in the hypolimnion than

in the epilimnion. Only minor diel vertical plankton migrations have been demonstrated in Lake Takvatn. This suggests that the *Bosmina* in the stomachs of the parr had been eaten in shallower water. The occurrence of littoral benthos in the stomach contents, above all *Eurycercus lamellatus*, supports this assumption. These findings indicate that profundal parr can undertake migrations into shallower water to feed, and then descend again. They were caught at 30 m during the night, indicating that the feeding trips must have taken place during the preceding day, possibly at dusk. For most parts of the lake, the distance along the bottom profile between 30 m and 10 m depths are in the order of a few hundred meters (Fig. 1). In the sublittoral zone, both shore-near, epilimnic plankton and benthos are accessible prey.

There is an important seasonal element in the availability of profundal prey for the parr. In the early part of the season the pupae of *H. subpilosus* were strongly preferred prey. The parr had eaten nothing else and the selection indices were positive. These pupae are mobile and probably appear on the surface of the sediments before emergence. For a short period the species is highly exposed to fish predation. The larvae on the other hand are probably confined within tubes in the sediment (Oliver 1971) and are much less exposed. Their importance in the diet of the parr was much less than that of the pupae, and the selection indices were always negative. Because *H. subpilosus* dominated the profundal macrobenthos completely, the feeding conditions for the parr change dramatically when the pupal generation of the year has emerged. The *H. subpilosus* population is reduced by approximately one half, and are only present as larvae which are well concealed. There is very little alternative prey available. This strong negative step in the profundal prey availability must be an important driving force behind the observed increase in the diversity in the diet of these charr with season, and their probable feeding trips into shallower water.

The growth through the 1985 season of the age 2 parr is the highest growth recorded for any Takvatn charr. A similar growth is indicated for the age 1 group (Fig. 4), but the sample is too small

to be conclusive. The 2+ parr also had the highest food consumption estimates found in Lake Takvatn, with July and August values of daily ration three times higher than for the 3+ fish from the same samples. The estimates for 3+ fish were very close to the values for stunted, littoral charr found by Amundsen and Klemetsen (1988), which gave little scope for growth in the summer and no scope for growth in the autumn. Following Winberg (1956), see also Mann (1978), Amundsen and Klemetsen (1988) calculated the daily food requirements at activity level for littoral charr to be about half of the present consumption values for 2+ fish in the summer. Given the lower temperatures in the hypolimnion, in which these fish live at least part of the time, this leaves a considerable scope for growth for the 2+ parr.

In spite of their larger size, the 3+ parr were not able to consume more food than their smaller and one year younger mates (Fig. 9). As discussed above, the diversity and availability of prey for a charr based in the profundal zone is severely restricted, especially as the season develops. The quantitative food intake estimates and the growth values strongly indicate that the profundal habitat is suitable only for the smallest charr parr. The shift from 3+ to 2+ fish as the dominant yearclass between July and August and the correspondent sharp drop in CPUE (Fig. 3) supports this hypothesis.

The main conclusion to be drawn from the present study is that the profundal zone of Lake Takvatn is a marginal habitat for charr. Only the smallest parr seems to be able to gain a positive output from the available production. Most probably, the profundal zone is inhabited by charr as a direct consequence of a heavy predation and competition risk in the littoral zone. A high density in the charr population itself is an important factor in this respect. These conclusions may have general application to charr lakes.

Acknowledgments

We thank Anton A. Giæver for his contribution to the field work, Ole A. Sæther and Endre Willassen at Zoological Museum, Bergen for their help with chironomid preparation and identification, and

Jeff Wallace for grammatical corrections to the manuscript. The comments by one anonymous reviewer led to the omission of unnecessary detail, and also some unsupported speculation, from the discussion.

References

- Amundsen, P.-A. 1989. Effects of intensive fishing on food consumption and growth of stunted Arctic charr (*Salvelinus alpinus* (L.)) in Takvatn, northern Norway. - *Physiol. Ecol. Japan, Spec. Vol. 1*: 265-278.
- Amundsen, P.-A. and A. Klemetsen. 1986. Within-sample variabilities in stomach contents weight of fish - implications for field studies of consumption rate. p. 307-314 - In: Simenstad C. A. and G.M. Cailliet (eds.). *Contemporary studies on fish feeding*. Junk, Dordrecht.
- Amundsen, P.-A. and A. Klemetsen. 1988. Diet, gastric evacuation rates and food consumption in a stunted population of arctic charr, *Salvelinus alpinus* L., in Takvatn, northern Norway. - *J. Fish Biol.* 33: 697-709.
- Bajkov, A.D. 1935. How to estimate the daily food consumption of fish under natural conditions. - *Trans. Amer. Fish. Soc.* 65: 288-289.
- Brundin, L. 1949. Chironomiden und andere Bodentiere der Sudschwedischen Urgebirgseen. - *Rep. Inst. Freshw. Res., Drottningholm* 30: 1-914.
- Eggers, D.M. 1979. Comments on some recent methods for estimating food consumption by fish. - *J. Fish. Res. Board Can.* 36: 1018-1019.
- Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. - *Freshw. Biol. Assoc. Sci. Publ.* 25: 1-160.
- Elliott, J.M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. - *J. Anim. Ecol.* 47: 977-993.
- Fürst, M. and J. Hammar. 1984. Effects of water level fluctuations on the recruitment of Arctic charr. p. 303-311. - In: Johnson L. and B. Burns (eds.). *Biology of the Arctic charr*. University of Manitoba Press, Winnipeg.
- Fürst, M. U. Boström and J. Hammar. 1978. Effects of new fish-food organisms in Lake Blåsjön. - *Inform. Inst. Freshw. Res., Drottningholm* (15). 1-94 p. (In Swedish with English summary.)
- Fürst, M. U. Boström and J. Hammar. 1981. Effects of introduced *Mysis relicta* on fish in Lake Torrön. - *Inform. Inst. Freshw. Res., Drottningholm* (1). 48 p. (In Swedish with English summary.)
- Hindar, K. and B. Jonsson. 1982. Habitat and food segregation of dwarf and normal Arctic char (*Salvelinus alpinus*) from Vangsvatnet lake, western Norway. - *Can. J. Fish. Aquat. Sci.* 39: 1030-1045.
- Hynes, H.B.N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of the methods used in studies of the food of fishes. - *J. Anim. Ecol.* 19: 36-58.

- Johnson, L. 1983. Homeostatic characteristics of single species fish stocks in arctic lakes. - *Can. J. Fish. Aquat. Sci.* 40: 987-1024.
- Kildemo, K. 1982. Livssyklus, verikalfordeling og døgnmigrasjon hos krepsdyrplanktonet i en nordnorsk innsjø (Takvatnet). - Cand. scient. thesis. University of Tromsø, Norway. (In Norwegian.)
- Kirchis, F.W. 1976. Reproductive biology and early life history of the Sunapee trout of Floods pond, Maine. - *Trans. Amer. Fish. Soc.* 105: 615-619.
- Klemetsen, A., P.A. Amundsen, H. Muladal, S. Rubach and J.I. Solbakken. 1989. Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. - *Physiol. Ecol. Japan, Spec. Vol. 1*: 187-200.
- Kristoffersen, R., 1987. *Diphyllbothrium* in Lake Takvatn charr. - *ISACF Inform. Ser., Inst. Freshw. Res., Drottningholm* 4: 93-98.
- Lindström, T. 1955. On the relation fish size - food size. - *Rep. Inst. Freshw. Res., Drottningholm* 36: 133-147.
- Mann, R.K.H. 1978. Estimating the food consumption of fish in nature. p. 250-273. - In: Gerking, S.D. (ed.) *Ecology of freshwater fish production*. Blackwell, Oxford.
- Nordeng, H. 1983. Solution to the "char problem" based on Arctic char in Norway. - *Can. J. Fish. Aquat. Sci.* 40: 1372-1387.
- Oliver, D.R. 1971. Life history of the Chironomidae. - *Ann. Rev. Entomol.* 16: 211-235.
- Riget, F.F., K.H. Nygaard and B. Christensen. 1986. Population structure, ecological segregation, and reproduction in a population of Arctic char (*Salvelinus alpinus*) from Lake Tassersuaq, Greenland. - *Can. J. Fish. Aquat. Sci.* 43: 985-992.
- Sandlund, O.T., H.J. Malmquist, B. Jonsson, S. Skulason, S.S. Snorrason, P.M. Jonasson, R. Gydemo and T. Lindem. 1988. Density, length distribution, and diet of age-0 Arctic charr, *Salvelinus alpinus*, in the surf zone of Thingvallavatn, Iceland. - *Env. Biol. Fish.* 23: 183-195.
- Sparholt, H. 1985. The population, survival, growth, reproduction and food of Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. - *J. Fish Biol.* 26: 313-330.
- Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index for food selection. - *Trans. Amer. Fish. Soc.* 108: 344-352.
- Svenning, M.-A. 1985. Økotypisk formdannelse hos røye (*Salvelinus alpinus*) i Takvatnet, Troms. - Cand. real. thesis. University of Tromsø, Norway. (In Norwegian.)
- Svenning, M.-A. and P. Grotnes 1991. Stationarity and homing ability of landlocked Arctic charr. - *Nordic J. Freshw. Res.* 66: 36-43.
- Sæther, O.A. 1979. Chironomid communities as water quality indicators. - *Holarctic Ecol.* 2: 65-74.
- Wiederholm, T. 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. - *Entomol. Scand., Suppl.* 19: 1-457.
- Wiederholm, T. 1986. Chironomidae of the Holarctic region. Keys and diagnoses. Part 2. Pupae. - *Entomol. Scand., Suppl.* 28: 1-482.
- Winberg, G.G. 1956. Rate of metabolism and food requirements of fish. - *Fish. Res. Board Can., Transl. Ser.* 194: 1-253.

Differences in Rheotactic Response and Attraction to Population-Specific Odours in Baltic Salmon (*Salmo salar* L.) Parr

CARL FOLKE¹, HÅKAN OLSÉN², SVANTE WINBERG², RICKARD BJERSELIUS² and LARS KARLSSON³

¹ Department of Systems Ecology, Stockholm University, S-106 91 Stockholm, Sweden.

² Department of Zoophysiology, University of Uppsala, Box 560, S-751 22 Uppsala, Sweden.

³ Salmon Research Institute, S-810 70 Älvkarleby, Sweden.

Abstract

Responses to chemical cues in two river populations of Baltic salmon (*Salmo salar* L.) parr were studied in a large Y-maze to determine whether population-specific odours are present in this reproductively isolated race of the Atlantic salmon. The experiment was performed in the home river water of one of the populations. Parr tested in an unknown river water had a significantly stronger motivation for upstream movement. Immature parr of this population were attracted to population-specific odours, providing evidence that such odours exist in the Baltic salmon. However, motivation or capacity for odour discrimination differ as precocious males of the responding population and parr tested in their home river water showed no significant preference for either odour. It is proposed that the lower motivation for upstream movement of the home river parr in comparison with young salmon from the other river is an effect of familiarity with their natural odourous background.

Key words: Population-specific odours, chemoattraction, olfaction, salmonid behavior.

Introduction

Local populations are important ecological units both in anadromous and landlocked salmonids, since mature fish during spawning migration returns with high precision to their natal river, which is often a small tributary (Ricker 1982, Bams 1976, Stabell 1984). The mature fish recognizes and is guided back to the home river by the special smell of the river (e.g. Wisby and Hasler 1954, Toft 1975, Bertmar 1979). Some authors have suggested that the home river odour is composed of population-specific substances emitted by conspecific salmonids (Nordeng 1971, 1977, Solomon 1973). In fact, several studies have provided evidence that salmonids emit chemical substances which carry information about kinship and genetic identity, and that these substances attract both juvenile fish (Stabell 1982, 1987, Olsén 1985, 1986a, 1989, Quinn and Busack 1985, Quinn and Tolson 1986, Quinn and Hara 1986, Courtenay

1989) and homing adults (Selset and Döving 1980, Groot et al. 1986, Quinn and Tolson 1986).

The aim of this study is to investigate the possible occurrence of intraspecific odour attraction in Baltic salmon (*Salmo salar* L.) parr. The juvenile salmon were tested in a much larger maze than in previous experiments concerned with conspecific odour attraction. The conditions more resembled a field or in situ situation when taking water flow, water temperature changes and space in the test chamber into consideration.

Materials and methods

Experimental fish

One-year-old Baltic salmon parr from two Swedish rivers, viz. the River Indalsälven and the River Dalälven, were used in this study. The parr belonged to two river populations, which have been

reared in hatcheries for almost half a century. We used hatchery reared fish since most salmon rivers of the Baltic drainage basin have been exploited for hydro-electric power stations, destroying rearing and spawning areas for Baltic salmon. Natural stocks have been replaced by hatchery reared smolts (e.g. Johansson 1981).

The experiment was performed at the Salmon Research Institute hatchery at the River Dalälven from October 18 to October 27, 1988. Two weeks prior to the experiment, 300 immature and 300 ripe precocious male parr (flowing milt) were brought from the River Indalsälven hatchery (Bergeforsen) to the River Dalälven hatchery. These parr and 300 immature parr from the River Dalälven population, raised at the River Dalälven hatchery, were kept separately in concrete tanks with separate supply of water from the River Dalälven. Fish were fed with granulated food (EWOS) every morning. The mean weights were 48 g (range 34-80 g, $n=210$) for immature parr from the River Indalsälven, 42 g (range 20-108 g, $n=290$) for precocious males from the River Indalsälven, and 90 g (range 36-148 g, $n=255$) for immature parr from the River Dalälven.

Natural spawning is negligible in these two rivers. Salmon populations are maintained through artificial breeding and hatchery-reared offsprings are released as smolts. In each of these two salmon rivers migration is hindered by a hydro-electric power dam. Salmon hatcheries of the two rivers are located below these dams. The water supplied to the River Dalälven hatchery, where the present experiment was performed, comes from the river above the dam.

Apparatus and Experimental Procedures

The experiment was performed in two identical Y-mazes similar to that used by Stabell (1987) although much bigger in size (Fig. 1). The great amount of water available at the hatchery made it possible to use a large maze with a high water flow through the migration pipes, similar to that of previous experiments done with adult salmonids (e.g. Sutterlin and Gray 1973, Brannon et al. 1984, Groot et al. 1986). Also much larger, and with a

greater water depth in the main test tank, than in any other corresponding experiments with juvenile salmonids. The large size of the apparatus should decrease the amount of stress fish may be exposed to during a test.

The Y-mazes were placed outside the River Dalälven hatchery. River water flowing through the migration pipes was introduced from a plastic head tank (63 x 35 x 60 cm) placed on a frame of stainless steel on top of a plastic trap tank (105 x 65 x 74 cm). From the head tank equal amounts of river water (76-77 L min⁻¹) were distributed between two separate compartments of the trap tank. Traps, with a wooden frame covered with plastic net, were placed in the trap tank (Fig. 1B). The pipes and the main tank were covered with opaque black plastic during the tests.

One hundred juvenile parr were used as odour donors and were held in covered glass fibre tanks (160 L) during each trial. Less than 50% of the water from the two odour-donor tanks entered the compartments of the trap tank and was added to the river water at an approximate ratio of 1:50 in volume. Donor fish were exchanged every second morning, and were left undisturbed in the donor tank for more than six hours prior to the initial trial.

Thirty minutes before a trial 30 parr were released into the main tank (250 x 120 x 60 cm plywood tank, 30 cm water level). After a 30 min. adaptation period, fish were allowed to enter the two migration pipes (100 cm long transparent plexiglass tubes of 20 cm in diameter). After each trial, the test fish were put into a concrete tank, and thirty new fish were brought to the Y-maze. Each test fish was used only once. For practical reasons three trials were performed daily in each of the two Y-mazes; from 17:15-18:00 h to 19:15-20:00 h, from 20:30-21:15 h to 22:30-23:15 h, and from 00:00-00:45 h to 08:45-09:30 h. After each trial the supply of unscented water and water scented by conspecifics were switched from one side of the trap tank to the other. The apparatus was drained between each trial. After a series of three trials each Y-maze was brushed with 95% ethanol and rinsed with water.

The preference of immature fish from both populations, and that of precocious males from the

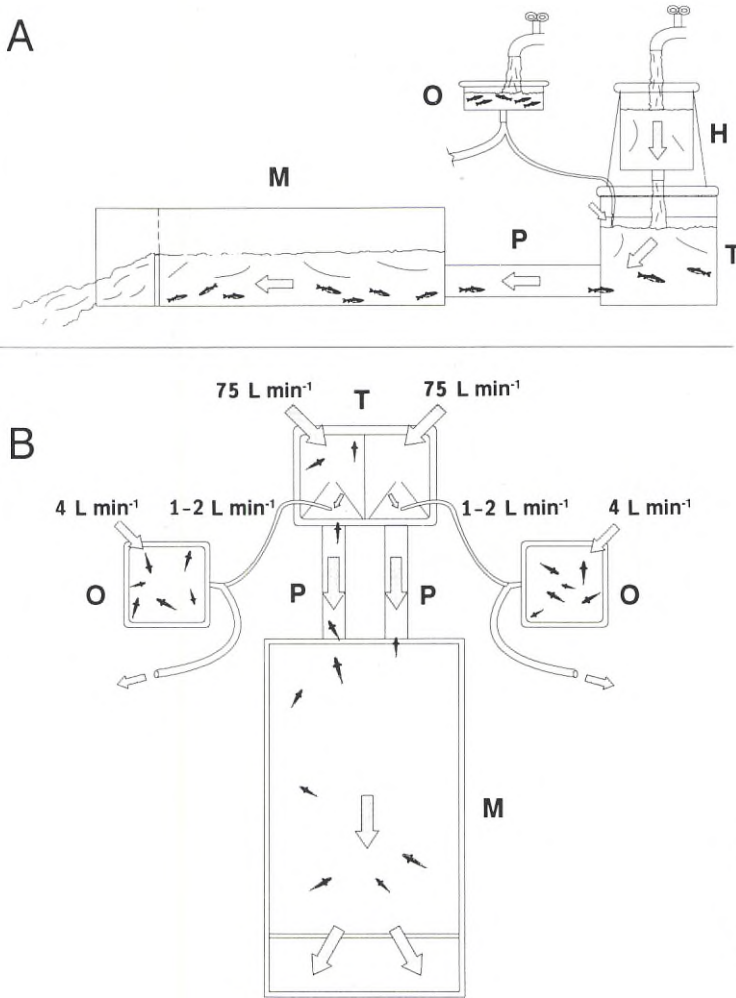


Fig. 1. The Y-maze used to measure behavioral response to population-specific odours. A: side view, B: from above. Arrows indicate direction of water flows. M = main tank, T = trap tank, O = odor-donor tanks, P = migration pipes, H = head tank (not drawn in B).

River Indalsälven, were assessed in the presence of 1) unscented water from the River Dalälven against water scented by immature fish from their own population, and 2) river water scented with immature fish from each population. Six to eight trials were conducted for each combination and for each test group of fish. The number of fish in the migration pipes and in each compartment of the trap tank were counted immediately after each trial.

The overall distribution of fish in relation to different odour combinations was determined and compared to a random distribution. For this purpose, a paired t-test was used with each trials of 30

individuals treated as an independent observation (see Table 1). Differences in the rate of upstream movement were analyzed using the Wilcoxon's two-sample test.

Results

Responses to population-specific odours

The immature parr from the River Indalsälven preferred unconditioned River Dalälven water to River Dalälven water scented with parr from its own population (Table 1). However, when given a choice between River Dalälven water scented with

Table 1. Responses of Baltic salmon parr in paired-choice tests, when exposed to odours of their own population against unscented river water, and to odours of their own population against odours of another population. Parr from the River Dalälven were tested in their home river water. Indal=River Indalsälven, Dal=River Dalälven.

a) Test fish: immature parr from the River Indalsälven, * $p < 0.05$, paired t-test

Date October	Odour donor parr A	Odour donor parr B	No. of choices for		Fish remaining in tank		Experimental period
			A	B	no.	(%)	
18	Indal	none	3	11	16	(53)	II
19	Indal	none	5	7	18	(60)	III
19	Indal	none	6	12	12	(40)	III
19	Indal	none	3	18	9	(30)	I
23	Indal	none	0	2	28	(93)	I
23	Indal	none	5	13	12	(40)	II
Total			22	63*	95	(53)	
21	Dal	Indal	1	3	26	(87)	I
21	Dal	Indal	6	11	13	(43)	II
22	Dal	Indal	2	13	15	(50)	III
22	Dal	Indal	2	7	21	(70)	I
22	Dal	Indal	11	11	8	(27)	II
23	Dal	Indal	2	17	11	(37)	III
Total			24	62*	94	(52)	

b) Test fish: immature parr from the River Dalälven

23	Dal	none	3	1	26	(87)	I
23	Dal	none	2	3	25	(83)	II
24	Dal	none	4	2	24	(80)	III
24	Dal	none	2	3	25	(83)	I
24	Dal	none	2	3	25	(83)	II
25	Dal	none	6	12	12	(40)	III
Total			19	24	137	(76)	
21	Dal	Indal	0	4	26	(87)	I
21	Dal	Indal	5	4	21	(70)	II
22	Dal	Indal	6	10	14	(47)	III
22	Dal	Indal	0	0	30	(100)	I
22	Dal	Indal	4	0	26	(87)	II
23	Dal	Indal	0	2	28	(93)	III
Total			15	20	145	(80)	

c) Test fish: precocious males from the River Indalsälven, ** trials run in a water temperature < 4 °C

19	Indal	none	5	8	17	(57)	II
19	Indal	none	12	5	13	(43)	III
20	Indal	none	4	7	19	(63)	I
20	Indal	none	6	6	18	(60)	II
24	Indal	none	7	6	17	(57)	III
26**	Indal	none	0	0	30	(100)	I
26**	Indal	none	1	0	29	(97)	II
27**	Indal	none	3	7	20	(67)	III
Total			38	39	163	(68)	
24	Indal	Dal	12	5	13	(43)	I
24	Indal	Dal	7	10	13	(43)	II
25	Indal	Dal	12	3	15	(50)	III
26**	Indal	Dal	1	0	29	(97)	I
26**	Indal	Dal	3	2	25	(83)	II
27**	Indal	Dal	4	4	22	(73)	III
Total			39	24	117	(65)	

River Indalsälven parr, and River Dalälven water scented with River Dalälven parr, the River Indalsälven parr preferred their own population odour.

Neither did the River Dalälven parr nor precocious males from the River Indalsälven prefer the unconditioned River Dalälven water to the River Dalälven water scented with odours from their own population. Nor did these fish show any preference when given a choice between odours from their own and odours from the other river population.

Rheotactic response

The river water temperature decreased from 7.6 °C to 3.6 °C during the trial period. 32 trials out of 38 were performed at temperatures higher than 4 °C. There were no significant differences in upstream

movement within river populations in these 32 trials. Only precocious males from the River Indalsälven were tested at a temperature below 4 °C, and their locomotor activity was significantly less than that of precocious males from the River Indalsälven tested at higher temperatures (Fig. 2). We excluded these lower temperature tests from further analysis.

Immature and precocious male parr from the River Indalsälven showed a significantly greater preference for upstream movement than immature River Dalälven parr. The number of immature Indalsälven parr moving upstream was 2.2 times higher than among the River Dalälven parr. We did not find any significant difference in activity level between precocious males and immature parr from the River Indalsälven (Fig. 2). Nor did we find any difference in activity between larger and smaller fish within populations.

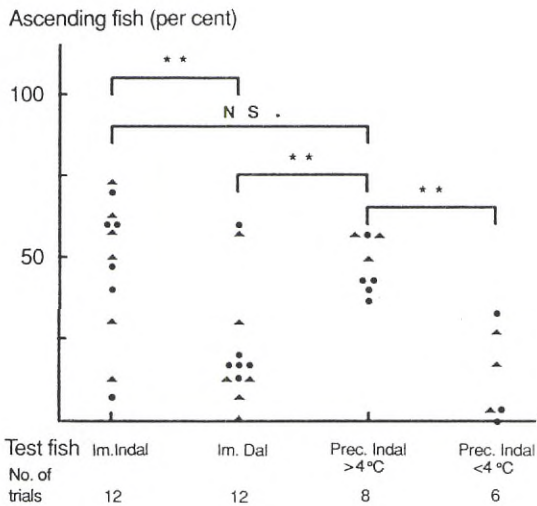


Fig. 2. Percentage of 30 fish moving upstream in the Y-maze. Trials were performed in the home water of the River Dalälven population. Parr were exposed to the following odour combinations; ● = water scented with fish from their own population against unconditioned river water, ▲ = water scented with fish from their own population against water scented with the unfamiliar population. Each ● and ▲ represents one trial and the performance of 30 fish. ** $p < 0.01$ Wilcoxon's two-sample test.

Discussion

The present results indicate that population-specific odour attraction also exists in the Baltic salmon. The study also reveals population differences in odour preference and differences in tendency of upstream movement.

Rheotactic response

Salmonid parr displaced out of their home area will often return there (Saunders and Gee 1964). Olfaction is of significance for this orientation (Halvorsen and Stabell 1990). The River Indalsälven parr were, in the present study, transferred to a river different from their home river. Presumably, they were not familiar with the unknown River Dalälven water, while the River Dalälven parr were acquainted with the natural odourous of their home river water, which always contains odours from river Dalälven fry reared in ponds upstream the hydro-electric power dam. We suggest that the significant difference in positive rheotactic response between these two populations (Fig. 2) might be due to that the River Indalsälven parr were actively searching for their

home area. As a consequence the exploratory behavior of the River Indalsälven parr were much stronger than among the River Dalälven parr.

Population-specific odour attraction

In the present study immature River Indalsälven parr showed a similar response to that which has been described by Stabell (1982) for Atlantic salmon. Fish avoided water scented by their own population and preferred unconditioned water. However, when fish had to choose between water scented by immature parr from their own and water scented by fish from another population, they significantly preferred their own population. Nitrogenous excretory products may in part be responsible for the repellent effect (Olsén 1986b,c 1987). It is possible that the 100 parr used as donors in the present study were under stress, and consequently emitted repellents, which were present in only one of the two water currents. But when both salmon populations were used as donors repellent odours were present in both water currents, but differed in the population-specific odours. Our results also indicate differences in preference behavior between mature and immature parr of the same population as precocious males of the River Indalsälven population in contrast to immature fish from the same population were indifferent to the odour combinations. No difference in activity levels were, however, shown. We are not at present able to explain this discrepancy in preference behavior between precocious males and immature fish.

Both behavioral and electrophysiological experiments have confirmed that salmonids are able to discriminate between water scented with their own population and water scented with a unfamiliar population. However, in all behavioral studies, with the exception of a comprehensive study with coho salmon (*Oncorhynchus kisutch*) (Courtenay, 1989), only one of the two population studied have been able to discriminate between their own and an unknown population odour (Groot et al. 1986, Olsén 1986a, Quinn and Tolson 1986). Also in our study only one of the two river populations showed preference for their own population. The other

population was indifferent. Based on studies of preference behavior and gene frequency analysis of serum esterases, Olsén (1986a) suggested that the lack of discriminatory ability in one of two sympatric populations of Arctic charr was due to a lesser genetic homogeneity, and that the quality of the emitted attractants therefore could be inherited giving rise to population-specific odours.

Olsén (1989) suggested that a hierarchy of odours act in chemical communication in salmonids. Fish may emit a bouquet composed of several substances which are to a greater or lesser degree shared by different specimens, and the extent to which such chemical cues are shared could be related to the genetic similarity between individuals (e.g. species-populations-siblings) (Olsén 1989). Recent results suggest that at least in Arctic charr (Winberg and Olsén, in press), and in coho salmon (Courtenay 1989) the specific odours of relatives are learned at an early development stage. These substances may in juvenile charr be of significance during schooling in the same way as has been suggested for schooling in cyprinides (Wrede 1932, Keenleyside 1955, Hemmings 1966). The relative importance of conspecific odours for imprinting of home stream odours (Hasler and Wisby 1951, Hasler and Scholz 1983, Morin et al. 1989) is still uncertain, although evidence for a hereditary component in the homing behavior of salmonids have been presented (e.g. Bams 1976, Black and Dempson 1986, McIsaac and Quinn 1988).

Acknowledgments

Many thanks to the staff at the Salmon Research Institute, and at the hatchery of the National Board of Fisheries, Älvkarleby, for your keen interest and assistance, to Jonas Sahlin and Lars Hedman at the Bergforsen hatchery for your cooperation and the experimental fish, and to Ole Stabell who kindly participated in various phases of this work.

The study was supported by grants from the Swedish Council for Forestry and Agricultural Research and the Helge Ax:son Johnson Stiftelse.

References

- Bams, 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*) - J. Fish. Res. Board Can. 33: 2716-2725.
- Bertmar, G. 1979. Home range, migrations and orientation mechanisms of the River Indalsälven trout, *Salmo trutta* - L. Rep. Inst. Freshw. Res., Drottningholm 58: 5-26.
- Black, G.A. and J.B. Dempson. 1986. A test of the hypothesis of pheromone attraction in salmonid migration. - Env. Biol. Fish. 15: 229-235.
- Brannon, E.L., R.P. Whitman and T.P. Quinn. 1984. Responses of returning adult Coho salmon to home water and population-specific odors. - Trans. Amer. Fish. Soc. 113: 374-377.
- Courtenay, S.C. 1989. Learning and memory of chemosensory stimuli by under-yearling coho salmon, *Oncorhynchus kisutch* (Walbaum). - PhD-thesis. Department of Zoology, The University of British Columbia, Vancouver, Canada.
- Groot, C., T.P. Quinn and T.J. Hara. 1986. Responses of migrating adult sockeye salmon (*Oncorhynchus nerka*) to population-specific odours. - Can. J. Zool. 64: 926-932.
- Halvorsen, M. and O.B. Stabell. 1990. Homing behaviour of displaced stream-dwelling brown trout. - Anim. Behav. 39: 1089-1097.
- Hasler, A.D. and W.J. Wisby. 1951. Discrimination of stream odours by fishes and relation to parent stream behaviour. - Am. Nat. 85: 223-238.
- Hasler, A.D. and A.T. Scholz. 1983. Olfactory imprinting and homing in salmon. - Zoophysiology 14. Springer Verlag, N.Y. 134 p.
- Hemmings, C.C. 1966. Olfaction and vision in fish schooling. - J. Exp. Biol. 45: 449-464.
- Johansson, N. 1981. General problems in Atlantic salmon rearing in Sweden. - Ecol. Bull., Stockholm 34: 75-83.
- Keenleyside, M.H.S. 1955. Some aspects in schooling behaviour of fish. - Behaviour 8: 183-248.
- McIsaac, D.O. and T.P. Quinn. 1988. Evidence for a hereditary component in homing behavior of chinook salmon (*Oncorhynchus tshawytscha*). - Can. J. Fish. Aquat. Sci. 45: 2201-2205.
- Morin, P.-P., J.J. Dodson and F.Y. Doré. 1989. Cardiac responses to a natural odourant as evidence of a sensitive period for olfactory imprinting in young Atlantic salmon, *Salmo salar*. - Can. J. Fish. Aquat. Sci. 46: 122-130.
- Nordeng, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? - Nature 233: 411-413.
- Nordeng, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. - Oikos 28: 155-159.
- Olsén, K.H. 1985. Chemoattraction between fry of Arctic char (*Salvelinus alpinus*) studied in a Y-maze fluvium. - J. Chem. Ecol. 11: 1009-1017.
- Olsén, K.H. 1986a. Chemoattraction between juveniles of two sympatric stocks of Arctic char (*Salvelinus alpinus*) and their gene frequency of serum esterases. - J. Fish Biol. 28: 221-231.
- Olsén, K.H. 1986b. Emission rate of amino acids and ammonia and their role in olfactory behaviour of juvenile Arctic char, *Salvelinus alpinus* (L.). - J. Fish. Biol. 28: 255-265.
- Olsén, K.H. 1986c. Modification of conspecific chemo-attraction in Arctic char (*Salvelinus alpinus* L.) by nitrogenous excretory products. - Comp. Biochem. Physiol. 85A: 77-81.
- Olsén, K.H. 1987. Chemoattraction of juvenile Arctic char (*Salvelinus alpinus* L.) to water scented by conspecific intestinal content and urine. - Comp. Biochem. Physiol. 87A: 641-643.
- Olsén, K.H. 1989. Sibling recognition in juvenile Arctic char, *Salvelinus alpinus* L. - J. Fish Biol. 34: 571-581.
- Quinn, T.P. and C.A. Busack. 1985. Chemosensory recognition of siblings in juvenile coho salmon (*Oncorhynchus kisutch*). - Anim. Behav. 33: 51-56.
- Quinn, T.P. and T.J. Hara. 1986. Sibling recognition and olfactory sensitivity in juvenile coho salmon (*Oncorhynchus kisutch*). - Can. J. Zool. 64: 921-925.
- Quinn, T.P. and G.M. Tolson. 1986. Evidence of chemically mediated population recognition in coho salmon (*Oncorhynchus kisutch*). - Can. J. Zool. 64: 84-87.
- Ricker, W.E. 1972. Hereditary and environmental factors effecting certain salmonid populations. p. 27.160. - In: The stock concept in Pacific salmon. R.C. Simon and P.A. Larkin. (eds.). H.R. McMillan Lectures in Fisheries. University of British Columbia, Vancouver, B.C., Canada. p. 27-160.
- Saunders, R.L. and J.H. Gee. 1964. Movements of young Atlantic salmon in a small stream. - J. Fish. Res. Board Can. 21: 27-36.
- Selset, R. and K.B. Döving. 1980. Behavior of mature anadromous char (*Salmo alpinus* L.) towards odorants produced by smolts of their own population. - Acta Physiol. Scan. 108: 113-122.
- Solomon, J.B. 1973. Evidence for pheromone-influenced homing by migrating Atlantic salmon, *Salmo salar*. - Nature 244: 231-232.
- Stabell, O.B. 1982. Detection of natural odorants by Atlantic salmon parr using positive rheotaxis olfactometry. p. 71-78. - In: E.L. Brannon and E.O. Solo (eds.). Proceedings of the Salmon and Trout Migratory Behaviour Symposium, June 1981. University of Washington. Seattle.
- Stabell, O.B. 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. - Biol. Rev. 59: 333-388.
- Stabell, O.B. 1987. Intraspecific pheromone discrimination and substrate marking by Atlantic salmon parr. - J. Chem. Ecol. 13: 1625-1643.
- Sutterlin, A.M. and R. Gray. 1973. Chemical basis for homing of Atlantic salmon (*Salmo salar*) to a hatchery. - J. Fish. Res. Board Can. 30: 985-989.
- Toft, R. 1975. Lukt- och synsättets roll för lekvandningsbeteendet hos Östersjö lax. - Salm. Res. Inst. Rep., Älvkarleby, Sweden. 10/1975. (In Swedish.)
- Winberg, S. and K.H. Olsén. The influence of rearing conditions on the sibling odor preference of juvenile Arctic char (*Salvelinus alpinus*). - Anim. Behav. (In press.)
- Wisby, W.J. and A.D. Hasler. 1954. Effect of olfactory occlusion on migrating silver salmon (*Oncorhynchus kisutch*). - J. Fish. Res. Board Can. 11: 472-478.
- Wrede, W.L. 1932. Versuche über den artduft der elritzen. - Z. Vergl. Physiol. 17: 510-519.

Differences in the Ecology of two Vendace Populations separated in 1895

ODD TERJE SANDLUND

Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway

Abstract

The vendace (*Coregonus albula*) in the Lake Osensjøen are descendants from 90,000 fry of the Lake Mjøsa stock introduced in 1895. Today, the two stocks have similar feeding habitats and diets, and juvenile growth rates are similar. However, the stocks differ in age at maturity, in asymptotic body length, spawning habitat and egg incubation time. The ages at maturity are 2+ and 3+ - 4+, and asymptotic lengths are 236 mm and 284 mm in Lake Mjøsa and Lake Osensjøen, respectively. Vendace in Lake Mjøsa spawn in an inlet river, whereas the Osensjøen stock spawns at approximately 10 m depth on the bottom of the lake. Peak spawning occurs around October 20 in both lakes, but as water temperature during incubation is higher in the lake, the populations differ significantly in incubation time as measured by degree-days (165 degree-days in the Mjøsa stock vs. 575-665 degree-days in the Osensjøen stock).

Introduction

The plasticity in morphology, life history, and ecology of fish species is clearly demonstrated when they are introduced into new and different environments (Alm 1959, Lindsey 1981, Reznick and Bryga 1987). Within one or a few generations the new environment may result in changes in a number of population characteristics compared to the donor population. The changes may be due to phenotypic plasticity or genetic changes. Among important environmental factors are food quality and abundance (Alm 1959), and presence or absence of competing fish species (Lindsey 1981).

Long term changes may involve changes in genotype (Vuorinen et al. 1991). These changes may be due to genetic drift and founder effect if the number of introduced individuals surviving to reproduce is low. The introduced stock may also be subject to selection pressures differing significantly from the donor stock.

The ability to become adapted to a new environment appears to vary among species. Generalists are believed to be particularly adaptive, whereas specialists are less able to change (Nikolskii 1969). Among coregonids, the whitefishes (*Coregonus*

lavaretus s.l.), with their terminal or subterminal mouths and variable gillraker numbers, are considered generalists. The ciscoes, on the other hand, with their superterminal mouths and high gillraker numbers, are considered specialized pelagic zooplanktivores (Scott and Crossman 1964). The north European cisco, vendace (*Coregonus albula* L.), is even considered the most specialized zooplanktivore in the Scandinavian freshwater fish fauna (Svårdson 1976).

The whitefishes have been subject to innumerable introductions all over their area of distribution, and many of the cases have been well documented (reviews in Svårdson 1979 and Lindsey 1981). Relative to whitefish, vendace have rarely been transplanted into new lakes (Svårdson 1966, Viljanen 1986), and morphological and ecological changes following introduction have not been documented (Lindsey 1981). Vendace is considered to vary little in ecological and morphological characters among natural populations (Svårdson 1966). Consequently, introduced populations are expected to be similar to their donor populations.

The two Norwegian lakes Mjøsa and Osensjøen, offer a rare opportunity to study changes in transplanted vendace. In 1895 90,000 vendace

fry from the Lake Mjøsa population were transferred to Lake Osensjøen (Nysæther 1977), which is situated outside the natural distribution area of vendace (Huitfeldt-Kaas 1923). The introduction has not been repeated. Thus, the present vendace in Lake Osensjøen are descendants from the introduction in 1895.

Here, I investigated the possible differences in morphology, life history, habitat and diet of the vendace populations in Lakes Mjøsa and Osensjøen. The genetic divergence has been investigated by Vuorinen et al. (1991). My null hypothesis is that there are no major differences between the introduced and donor population of vendace in terms of morphology, life history characters, and habitat use.

Material and methods

Study area

Lakes Mjøsa and Osensjøen are situated in the southeastern part of Norway (Fig. 1). Due to the difference in altitudes, the air temperature is lower in the area of Lake Osensjøen than Lake Mjøsa (Table 1). Annual pelagic primary productivity is higher in Lake Mjøsa than in Lake Osensjøen. The epilimnic zone is smaller in Lake Osensjøen, and due to the high humic content, Secchi disc transparency is also lower than in Lake Mjøsa. The

water level fluctuations due to regulations differ between the lakes, but in both cases littoral benthic production is reduced (Lien et al. 1981, Kjellberg 1986).

The dominating zooplankton species in Lake Mjøsa are *Daphnia galeata*, *D. cristata*, *Bosmina longispina*, *Limnocalanus macrurus*, *Eudiaptomus gracilis* and *Cyclops lacustris* (Kjellberg 1986). In Lake Osensjøen, the zooplankton is dominated by *Arctodiaptomus laticeps*, *C. scutifer*, *B. longispina* and *D. cristata* (Løvik and Kjellberg 1982). Reflecting the higher productivity, zooplankton biomass in Lake Mjøsa is higher compared to that in Lake Osensjøen (Table 1).

Twenty species of fish occur in Lake Mjøsa (Sandlund et al. 1985b). Of these whitefish, *C. lavaretus*, and smelt, *Osmerus eperlanus*, are co-occurring with vendace in the pelagic zone. Brown trout, *Salmo trutta*, is a pelagic predator. In Lake Osensjøen, there are 9 fish species. Only whitefish and brown trout occur in the pelagic zone with vendace (Sandlund 1979). The pelagic brown trout of Lake Osensjøen is small-sized and fish is rarely found in their diet (Sandlund and Næsje 1983). Although the lakes belong to the same river system, no migration between them by lacustrine fishes like vendace have been possible due to water falls.

In Lake Mjøsa the vendace population is subject to commercial exploitation. In the 1960's, the yield was approximately 3.6 kg ha⁻¹ yr⁻¹ (Aass 1978). In Lake Osensjøen, fishing for vendace is negligible, and the yield is less than 0.1 kg ha⁻¹ yr⁻¹.

Sampling

In Lake Mjøsa sampling was performed with pelagic and benthic gillnets of mesh size 8-52 mm during 1978-80 (Sandlund et al. 1985b). In 1987, vendace was caught with a beach seine (mesh size 20 mm). In Lake Osensjøen, sampling was performed with pelagic and benthic gillnets of mesh size 10-52 mm during 1976-78 and 8-52 mm in 1985, and with benthic gillnets (mesh size 26 - 32 mm) on the spawning sites of vendace in 1977- 79, 1981-85, and 1987. Altogether 1,248 and 2,623 vendace were analyzed from Lake Mjøsa and Lake Osensjøen, respectively.

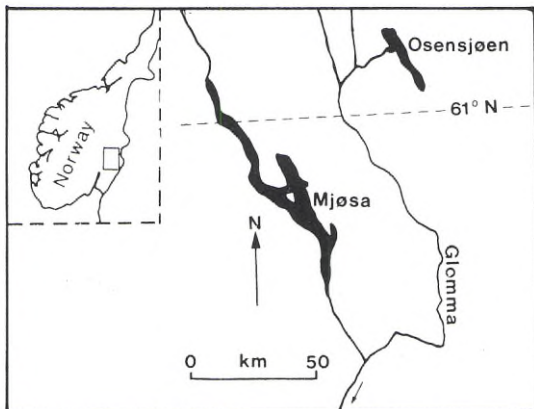


Fig. 1. Locations of Lakes Mjøsa and Osensjøen, Norway.

Table 1. Physical and chemical characteristics of Lakes Mjøsa and Osensjøen (data from Lindem 1978, Lien et al. 1981, Rognerud and Kjellberg 1984, Kjellberg 1986, Linløkken and Qvenild 1986, and The Norwegian Meteorological Institute).

	L. Mjøsa	L. Osensjøen
Altitude (m a.s.l.)	121	437
Air temperature (°C, 30 yr mean for July)	15.9	11.7
Surface area (km ²)	365	53
Maximum depth (m)	449	117
Mean depth (m)	153	37
Theoretical retention time (yrs)	5.6	2.7
Regulation amplitude (m)	3.2	6.6
Secchi disc transparency (m)	2.5-8.0	3.4-6.4
Thermocline level	12-20	8-15
pH	6.7-7.4	6.4-6.7
Conductivity (µS cm ⁻¹)	20-40	18-19
Primary production (g C yr ⁻¹)	20	8
Zooplankton biomass (g wet weight m ⁻²)	30	9.8
Pelagic fish biomass (kg ha ⁻¹)	26	4

Treatment of material

The fish was weighed (1 g), and body length was measured (1 mm) as natural tip length (Ricker 1979). Sex and degree of sexual maturation were recorded (Dahl 1917). Age was determined by burning and cutting otoliths (Christensen 1964). The gillrakers were counted on the anterior left gill arch dissected out of adult fish. Diet was investigated by identifying and counting the stomach contents under a stereo microscope, and per cent wet weight composition was calculated based on weights of undigested prey items.

On 50 fish from each lake the number of scales along the lateral line was counted, and the following meristic characters were measured with a caliper (0.1 mm): Head length, eye diameter, snout length, upper jaw length, and lower jaw length (Fig. 2).

Mensural characters adjusted for fish length were analysed with discriminant function analysis (SPSS software). To obtain length-adjusted characters, linear regressions of \log_e -transformed measurements on \log_e fish length was performed, and length-adjusted parameters calculated (Humphries et al. 1981, Hénault and Fortin 1989).

Van Bertalanffy growth parameters were calculated as described by Dickie (1978). Length/weight relationship was calculated by linear regression of \log_e -transformed data (Bagenal and Tesch 1978).

Individual fecundity was based on female gonads in maturity stage 5. Gonadosomatic index (GSI) was calculated according to Mills and Eloranta (1985):

$$\text{GSI} = W_g(W_t - W_g)^{-1}$$

where W_g is the weight of gonads, and W_t is total body weight.

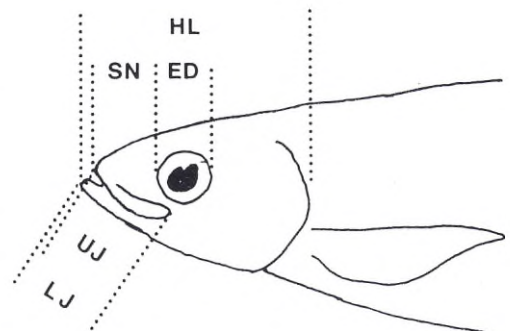


Fig. 2. Mensural characters measured on vendace: HL = head length, SN = snout length, ED = eye diameter, UJ = upper jaw, LJ = lower jaw.

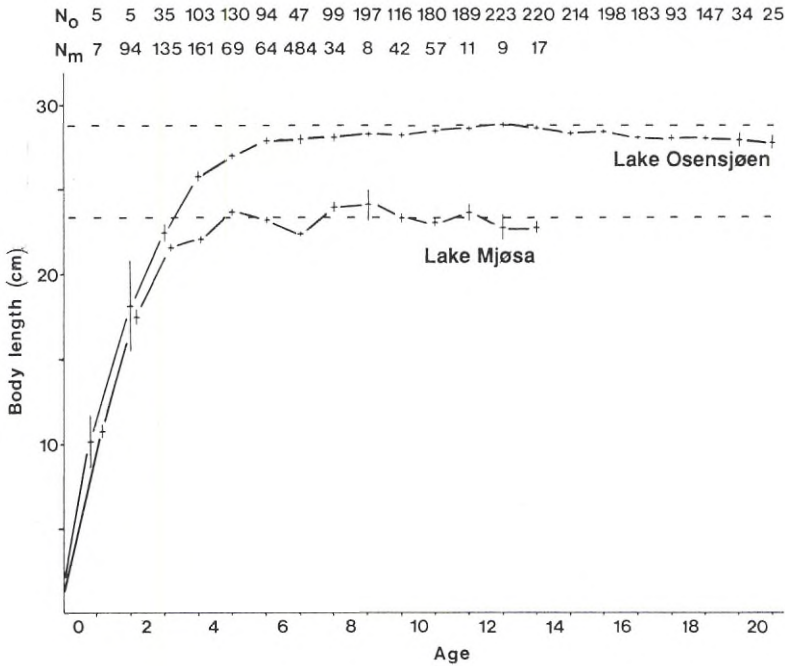


Fig. 3. Empirical growth of vendace in Lakes Mjøsa and Osensjøen. N_o =number of fish in Lake Osensjøen, N_m =number of fish in Lake Mjøsa. Vertical lines indicate 95% confidence limits. Broken horizontal lines indicate asymptotic lengths.

Results

Growth pattern and sexual maturation

The growth rates of juvenile vendace in Lakes Mjøsa and Osensjøen were similar (Fig. 3), and there was no significant difference in body lengths

Table 2. Population characteristics of vendace in Lakes Mjøsa and Osensjøen. GSI = gonadosomatic index (Mills and Eloranta 1985). Fecundity sample size: Mjøsa, $N = 8$; Osensjøen, $N = 21$.

	L. Mjøsa	L. Osensjøen
Von Bertalanffy parameters:		
L_{∞} (mm)	236	284
K (Brody's growth coef.)	0.82	0.60
t_0	0.45	1.24
Spawning locality	inlet river	lake
Spawning time	15-30 Oct.	15-30 Oct.
Incubation time (degree-days)	165	575-665
Mean ind. fecundity (no of eggs) $\pm 95\%$ c.l.	7,350 ± 845	11,890 $\pm 1,317$
GSI $\pm 95\%$ c.l.	0.25 ± 0.02	0.29 ± 0.02
Mean body weight (W)	124.9 ± 6.7	225.4 ± 7.5
No of eggs per g body weight	60.3	52.8

after the first and second growth season (t-tests, $p > 0.05$). However, growth stagnation appeared one year later in Lake Osensjøen (at age 4-5) than in the Mjøsa stock (at age 3-4), resulting in asymptotic lengths: $L_{\infty} = 284$ mm, and $L_{\infty} = 236$ mm, respectively (Fig. 3, Table 2). Brody's growth coefficient (K) is somewhat higher in Lake Mjøsa (0.82) than in Lake Osensjøen (0.60).

In both sexes, the age at sexual maturity differed significantly between lakes ($Z^* = 37.65$, $df = 2$, $p < 0.005$; and $Z^* = 23.54$, $df = 4$, $p < 0.005$; for males and females, respectively; Siegel 1956). In Lake Mjøsa, nearly all males and 75% of the females were mature at age 2+ (Fig. 4). In Lake Osensjøen, 35-40% of the fish were mature at age 2+, but 100% maturity was only reached in age 4+ and 5+ for males and females, respectively.

Individual fecundity was significantly higher in the larger Lake Osensjøen vendace ($t = 6.5$, $df = 49$, $p < 0.001$; Table 2). For the two populations combined, \log_e individual fecundity was significantly correlated to \log_e fish length ($R^2 = 0.44$, $p < 0.0005$). Within populations, however, the corresponding correlations were not significant ($p > 0.05$). The

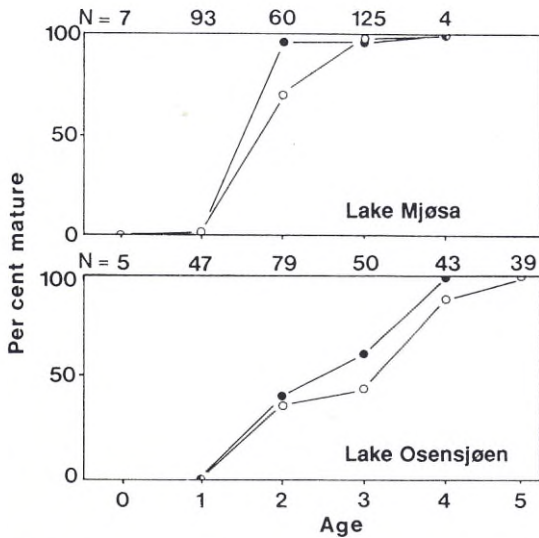


Fig. 4. Per cent sexually mature vendace females (o) and males (●) in Lakes Mjøsa and Osensjøen, based on fish caught in July-October. N indicates number of fish.

gonadosomatic index was significantly higher in Osensjøen vendace ($t=2.87$, $df=49$, $p<0.006$), but the mean number of eggs per gram somatic weight was not significantly different between the two populations ($t=0.35$, $p>0.05$).

Both populations were iteroparous (Sandlund et al. 1991). In Lake Mjøsa more than 10 age groups, and in Lake Osensjøen more than 15 age groups were present in the adult stock (Fig. 3).

Morphology

Differences in body length in adult fish were reflected in the mensural head characters of the two populations (Table 3). All mensural characters were significantly larger in the Lake Osensjøen vendace (t -tests, $p<0.05$). Discriminant function analysis showed that the mensural characters adjusted for fish length did not differ significantly between the two populations (Wilks' lambda=0.97, $p=0.72$). The number of scales along the lateral line did not differ significantly between the two populations ($t=0.105$, $p>0.5$), whereas gillraker numbers were significantly lower in the introduced population in Lake Osensjøen as compared to that in Lake Mjøsa ($t=2.194$, $p<0.05$). The relative variance (as measured by the coefficient of variation) was larger in the Lake Osensjøen vendace in all characters except upper jaw length (Table 3). There was also a difference in body colouration, as the Lake Osensjøen population frequently exhibited red pectoral and pelvic fins. This was never observed in Lake Mjøsa.

The weight/length equations of the two populations show that the Lake Osensjøen vendace has a somewhat lower weight/length ratio than the Lake Mjøsa vendace (Table 4), but the regression slopes were not significantly different ($F_{1,299}=0.199$, $p>0.05$).

Table 3. Mean length (mm), length of various head characters (mm), number of scales along the lateral line, and gillraker number of 50 sexually mature vendace from Lakes Mjøsa and Osensjøen. SD = standard deviation, C.V. = coefficient of variation (SD/mean).

	L. Mjøsa			L. Osensjøen		
	Mean	SD	C.V.	Mean	SD	C.V.
Body length	239.9	7.6	0.032	280.8	11.7	0.041
Head length	44.9	2.2	0.043	52.9	3.1	0.059
Eye diameter	9.8	0.6	0.064	11.3	1.1	0.095
Snout length	10.8	0.7	0.067	13.2	1.1	0.081
Upper jaw	15.1	1.0	0.064	18.2	1.1	0.061
Lower jaw	16.0	1.0	0.065	18.7	1.8	0.098
No of scales	77.1	2.2	0.028	77.0	3.4	0.044
Gillrakers	44.6	1.5	0.034	43.9	1.8	0.041

Table 4. Linear regression of the natural logarithms of weight (W, g) vs. length (L, mm) for vendace from Lakes Mjøsa and Osensjøen. R=correlation coefficient, N=number of fish, Min.-max.=minimum and maximum length (in mm) of fish included.

Locality	Equation	R	N	Min.-max.
L. Mjøsa	$\log_e W = -14.22 + 3.46 \log_e L$	0.97	179	106-258
L. Osensjøen	$\log_e W = -10.56 + 2.80 \log_e L$	0.98	124	65-310

Habitat and diet

Spawning occurred during late October in both lakes. However, the spawning habitat differed between the populations. The Lake Mjøsa population spawn in the main inlet river, whereas the Lake Osensjøen population spawn on the lake bottom at 10-20 m depth. In Lake Mjøsa, the incubation period from peak spawning until hatching corresponds to approximately 165 degree-days (Næsje et al. 1986a). The river temperature at spawning varies between 5-9 °C, but decreases swiftly below 1 °C. In spring, temperature starts to increase in late April, and is usually between 2-8 °C at hatching in May. In Lake Osensjøen, the actual date of hatching is not known, but it presumably occurs some time before or around ice-break. As the coregonid larvae are visual feeders, and probably need exogeneous food within a month after hatching (Braun 1978), it appears reasonable that hatching must occur close to ice-break. While the lake is ice-covered, light conditions will make searching for food difficult. The period from peak spawning until ice-break around May 15 in this lake corresponds to approximately 665 degree-days. Water temperature at the spawning site in the lake stays at about 3-4 °C throughout incubation time (Lien et al. 1981). Assuming a water temperature of 3 °C in April, hatching approximately one month before ice-break would correspond to 575 degree-days from peak spawning.

In Lake Mjøsa, newly hatched larvae drift from the spawning area in the river into the lake and stays in the littoral zone from spring until late summer (Næsje et al. 1986b). In Lake Osensjøen a few age-0 fish were caught in benthic nets and none in pelagic nets, which may indicate a littoral habitat choice also in this lake. Catches of age-0

vendace in Lake Osensjøen were, however, small. The smallest mesh sizes used, 8 and 10 mm bar mesh, appear to be efficient in catching juvenile coregonids from 70 and 90 mm in length in localities where they are abundant (Sandlund and Næsje 1986, 1989). Thus, by autumn, age-0 vendace in both lakes have reached lengths susceptible to the gillnets used (Fig. 3).

In both lakes subadult and adult vendace utilize the upper 20 m of the pelagic zone. Gillnet catches were low in the benthic zone throughout the year, and in the pelagic zone during winter, spring and early summer. Pelagic catches increased from late July and stayed high until early October, when spawning migrations started.

The diet of vendace was completely dominated by crustacean zooplankton in both lakes. Prey species constituting more than 10% by number at any sampling date were in Lake Mjøsa, numbers in parentheses indicate mean size (mm) in stomachs: *Daphnia galeata* (1.25), *Bosmina longispina* (0.50), *Eudiaptomus gracilis* (1.15), *Cyclops lacustris* (1.12), and *Limnocalanus macrurus* (1.78). Corresponding prey species in Lake Osensjøen were: *D. cristata* (1.11), *D. galeatalongispina* (2.13), *B. longispina* (0.65), *Arctodiaptomus laticeps* (1.48), *C. scutifer* (1.03), and *Heterocope appendiculata* (2.08) (Sandlund et al. 1987, 1991).

In Lake Mjøsa, smelt and whitefish coexist with vendace in the pelagic zone. Pelagic whitefish generally utilize the same depth zones as vendace, whereas smelt live from the surface to at least 80 m depth (Sandlund et al. 1985b). Biomass estimates indicate that vendace, smelt and whitefish constitute c. 36%, 11%, and 53%, respectively, of total pelagic fish biomass (Kjellberg and Sandlund 1983). Crustacean zooplankton consti-

tute approximately 50% of the smelt diet, and 70% of the whitefish diet.

In Lake Osensjøen, pelagic whitefish show a nearly complete habitat overlap with vendace, constituting less than 50% of pelagic gillnet catches. Zooplankton constitute nearly 100% of the diet of pelagic whitefish in this lake. The two fish species segregate in diet: whereas copepods dominate in vendace diet, cladocerans dominate in whitefish diet (Sandlund 1979).

Discussion

The null hypotheses, that there are no major differences between the introduced and donor population of vendace, must be rejected. The introduced vendace population differed from the donor population in spawning environment and incubation time from spawning till hatching, and age and size at sexual maturity.

As a consequence of spawning in the lake where winter temperatures are higher than in the river, the population in Lake Osensjøen experiences a higher energy supply (as measured by degree-days) during egg incubation than the river spawning population in Lake Mjøsa. At the spawning site in Lake Osensjøen, where peak spawning occurs around October 20, at a water temperature of approximately 7 °C, 200 degree-days are reached already in late November. In laboratory experiments with vendace eggs, Luczynski and Kirklewska (1984) found a variation between approximately 200 and 510 degree-days from fertilization till hatching at various constant temperatures (1.1–9.9 °C). This difference between batches from the same population is similar to the difference between the Mjøsa and Osensjøen stocks. Investigations on the hatching of the river spawning vendace and whitefish in Lake Mjøsa indicate that hatching may be triggered by mechanical disturbances of the eggs caused by the start of the river spring spate, and the larvae drift into the lake soon after ice-break (Næsje et al. 1986a,b). The mechanical disturbances caused hatching at about 50% of the incubation time needed if hatching was caused by water temperature (Næsje and Jonsson

1988). In the lake spawning population, the mechanical disturbance of the eggs, if present at all at depths of more than 10 m, will be due to the weak currents created by the spring circulation after ice-break. In the lake, hatching is more probably caused by one or both of the factors: water temperature increase at spring circulation (Lindroth 1957, Luczynski 1985), or internal physiological conditions of the embryo (Colby and Brooke 1973, Luczynski and Kirklewska 1984). It may also be speculated that the change in light conditions at ice-break may cause increased embryo activity leading to hatching (Smith 1957). The difference in incubation time between the closely related populations indicate that, once a sufficient amount of energy to complete embryonal development is provided, incubation time may vary greatly according to local conditions. The occurrence of sympatric autumn and winter/spring spawning populations of vendace (Svårdson 1979, Vuorinen 1987) may also be related to this apparent flexibility in incubation time of this species.

Asymptotic length and sexual maturity was attained one year later and at a larger size in the Lake Osensjøen than in the Lake Mjøsa vendace. Juvenile growth rates were very similar, but the higher *K* (Brody's growth coefficient) in Lake Mjøsa indicates a more abrupt growth stagnation in this stock. Age and size at maturity is strongly related to individual fitness, and determined mainly by juvenile mortality and individual growth rate (Jonsson et al. 1984, Stearns and Koella 1986, Reznick and Bryga 1987). In the present vendace stocks, juvenile mortality due to predation probably decreases quickly when the fish reach a size of 10–15 cm, i. e. after the first growth season. The main predators in these localities appear to take smaller prey (Sandlund et al. 1985a, Taugbøl et al. 1989). However, no information is available on possible differences in juvenile mortality between localities.

Growth rate and asymptotic length is dependent on the abundance and type of food. The sizes of zooplankton eaten in the two lakes are similar. Thus, differences in prey sizes does not appear to be the reason for different asymptotic lengths. However, the density of zooplanktivorous fish in

Lake Mjøsa is 6.5 times higher than that in Lake Osensjøen, whereas the corresponding zooplankton biomass in Lake Mjøsa is only 3.1 times higher. This gives ratios of fish biomass relative to crustacean zooplankton biomass at approximately 0.09 in Lake Mjøsa and 0.04 in Lake Osensjøen, indicating higher food availability for individual fish in Lake Osensjøen. The community of pelagic zooplanktivore fish consists of three species (vendace, whitefish, smelt) in Lake Mjøsa, and two species (vendace, whitefish) in Lake Osensjøen. The habitat of vendace (the upper 20 m epilimnetic zone) is also utilized by the other species. This indicates that the niche available for the Osensjøen vendace is somewhat wider than the niche in Lake Mjøsa.

The observed differences between the populations in mensural characters of the head are apparently due to differences in body length. Number of scales along the lateral line did not differ between populations, and although the mean gill-raker count in Lake Osensjøen vendace was somewhat lower than in Lake Mjøsa, the difference was small. These observations support the notion that vendace is a morphologically stable species (Svärdson 1979). Habitat and diet of the two populations differed very little, confirming vendace as a specialist pelagic zooplanktivore species (Svärdson 1976).

In conclusion, it appears that vendace adapt well to changes in spawning environment, and also is able to adapt to the prey abundance in a new environment by changes in size and age of sexual maturation. The morphology, habitat use and diet of the species, however, does not differ much between the introduced and donor populations.

Acknowledgments

I want to thank Leif Gjestad, Helge Hagen, Gerd Justås, Gösta Kjellberg and Tor F. Næsje, and Jon Mørstad, Nils Myrene, Karsten Nohr and Edvinn Odden, for their assistance during field work in Lake Mjøsa and Lake Osensjøen, respectively. Bror Jonsson and Tor F. Næsje commented critically on drafts of this paper.

References

- Aass, P. 1978. The whitefish and cisco fisheries in Lake Mjøsa, Norway. - Fauna 31: 80-83. (In Norwegian with English summary.)
- Alm, G. 1959. Connection between maturity, size and age in fishes. - Rep. Inst. Fresw. Res., Drottningholm 40: 5-145.
- Bagenal, T.B. and F.W. Tesch. 1978. Age and growth. p. 101-130. - In: T.B. Bagenal (ed.) Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.
- Braun, E. 1978. Ecological aspects of the survival of fish eggs, embryos and larvae. p. 102-131. - In: S.D. Gerking (ed.) Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.
- Christensen, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. - J. Cons. Int. Explor. Mer. 29: 73-81.
- Colby, P.J. and L.T. Brooke. 1973. Effects of temperature on embryonic development of lake herring (*Coregonus artedii*). - J. Fish. Res. Board Can. 30: 799-810.
- Dahl, K. 1917. Trout and trout waters in Norway. - Centraltrykkeriet, Kristiania. 107 p. (In Norwegian.)
- Dickie, L.M. 1978. Mathematical models of growth. p. 130-136. - In: T.B. Bagenal (ed.) Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.
- Hénault, M. and R. Fortin. 1989. Comparison of meristic and morphometric characters among spring- and fall-spawning ecotypes of cisco (*Coregonus artedii*) in southern Quebec, Canada. - Can. J. Fish. Aquat. Sci. 46: 166-173.
- Huitfeldt-Kaas, H. 1923. Einwanderung und Verbreitung der Süßwasserfische in Norwegen mit einem Anhang über den Krebs. - Arch. Hydrobiol. 14: 223-314.
- Humphries, J.M., F.L. Bookstein, B. Chernoff, G.R. Smith, R.L. Elder and S.G. Poss. 1981. Multivariate discrimination by shape in relation to size. - Syst. Zool. 30: 291-308.
- Jonsson, B., K. Hindar and T.G. Northcote. 1984. Optimal age at sexual maturity of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. - Oecologia (Berlin) 61: 319-325.
- Kjellberg, G. 1986. Monitoring of Lake Mjøsa. Summary, trends and comments 1976-85. - Norwegian Institute of Water Research. Report O-8000203 (241/86). 80 p. (In Norwegian.)
- Kjellberg, G. and O.T. Sandlund. 1983. Trophic relationships in the pelagic zone of Mjøsa. - Directorate of Wildlife and Freshwater Fish. The Mjøsa Project. Report 6. 61 p. (In Norwegian.)
- Lien, L., Å. Bakketun, E. Bendiksen, R. Halvorsen, G. Kjellberg, E.-A. Lindstrøm, M. Mjelde, O.T. Sandlund, T. Tjomsland and K.J. Aanes. 1981. Impact of hydroelectrical power developments in Osensjøen and Søre Osa. - Norwegian Institute of Water Research. Report O-77084. 112 p. (In Norwegian.)

- Lindem, T. 1978. Recordings of pelagic fish in Mjøsa by use of hydroacoustics. - Institute of Physics, Univ. of Oslo. Mimeographed report. 19 p. (In Norwegian.)
- Lindroth, A. 1957. A study of the whitefish (*Coregonus*) of the Sundsvall bay district. - Rep. Inst. Freshw. Res., Drottningholm 38: 70-108.
- Lindsey, C.C. 1981. Stocks are chameleons: Plasticity in gill rakers of coregonid fishes. - Can. J. Fish. Aquat. Sci. 38: 1497-1506.
- Linløkken, A. and T. Qvenild. 1986. Hydroacoustic recordings in Storsjøen (Rendalen), Osensjøen and Engeren, summer and autumn 1985. - Hedmark County, Dept. of the Environment, Hamar. Report no. 6. 15 p. (In Norwegian.)
- Løvik, J.E. and G. Kjellberg. 1982. The Glåma watercourse in Hedmark. Report on zooplankton 1978-80. - Norwegian Institute of Water Research. Report No. O-78045-III. 58 p. (In Norwegian.)
- Luczynski, M. 1985. Survival of *Coregonus albula* (L.) (Tel-osteii) embryos incubated at different thermal conditions. - Hydrobiologia 121: 51-58.
- Luczynski, M. and A. Kirklewska. 1984. Dependence of *Coregonus albula* embryogenesis rate on the incubation temperature. - Aquaculture 42: 43-55.
- Mills, C.A. and A. Eloranta. 1985. Reproductive strategies in the stone loach *Neomacheilus barbatus*. - Oikos 44: 341-349.
- Næsje, T.F. and B. Jonsson. 1988. Impacted stress: a causal agent of reduced whitefish (*Coregonus lavaretus*) egg incubation time. - Can. J. Fish. Aquat. Sci. 45: 27-31.
- Næsje, T.F., B. Jonsson and O.T. Sandlund. 1986a. Drift of cisco and whitefish in a Norwegian river. - Trans. Amer. Fish. Soc. 155: 89-93.
- Næsje, T.F., O.T. Sandlund and B. Jonsson. 1986b. Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*. - Env. Biol. Fish. 15: 309-314.
- Nikolskii, G.V. 1969. Fish population dynamics. - Oliver and Boyd, Edinburgh. 323 p.
- Nysæther, J.K. 1977. The fisheries in Osensjøen. p. 249-267. - In: T. Fossum (ed.) Yearbook, The Norwegian Museum of Forestry, Hunting and Fishing. No. 8, 1976-1977. Elverum, Norway. (In Norwegian with English summary.)
- Reznick, D.N. and H. Bryga. 1987. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. - Evolution 41: 1370-1385.
- Ricker, W.E. 1979. Growth rates and models. p. 677-743. - In: W.S. Hoar, D.J. Randall and J.R. Brett (eds.) Fish physiology. Vol. 8. Bioenergetics and growth. Academic Press, New York.
- Rognerud, S. and G. Kjellberg. 1984. Relationships between phytoplankton and zooplankton biomass in large lakes. - Verh. Internat. Verein. Limnol. 22: 666-671.
- Sandlund, O.T. 1979. Whitefish and vendace in Osensjøen. - Investigations in fish biology in the Osen area. Report no. 6. 57 p. (In Norwegian.)
- Sandlund, O.T., B. Jonsson, T.F. Næsje and P. Aass. 1991. Year-class fluctuations in vendace (*Coregonus albula*): Who's got the upper hand in intraspecific competition? - J. Fish Biol. 38: 873-885.
- Sandlund, O.T., L. Klyve and T.F. Næsje. 1985a. Growth, habitat and food of burbot *Lota lota* in Lake Mjøsa. - Fauna 38: 37-43. (In Norwegian with English summary.)
- Sandlund, O.T. and T.F. Næsje. 1983. The brown trout in Osensjøen. - Investigations in fish biology in the Osen area. Report no. 11. 23 p. (In Norwegian.)
- Sandlund, O.T. and T.F. Næsje. 1986. The whitefish stock in Femund 1982-84. - Directorate for Nature Management. Fish Res. Div. Report 2. 51 p. (In Norwegian.)
- Sandlund, O.T. and T.F. Næsje. 1989. Impact of a pelagic gill-net fishery on the polymorphic whitefish (*Coregonus lavaretus* L. s.l.) population in Lake Femund, Norway. - Fish. Res. 7: 85-97.
- Sandlund, O.T., T.F. Næsje, L. Klyve and T. Lindem. 1985b. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill net catches and echo sounder. - Rep. Inst. Freshw. Res., Drottningholm 62: 136-149.
- Sandlund, O.T., T.F. Næsje and G. Kjellberg. 1987. The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occurring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*). - Arch. Hydrobiol. 110: 357-363.
- Scott, W.B. and E.J. Crossman. 1964. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 1-966.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. - McGraw-Hill, New York. 312 p.
- Smith, S. 1957. Early development and hatching. p. 323-359. - In: M.E. Brown (ed.) The physiology of fishes. Academic Press, New York.
- Stearns, S.C. and J.C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. - Evolution 40: 893-913.
- Svärdson, G. 1966. The distribution and growth of vendace. Inform. Inst. Freshw. Res., Drottningholm (4). 24 p. (In Swedish.)
- Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshw. Res., Drottningholm 55: 144-171.
- Svärdson, G. 1979. Speciation of Scandinavian *Coregonus*. - Rep. Inst. Freshw. Res., Drottningholm 57: 3-95.
- Taugbøl, T., O. Hegge, T. Qvenild and J. Skurdal. 1989. The diet of brown trout in Mjøsa. - Oppland County. Dept. of the Environment, Lillehammer. Report no. 15. 17 p. (In Norwegian.)
- Viljanen, M. 1986. Biology, propagation, exploitation and management of vendace (*Coregonus albula* L.) in Finland. - Arch. Hydrobiol. Beih. Ergebn. Limnol. 22: 73-97.
- Vuorinen, J. 1987. Genetic differences of vendace (*Coregonus albula* L.) stocks and their management implications. - Publ. Univ. Kuopio, Nat. Sci. Statistics and Reviews 1: 5-17.
- Vuorinen, J., T.F. Næsje and O.T. Sandlund. 1991. Genetic changes in a vendace *Coregonus albula* (L.) population, 92 years after introduction. - J. Fish Biol. 39 (Suppl. A): 193-201.

Fish Assemblages in Swedish Streams

ERIK DEGERMAN and BERIT SERS

Institute of Freshwater Research, S-178 93 Drottningholm, Sweden

Abstract

Swedish streams have low diversity and the fish fauna is dominated by a few species. Electrofishing results from 981 localities throughout the country were used in three Principal Component Analyses (PCA) to ordinate electrofishing sites by abiotic factors, species occurrences and species abundances. The abiotic variables were reduced to five major components: climate, colonisation probability, stream order, depth of the locality and distance to the nearest lake. From the ordination of localities by species four major fish assemblages could be interpreted; the lake fish assemblage, the sea-run fish assemblage, the stream fish assemblage and the headwater fish assemblage. Proximity to the sea/lakes and environmental stability were thought to be the main factors influencing division into these assemblages. A possible effect of predation is also discussed. The result is in accordance with the idea of the river continuum, with the effects of lakes added. Salmonid species were more frequent and abundant in extreme environments where other species could not thrive, suggesting that salmonids are sensitive to biotic interactions.

Introduction

Streams represent a variable milieu owing to variations in water discharge and temperature. The characteristics of the environment are determined mainly by climate and catchment area. These variables have a profound effect on the occurrence and abundance of fish. Several studies have described the response of single salmonid species to **micro-habitat** variables (e.g. DeVore and White 1978, Heggenes and Saltveit 1990) or to **macro-habitat** (e.g. Osborne et al. 1991). When studying larger geographic regions geomorphological variables or the size of the catchment area (**meta-habitat**) have been used to predict salmonid abundance (Lanka and Hubert 1987, Kozel and Hubert 1989). On a still larger scale, zoogeographic studies (**super-habitat**) of the Scandinavian fish fauna were performed at the beginning of the century (Huitfeldt-Kaas 1918, Ekman 1922). At this time the main focus was on colonisation after the last glaciation. Later studies have shown that distribution and abundance of species is also dependent on biotic variables, e.g. species interactions (e.g. Svårdson 1976) and food organisms (Eloranta and Olkio 1987). However, most studies have dealt

with lakes. Small streams hold omnivorous species (Vadas 1990), whereas fish in large rivers, which represent a more stable milieu, tend to specialize in food choice (Mann 1965). Few studies have shown predators to affect the abundance of salmonids in streams (Thorpe 1986). But the presence of predators has been shown to decrease salmonids use of pools (Greenberg 1992), and Resetarits (1991) discussed how a coevolution between predator and prey has led the latter to occupy different habitats in the presence of predators.

Owing to a close correlation between abiotic variables and between fish species it is seldom possible to assess the impact of a single abiotic or biotic variable on a single species. The joint effect of different variables on the species within a fish community must be considered (Appelberg and Degerman 1991). One step towards an understanding is a descriptive study of abiotic variables in order to reduce them to a few major components. Further a definition of biotic communities or assemblages is needed. Interaction within and between assemblages may then be observed and eventually quantified.

There has been an increasing number of studies of fish communities in running waters in the last

decade. Most studies rely on the basic concept of "the river continuum" (Vannote et al. 1980), i.e. an increased productivity with stream order and a shift from abiotic regulation of biota to biotic regulation downstream. In Scandinavia such studies are rare, since streams have low diversity and often are dominated by a few species (Larsen 1955). Really large rivers are few. The young landscape is instead dominated by lakes and streams and most studies concentrate on stream-dwelling salmonids (Bohlin 1977, 1978, Näslund 1991, Titus 1991).

The present study aims to describe fish assemblages in running waters in Sweden. The emphasis is on hard bottom biotopes, although soft bottom stream sites have also been investigated. The same species occur in both habitats (Degerman and Appelberg 1992), although in different proportions.

Methods

Electrofishing data were obtained from a national database containing electrofishing results in Sweden since 1989. The database is kept at the Institute of Freshwater Research, Drottningholm, and the included parameters are thoroughly defined (Sers 1991). The electrofishing methods used are the common practice for investigations recommended by the National Board of Fisheries, i.e. successive removals (Karlström 1976, Johlander and Degerman 1991). Data were available from 981 localities fished during June-October. The physical data recorded for each locality included sampling site location (latitude, longitude and altitude), stream width, average depth and maximum depth. On average, the localities represented a 70 m section of the stream. The bottom substrate was classified into five categories (fine <0.0002 m, sand 0.0002-0.002 m, gravel 0.002-0.02 m, stones 0.02-0.2 m, boulders >0.2 m), coarser particles being given a higher value. Water velocity was classified into three categories (<0.2 m s⁻¹, 0.2-0.7 m s⁻¹, >0.7 m s⁻¹). Additional information for each sampling locality included average annual air temperature, average air temperature in January and July and the length of the growing season, expressed as

number of days with an average temperature above 5 °C. The catchment area upstream of the sampling locality and the proportion of the catchment area consisting of lakes were estimated from maps. In addition, the distance from each sampling locality to lakes upstream and downstream was recorded. It was also noted for each locality whether it was located above or below the highest sea level occurring since the last ice age. All variables have been transformed using log₁₀.

Population parameters included were discrete, absence/presence, and continuous, the number of individuals of each species per 100 m². The latter variable was transformed log₁₀(x+1) to normalise the data.

The number of variables was reduced by principal component analysis (PCA). This was performed using environmental data, absence/presence data and species abundance. The primary ordination factors were subsequently rotated using varimax rotation and Kaiser normalisation. The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and Bartlett's test of sphericity were computed to check the accuracy of the PCA (Kaiser 1974). KMO values below 0.5 indicate a poor model. Only components with eigenvalues above 1 were accepted. Factor scores for each sampling locality were computed using the regression method.

Results

Localities studied

The electrofishing localities included in this study are located throughout Sweden (Fig. 1). Their altitude averaged 172 m above sea-level with extremes of 1 and 795 m (Fig. 2). Stream width was generally less than 15 m and averaged 8 m (range 0.5-175 m). Average depth of the sampling sites was 0.29 m (0.04-2.6 m). Only 14% of the sites had soft bottoms (mud-sand), 56% gravel or stones and 28% boulders as the predominant substrate (Fig. 2). The majority of localities (62%) were located below the highest marine level after the last glaciation. The catchment area upstream most localities was 10-100 km², and the proportion of catchment area consisting of lakes was often 5-10%.



Fig. 1. Electrofishing localities included in the study (n=981).

Species occurrence and abundance

Altogether 37 fish species were caught, but most of them occurred in low numbers and at few localities. The number of species averaged 2.4 per sampling location, with extremes of 0 and 9. Fish were absent from 7.9% of the localities, and only 4% of the localities had five or more species. Thus, the number of species was generally low, and 35.5% of the localities had only one species, usually brown trout (31.0%).

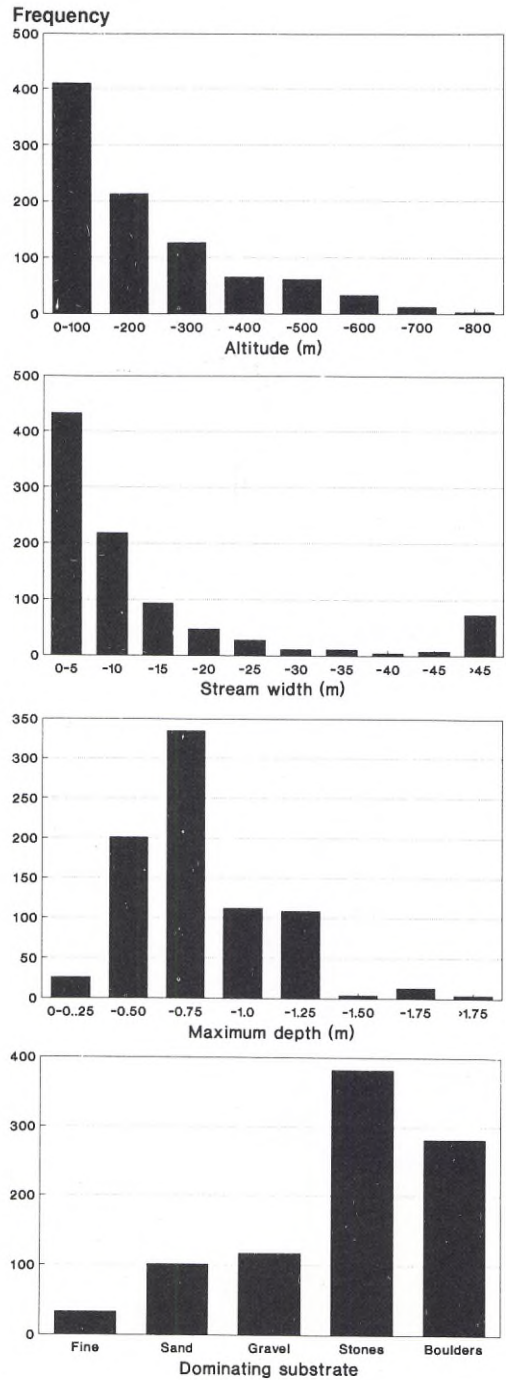


Fig. 2. Frequency distributions of altitude, stream width, stream maximum depth and dominant substrate at the 981 electrofishing localities.

The 13 most frequently caught species were used in the analysis. Brown trout (*Salmo trutta*) was the predominant species and was noted at 79.1% of the localities. Other common species were European minnow (*Phoxinus phoxinus*) (31.4%), burbot (*Lota lota*) (26.3%), northern pike (*Esox lucius*) (22.5%) and bullhead (*Cottus gobio*) (21.0%). All other species were found at fewer than 20% of the localities. Arctic char (*Salvelinus alpinus*) (1.5%) and alpine bullhead (*Cottus poecilopus*) (3.4%) were rare, both being more common at high altitudes. Parr of Atlantic salmon (*Salmo salar*) were caught at 14.8% of the localities, and European eel (*Anguilla anguilla*) occurred at 10.2%.

The number of individuals averaged 65.9 (SD 140) per 100 m². Brown trout alone averaged 24.2 individuals per 100 m², i.e. 37% of the total abundance. Other abundant species were European minnow (14.1% per 100 m²), bullheads (*Cottus gobio* and *C. poecilopus*, 12.7%) and Atlantic salmon (7.7%). These five species constituted 89% of the total number of individuals.

Brown trout predominated at several localities and was found together with several of the other species at many localities (Table 1). Brown trout was found at 80% or more of the localities holding Atlantic salmon, grayling (*Thymallus thymallus*) or brook lamprey (*Lampetra planeri*). Arctic char was only found together with burbot and/or brown trout. Apart from brown trout, only European

minnow and burbot were sympatric with other species at more than 50% of the localities where they occurred.

Ordination of localities by abiotic factors

PCA of the 18 environmental variables resulted in five components that explained 78% of the variation (Table 2). The KMO index of adequacy was 0.69, indicating an acceptable ordination. The resulting five components were interpreted as "climate", "colonisation probability", "stream order", depth of the locality ("habitat depth") and distance to nearest lake ("lake distance").

Ordination of localities by species occurrence

The PCA of species occurrence (presence/absence) resulted in five components (Table 3). The KMO index was 0.60 indicating a barely acceptable model. Only 54% of the variation was accounted for. The first factor included roach, perch, northern pike, burbot and, at the other end of the axis, brown trout (Table 3). The remaining four factors comprised two species each; grayling and bullhead, Atlantic salmon and European eel, alpine bullhead and European minnow, brook lamprey and Arctic char. The latter two were separated on the axis.

Table 1. The proportion (%) of localities where two species coexisted.

SPECIES	B.t.	A. s.	G.	A.b.	B.	A.c.	B.l.	E.m.	Eel	N.p.	P.	R.	B.
Brown trout	100	12	7	2	16	1	5	23	8	16	6	5	18
A. salmon	12	100	3	1	5	0	1	8	5	3	1	1	4
Grayling	7	3	100	1	2	0	1	4	0	2	1	1	5
A. bullhead	2	1	1	100	0	0	1	2	1	1	1	1	2
Bullhead	16	5	3	0	100	0	1	8	1	4	3	2	8
Arctic char	1	0	0	0	0	100	0	0	0	0	0	0	1
Br. lamprey	5	1	1	1	1	0	100	3	1	2	1	1	1
Eur. minnow	23	8	4	2	8	0	3	100	4	8	2	2	9
Eur. eel	8	5	0	1	1	0	1	4	100	3	1	2	2
Nort. pike	16	3	2	1	4	0	2	8	3	100	6	5	10
Perch	6	1	1	1	3	0	1	2	1	6	100	5	6
Roach	5	1	1	1	2	0	1	2	2	5	5	100	6
Burbot	18	4	5	2	8	1	1	9	2	10	6	6	100

Table 2. Factor loadings for the PCA of localities by environmental variables. Only loadings above 0.5 are shown.

	Environmental components				
	Factor 1 "climate"	Factor 2 "colonis. prob."	Factor 3 "stream order"	Factor 4 "hab. depth"	Factor 5 "lake dist."
Temperature (Jan)	0.91				
Annual temperature	0.91				
Growing period	0.90				
Latitude	-0.89				
Longitude	-0.60				
Highest shoreline		-0.85			
Temperature (Jul)		0.77			
Altitude		-0.76			
Stream width			0.84		
Catchment area			0.81		
Substrate			0.56		
Max. depth				0.91	
Average depth				0.82	
Cross-section area				0.81	
Lake distance (upstream)					0.87
Lake distance (total)					0.84
Proportion of lakes					-0.68
Lake distance (downstream)					0.52

As the input data consisted of species occurrence the results should be interpreted in terms of species occurring together. This does not necessarily mean that their population strengths were at their peaks together with the other positively correlated species on an axis.

Ordination of localities by species abundance

PCA of species abundance also resulted in five components with eigenvalues above 1. They explained 53.4% of the variation, with a KMO of 0.56 indicating a barely acceptable model. As with the PCA of localities by species occurrence, localities with roach and perch, as well as with northern pike and burbot were closely related (Table 4). Localities with Atlantic salmon and European eel were also grouped together. Factor three grouped localities with grayling and bullhead together, while factor four mainly separated localities with brook lamprey and brown trout from localities

with Arctic char. The fifth factor separated localities with European minnow from those with northern pike, burbot and alpine bullhead.

Correlation between abiotic and biotic ordinations

Factor scores for each locality from each PCA were computed and a correlation matrix from the three different PCA's was established (Table 5). Significant correlation ($p < 0.01$) involving most of the abiotic and biotic factors were noted. However, the abiotic factor 5 (lake distance) and the biotic factor 4 for occurrence (alpine bullhead and European minnow) lacked any significant correlations with other factors.

Localities with brown trout were grouped together with localities with several different species. Brown trout occurrence was low along with perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), northern pike and burbot. Brown trout abundance was high together with brook lamprey. The latter

Table 3. Factor loadings for the PCA of localities by species occurrence. Although only loadings above 0.5 are shown the sign (+/-) is given for species with lower loadings.

Species	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Roach	0.74				
Perch	0.74				
Northern pike	0.59				
Burbot	+				
Brown trout	-				
Grayling		0.68			
Bullhead		0.63			
Atlantic salmon			0.77		
European eel			0.75		
Alpine bullhead				0.82	
European minnow				+	
Brook lamprey					0.69
Arctic char					-0.65

Table 4. Factor loadings for the PCA of localities by species abundance. Although only loadings above 0.5 are shown the sign (+/-) is given for species with lower loadings.

Species	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Perch	0.79				
Roach	0.78				
Atlantic salmon		0.83			
European eel		0.79			
Bullhead			0.72		
Grayling			0.66		
Brook lamprey				0.67	
Brown trout				0.58	
Arctic char				-0.54	
Alpine bullhead					0.65
Burbot					+
European minnow					-
Northern pike					+

species hardly competes with trout, as it lies burrowed and feeds on detritus. Thus, brown trout was frequent and reached its highest abundances in low-competitive environments (Fig. 3). There was a significant correlation between the number

of fish species and the factor scores for the abiotic factors 2 and 3, i.e. colonisation probability and stream order (multiple regression, $R^2=0.39$, $p<0.001$). There was no correlation between trout abundance (single linear correlation) and these

Table 5. Correlation matrix between sites-by-species occurrence and sites-by-species abundance scores and the five environmental components. Correlations given are significant at the 0.01 level. Non-significant correlations are marked (+/-).

Biotic comp.	Environmental components				
	Factor 1 "climate"	Factor 2 "colonis.prob."	Factor 3 "stream order"	Factor 4 "hab. depth"	Factor 5 "lake dist."
OCCURRENCE					
Factor 1 (+roach,+perch,+pike,+burbot,-trout)	0.18	0.34	+	+	-
Factor 2 (+grayling,+bullhead)	-0.35	0.30	0.47	0.13	+
Factor 3 (+salmon,+eel)	+	0.20	0.42	-	+
Factor 4 (+alpine bullhead,+minnow)	+	-	+	-	+
Factor 5 (+lamprey,-Arctic char)	0.30	0.17	+	-	+
ABUNDANCE					
Factor 1 (+perch,+roach)	0.22	0.27	-	+	-
Factor 2 (+salmon,+eel)	0.20	0.14	0.30	-	+
Factor 3 (+bullhead,+grayling)	-0.24	0.31	0.30	0.13	+
Factor 4 (+lamprey,+trout,-Arctic char)	0.40	+	-0.11	-0.12	-
Factor 5 (+Alpine bullhead,+burbot,+pike,-minnow)	+	+	0.11	-	+

two factors, thus indicating that trout abundance was not directly influenced by colonisation probabilities or stream order, but rather by the number of coexisting species.

The ordination of sites by species occurrence and abundance gave similar results, and the occurrence of most species was generally favoured by the same abiotic factors that favoured species abundance. However, some differences were noted. Atlantic salmon and European eel (Factor 3 occurrence, Factor 2 abundance) occurred only at localities below the highest shoreline, and were more frequent in large streams. Their abundances also were positively correlated with warmer climate, but the occurrence of these species was not significantly favoured by a warm climate. Northern pike often occurred together with roach and perch

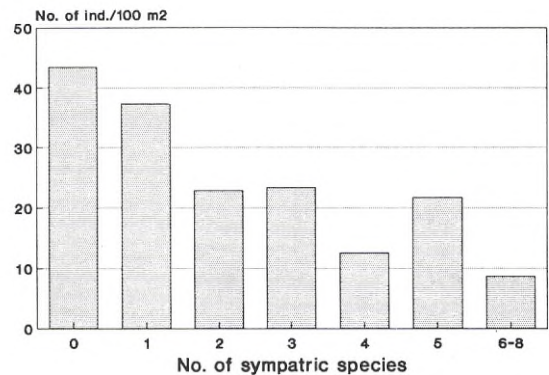


Fig. 3. The abundance (no. of individuals/100 m²) of brown trout in relation to the number of sympatric species at each locality.

(Factor 1 occurrence), but reached higher abundances together with burbot, European minnow and alpine bullhead (Factor 5 abundance). Thus, this predator frequently occurred on warmer localities close to lakes, but seemed to be most abundant in large streams. As for northern pike, localities with burbot were grouped together with localities that held several different species. Localities where burbot was more abundant were grouped together with localities with European minnow and alpine bullhead. Burbot was frequently found together with roach, perch and northern pike close to lakes. Localities with European minnow and alpine bullhead occurred together in the PCA of species (Factor 4 occurrence, Factor 5 abundance). There was a weak tendency for these species to be less abundant in large streams, although they occurred more often there. This suggests that they are subdominant species.

For the other species the results of ordination sites by fish occurrence or abundance were similar. Perch and roach (Factor 1 on occurrence and abundance) were favoured at easily accessible sites and by a warmer climate. Localities with these species more frequently were located below the highest shoreline, close to lakes and were in general deep. Localities with perch and roach often also held northern pike and burbot. All four species mainly occur in lakes. Localities with grayling and bullhead (Factor 2 occurrence, Factor 3 abundance) were more frequent and the species were more abundant in colder climate in large streams and at easily accessible sites. Localities with Arctic char and brook lamprey were placed on the same factor axis (Factor 5 occurrence, Factor 4 abundance) but with different signs. These two species never occurred together, but each were to be found along with brown trout at some localities. Arctic char was favoured by a cold climate, and to some extent by colonisation difficulties for other species.

Discussion

The results must be viewed with care, because they rely only on the abiotic parameters included. For instance, water quality data was not available,

which is unfortunate, since recent acidification of Swedish streams has had a major impact on fish (Degerman et al. 1990, Degerman and Appelberg 1992). Moreover, the localities chosen do not represent a random sample, as they were part of regional inventories or monitoring of salmonids. However, this drawback is compensated for by the extensive material used in the study and the wide geographic and abiotic variation between localities. Furthermore, the aim of this study was to identify different fish assemblages and not to quantify their occurrence.

The results showed that the streams have low diversity, and that brown trout was the most frequently occurring species. Brown trout was abundant when it occurred alone or together with brook lamprey, whereas its abundance was lower together with potential competitors and predators. The correlation between the abundance of brown trout and the number of coexisting species could be fallacious, since a negative correlation might only exist between the young stages (Young-of-the-Year, YOY) and other species, e.g. as a consequence of spawning habitat choice. YOY were separated from older trout in the material but the result was exactly the same. Thus, it is suggested that brown trout do suffer from interacting species.

The results revealed that four major assemblages of fish exist in Swedish streams. The species, however, show great overlap in distribution and high abundance is only achieved by a few species. In a similar study of Swedish lakes, Appelberg and Degerman (1991) recorded a higher explained variation using the biotic ordinations. Swedish lakes generally have more species than streams, as well as more segregation in food utilization (Nilsson 1965, Svårdson 1976). The stable lake environment permits specialists to establish and thrive. Competitive exclusion of species may thereby occur, which will lead to more distinct assemblages than in unstable running waters. Because of large environmental variation over the year the streams are only used for part of the year by some species. For instance, European minnow seem to migrate to streams to feed during summer and return to lakes for the winter (Degerman et al. 1990). Few species (brown trout, bullheads) seem

to be able to spend their whole life in the stream, instead they use them for feeding, migration routes or spawning. The former strategy is mainly employed by lake-dwelling species entering streams during low flow periods.

Perch and roach coexisted at 46% of the localities where roach was present. These two species were grouped together throughout. Northern pike and burbot also frequently occurred together with these two species. This group of species occurs in slow-flowing stretches, often close to lakes, and this assemblage of stream-dwelling fish could be referred to as "the lake fish assemblage". It should be noted that presence of a lake is not a prerequisite for this assemblage as these species also dominate in slow flowing stretches in streams and in large slow flowing rivers (Mann 1965). This assemblage had a relatively low occurrence of brown trout (approx. 50% of the localities) and brown trout had low abundance in this assemblage.

Localities with Atlantic salmon (anadromous) and European eel (catadromous) were ordinated together. Both species were more frequent and abundant on the Swedish west coast, but also occurred along the east coast. Sea-run brown trout frequently coexists with these two species. If the streams are swift-flowing and large, Atlantic salmon reaches higher abundances than brown trout (Degerman and Appelberg 1992), although brown trout is the more aggressive species (Kalleberg 1958). These species are naturally favoured in the easily accessible lower reaches of large streams. European eel is also favoured by a warm climate, and brown trout and Atlantic salmon reach higher abundances in warm regions in Sweden. These species occurred together with European minnow, which was subdominant and reached low abundances. This assemblage could be labelled "the sea-run fish assemblage".

Other species favoured by large streams were grayling and bullhead, often in coexistence with brown trout and occasionally with European minnow, burbot and northern pike. The latter two are members of the lake fish assemblage. The former four species occurred together in colder streams and preferably in the intermediate reaches where colonisation was not a problem. Access to the sea

was impossible at several sites. Several of the species present are able to live their whole lives in running water. This assemblage is labelled "the stream fish assemblage".

Arctic char occurred in small, cold northern streams, whereas brown trout was more frequent in warmer headwaters. This is called "the headwater fish assemblage", and may thus be divided into two subgroups. Brown trout often occurred alone, but sometimes together with brook lamprey. Both Arctic char and brown trout are susceptible to predation and competition (Svärdson 1976) and during the colonisation of waters after the last ice age these two species occupied most water in the country (Huitfeldt-Kaas 1918, Ekman 1922). With time and climatic changes other species followed and occupied the niche taken by these two salmonids (op.cit.). Whereas brown trout was able to coexist with several of the newcomers, Arctic char soon disappeared (op.cit., Hammar 1987). As a consequence, it is proposed that Arctic char and brown trout occupy a wider niche when living alone than in streams where they live sympatric with other species (e.g. Nilsson 1965). This could be noted for brown trout, since localities with allopatric brown trout showed a larger niche utilization than sympatric populations, i.e. the standard deviation around the average on each abiotic PCA axis was greater at localities with the allopatric populations. Too few localities with Arctic char were included for this analysis, but other authors have shown that lake-dwelling allopatric Arctic char occupy a larger food niche than sympatric populations (Hammar 1987). The species in "the headwater fish assemblage" are opportunistic low-competitive species and thrive in extreme environments, where specialists are excluded.

All thirteen species included in the analyses occur in lakes in Sweden. None or few specialists occur, probably because the streams are variable and the ecosystems are young (approx. 10,000 years since the last ice age). As the ecosystems slowly age, resulting in fewer lakes and more rivers, biotic interactions will increase and the salmonids will successively find fewer refuges, while cyprinids and the predatory guild will expand.

To sum up, access and proximity to the sea or lakes allowed two fish assemblages to establish (the sea-run fish and the lake fish assemblage). The fishes in these assemblages utilize the streams only during part of their lives. The headwater fish assemblage turns into the stream fish assemblage with increasing stream order, i.e. with increased habitat size, increased productivity and a more stable environment. This assemblage turns into the sea-run fish assemblage where access to the sea is possible. The results are in accordance with the old idea of succession with increasing stream order (Vannote et al. 1980). The lake fish assemblage, however, interrupts all of the other assemblages and is found along the entire stream order gradient. A major factor distinguishing the headwater fish assemblage from the other three could be that piscivorous predators, such as northern pike, European eel and burbot, were absent from the headwater fish assemblage.

Acknowledgments

Thanks to Magnus Appelberg, Larry Greenberg and Bill Tonn for comments.

References

- Appelberg, M. and E. Degerman. 1991. Development and stability of fish assemblages after lime treatment. - *Can. J. Fish. Aquat. Sci.* 48(4): 546-554.
- Bohlin, T. 1977. Habitat selection and intercohort competition of juvenile sea-trout *Salmo trutta*. - *Oikos* 29: 112-117.
- Bohlin, T. 1978. Temporal changes in the spatial distribution of juvenile sea-trout *Salmo trutta* in a small stream. - *Oikos* 30: 114-120.
- Degerman, E., E. Sjölander, A. Johlander, P. Sjöstrand, K. Höglind and L. Thorsson. 1990. Liming of acidified running waters to improve conditions for fish. - *Inform. Inst. Freshw. Res., Drottningholm* 4: 27-214. (In Swedish with English summary).
- Degerman, E. and M. Appelberg. 1992. The response of stream-dwelling fish to liming. - *Environmental Pollution*. (In press.)
- DeVore, P.W. and R.J. White. 1978. Daytime responses of brown trout (*Salmo trutta*) to cover stimuli in stream channels. - *Trans. Amer. Fish. Soc.* 107: 763-771.
- Ekman, S. 1922. Djurvärldens utbredningshistoria på skandinaviska halvön. - A. Bonniers förlag, Stockholm. 612 p. (In Swedish)
- Eloranta, A. and K. Olkio. 1987. Size, growth and density of brown trout (*Salmo trutta* L.) in the Arvanjoki watercourse, Finnish lake district. - *Biol. Res. Rep. Univ. Jyväskylä* 10: 167-188.
- Greenberg, L. 1992. The effect of discharge and predation on habitat use by wild and hatchery brown trout (*Salmo trutta*). - In: *Regulated rivers: Research and Management*. John Wiley and Sons Ltd. (In press.)
- Hammar, J. 1987. Zoogeographical zonation of fish communities in insular Newfoundland; A preliminary attempt to use the Arctic char population ecology to describe early postglacial colonisation interactions. - *Proceedings of the fourth workshop on Arctic char, 1986. ISACF Inform. Ser., Drottningholm* 4: 31-38.
- Heggenes, J. and S.J. Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. - *J. Fish Biol.* 36: 707-720.
- Huitfeldt-Kaas, H. 1918. Ferskvandfiskenes utbredelse og invandring i Norge - med et tillæg om krebsen. - *Centraltrykkeriet, Kristiania*. 106 p. (In Norwegian.)
- Johlander, A. and E. Degerman. 1991. Elfiske - kurs juni 1991 (Electrofishing manual). - National Board of Fisheries, Gothenburg, Sweden. 18 p. (In Swedish.)
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *Salmo trutta* L.). - *Rep. Inst. Freshw. Res., Drottningholm* 32: 55-98.
- Kaiser, H.F. 1974. An index of factorial simplicity - *Psychometrika* 39: 31-36.
- Karlström, Ö. 1976. Quantitative methods in electrical fishing in Swedish salmon rivers. - *ZOON* 4: 53-63.
- Kozel, S.J. and W.A. Hubert. 1989. Factors influencing the abundance of brook trout (*Salvelinus fontinalis*) in forested mountain streams. - *J. Freshw. Ecol.* 5(1): 113-122.
- Lanka, R.P. and W.A. Hubert. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. - *Trans. Amer. Fish. Soc.* 116: 21-28.
- Larsen, K. 1955. Fish population analyses in some small Danish trout streams by means of D.C. electrofishing. With special reference to the populations of trout (*Salmo trutta* L.). - *Medd. Danmarks Fisk. og Havunders. Ny Ser. Bind I, nr 10*. 69 p.
- Mann, K.H. 1965. Energy transformations by a population of fish in the River Thames. - *J. Anim. Ecol.* 34: 253-275.
- Nilsson, N.-A. 1965. Food segregation between salmonid species in north Sweden. - *Rep. Inst. Freshw. Res., Drottningholm*. 46: 58-78.
- Näslund, I. 1991. Partial migration and the development of seasonal habitat shifts in a land-locked Arctic char (*Salvelinus alpinus*) population. - *Dissertation, Umeå Univ.* 22 p.

- Osborne, L.L., B. Dickson, M. Ebbers, R. Ford, J. Lyons, D. Kline, E. Rankin, D. Ross, R. Sauer, P. Seelbach, C. Speas, T. Stefanavage, J. Waite and S. Walker. 1991. Stream habitat assessment programs in states of the AFS north central division. - *Fisheries* 16(3): 28-35.
- Resetarits, W.J. Jr. 1991. Ecological interactions among predators in experimental stream communities. *Ecology* 72(5): 1782-1793.
- Sers, B. 1991. Elfiskeregistret - en viktig och användbar databas . - PM no.1 Institute of Freshwater Research, Drottningholm. 17 p. (In Swedish.)
- Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - *Rep. Inst. Freshw. Res.* 55: 144-171.
- Thorp, J.H. 1986. Two distinct roles for predators in freshwater assemblages. - *Oikos* 47: 75-82.
- Titus, R.G. 1991. Population regulation in migratory brown trout (*Salmo trutta*). - Dissertation, Uppsala Univ. 24 p.
- Vadas, R.L. Jr. 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Env. Biol. Fish.* 27: 285-302.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The River Continuum concept. *Can. J. Fish. Aquat. Sci.* 37: 130-137.

Food Choice and Vertical Distribution of European Minnow, *Phoxinus phoxinus*, and Young Native and Stocked Brown Trout, *Salmo trutta*, in the Littoral Zone of a Subalpine Lake

TRYGVE HESTHAGEN,¹ OLA HEGGE² and JOSTEIN SKURDAL³

¹ Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway.

² County Environmental Administration, Statsetatenes hus, N-2600 Lillehammer, Norway.

³ Eastern Research Institute, P.O. Box 1066, Skurva, N-2601 Lillehammer, Norway

Abstract

The aim of this paper was to study interactions between European minnow (*Phoxinus phoxinus*) and young brown trout (*Salmo trutta*) through comparison of their diet and vertical distribution in the littoral zone of a lake. A significantly higher fraction of E. minnow was caught close to the bottom compared with both native - and stocked brown trout. Only stocked brown trout were caught in the upper part of the gillnets. The dominant food item for E. minnow was *Gammarus lacustris*, which comprised about 80 percent volume of the diet, as opposed to about 40 percent and 10 percent for native and stocked brown trout, respectively. Other dominant food items for brown trout were *Eurycercus lamellatus* and aquatic insects. Surface insects were only an important food source for stocked brown trout. We suggest the existence of exploitative competition between E. minnow and young brown trout for their common prey, *G. lacustris*.

Introduction

Since the 1920's, European minnow (*Phoxinus phoxinus*) have become widely distributed in subalpine and mountain lakes in southern Norway (Huitfeldt-Kaas 1918, Borgstrøm 1973, Lillehammer and Saltveit 1979, Saltveit and Brabrand 1991), probably mostly due to their use as live bait in angling. Previously, brown trout (*Salmo trutta*) was the only fish species present in most lakes in this region. *Gammarus lacustris* is an important food item for allopatric brown trout (Lien 1978). However, introductions of E. minnow have considerably reduced the abundance of *G. lacustris* and its consumption by brown trout in Norwegian lakes (Lien 1981, Brittain et al. 1988, Bruun 1988, Hansen 1988).

European minnow and brown trout are two dissimilar species which differ strongly in aspects such as behaviour. While E. minnow is typically a social species foraging in shoals (Pitcher 1986), brown trout is territorial and display agonistic behaviour (Bachman 1984). Nongame fishes are

considered to affect the production of salmonid fishes, but the actual evidence is weak (Brown and Moyle 1981). Resource partitioning, which can be caused by both exploitative and interference competition, has been documented in sympatric fish species (Nilsson 1963, 1965). Habitat segregation is most pronounced between closely related species, but may also occur between taxonomically more distant species (Nilsson 1967).

In Lake Tansbergfjorden, brown trout was originally the only fish species present, and the lake also supports *G. lacustris*. E. minnow was introduced into the lake during the 1950's. Our aim was to study the effect of E. minnow on juvenile brown trout by comparing their use of space and their food habits in the littoral zone in summer.

Study area

Lake Tansbergfjorden is located in southern central Norway at an altitude of 916 m a.s.l. The surface area of the lake is 99.4 hectare; 40% is less

than 3 m deep while maximum depth is 6 m. The catchment area of the lake is 15 km², and consists mainly of marsh with some birch and pine forest. Aquatic vegetation is sparse, and the bottom substrate mainly consists of a silty substrate with few stones in the littoral zone. pH was 6.5 and the concentration of calcium 1.5 mg L⁻¹.

In early September 1986, and late August 1987, the lake was stocked with 4,600 trout fry (age 0+) in equal numbers of pond and hatchery reared fish. Fish in the two groups were marked by cutting off the adipose fin in addition to the entire left and right lobe of the pelvic fin, respectively. We used Tunhovdfjord brown trout which originated from wild parents (Hesthagen and Skurdal 1989). The mean total length of the stocked fry varied between 47-66 mm (range 42-87 mm).

Sampling with chains of benthic nets of different mesh sizes showed that brown trout are commonly found at all depths between 0-6 m, while few individuals were caught in pelagic nets (unpubl. data). The stock is mainly exploited with gillnets of 35 mm as the minimum legal mesh size, and the annual yield was estimated to range between 190 and 290 kg (1988-90).

Methods

Gillnets of 10 mm mesh size (monofilament) which were 25 m long and 1.5 m deep were used to sample fish in 1987 (August) and 1988 (July and August). A total of 26 and 27 gillnets were used in 1987 and 1988, respectively. Each net was set perpendicular to the shore at 0-2.5 m. We divided each net into three horizontal panels: 0-0.5 m, 0.5-1.0 m and 1.0-1.5 m. Stomachs of randomly chosen fish were collected in August each year, and stored in alcohol for later identification under a stereo microscope. The percent volume (% vol.) of each taxonomic category in each stomach was determined by counting the number of specimens of each category and estimating their average size.

The degree of food overlap between populations was calculated according to Schoener's (1968) index

$$D = 1 - 0.5 \sum_{i=1}^n (p_i - q_i)$$

where p_i is proportion of food item i in population 1, q_i is proportion of food item i in population 2, and n the number of food categories. D varies between 0 and 1.0, representing no and complete food overlap, respectively.

Stomach fullness was subjectively estimated on a scale from 0-5, where 0 represents empty stomachs and 5 extended stomachs. Variation in stomach fullness between different groups of fish was tested using the non-adjusted G -statistics for test of independence (Sokal and Rohlf 1969).

Results

The catch per gillnet night on 10 mm mesh size of *E. minnow* and native/stocked brown trout in 1987 and 1988, ranged from 28.5-36.4 and 1.1-1.2 specimens, respectively (Table 1). Recapture of stocked fish included only individuals of age 1+. Native brown trout were also almost exclusively fish of age 1+ (92%).

The mean length of *E. minnow* was 98±5 mm (mean ±SD) (n=99). The corresponding lengths for native trout and stocked trout (age 1+) were 100±6 mm (n=63) and 105±7 (n=61), respectively, and did not differ significantly (t -test, $P>0.05$).

There was no significant difference in the vertical depth distribution of fish caught in the littoral zone in 1987 and 1988 in either fish category, and the data were therefore pooled (χ^2 -tests, $P>0.05$).

Table 1. Mean number ±SD of *E. minnow*, native brown trout and stocked brown trout caught per gillnet night on 10 mm mesh size in Lake Tansbergfjorden in 1987 (August) and 1988 (July and August). Total number of fish caught in parenthesis. N=number of gillnets used.

Fish category	1987 N=26	1988 N=27
<i>E. minnow</i>	36.4 ± 6.1 (946)	28.5 ± 4.5 (770)
Native trout	1.2 ± 1.0 (31)	1.2 ± 1.1 (32)
Stocked trout	1.1 ± 0.8 (28)	1.2 ± 0.9 (33)

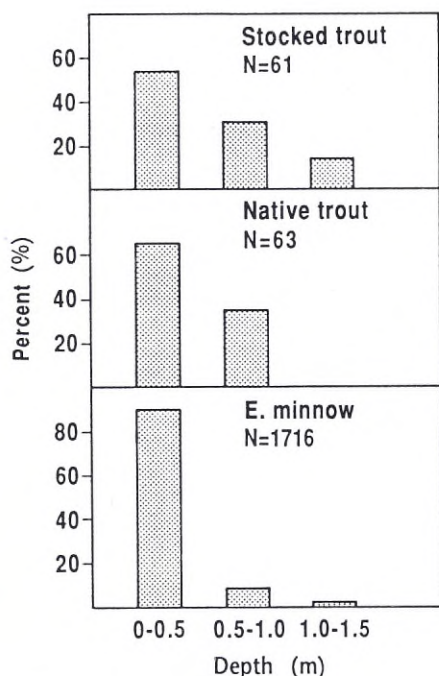


Fig. 1. Distribution (%) of stocked brown trout, native brown trout and E. minnow caught with 10 mm mesh size gillnets at three depths from the bottom: 0-0.5 m, 0.5-1.0 m and 1.0-1.5 m in Lake Tansbergfjorden in 1987 and 1988. N = number of fish caught.

Further, the vertical distribution of stocked trout, i.e. pond reared versus hatchery reared fish, was not significantly different ($\chi^2=0.70$, $P>0.05$). The vertical distribution of E. minnow differed signifi-

cantly from that of native ($\chi^2=52.4$, $P<0.05$) as well as stocked trout ($\chi^2=81.6$, $P<0.05$). Most (90%) E. minnow were caught between 0-0.5 m from the bottom (Fig. 1). The distribution of native and stocked brown trout was significantly different ($\chi^2=10.1$, $P<0.05$); as stocked individuals occurred more frequently in higher water strata compared with native trout.

The Schoener (1968) index D showed small overlap in the diets of E. minnow and both native trout ($D=0.49$) and stocked trout ($D=0.24$). However, overlap in diet between native and stocked trout was relatively high ($D=0.75$). The main food item for E. minnow both in 1987 and 1988 was *G. lacustris*, comprising 75 and 82% vol. of their stomach contents, respectively (Table 2). In native brown trout stomachs, the abundance of *G. lacustris* was much less than in E. minnow, which in addition to *Eurycercus lamellatus* were the predominant food items constituting 37 and 41% vol. of the diet. In stocked brown trout, the abundance of *Gammarus* constituted only 12 and 13% vol. of the diet in 1987 and 1988, respectively, for which *E. lamellatus* was the most important food item. *E. lamellatus* was of less importance as food for E. minnow. Surface insects made up a relatively high fraction of the diet only for stocked brown trout (20 and 22% vol.), while they constituted 3 and 4% vol. of the diet of native brown trout. Zoobenthos (mainly Trichoptera) were equally important as food for both native and stocked trout, ranging between 23 and 25% vol..

Table 2. Percent composition (volume) of major prey items for E. minnow, native brown trout and stocked brown trout caught in Lake Tansbergfjorden in 1987 and 1988. Number of stomachs analysed in parenthesis.

Food Category	E. minnow		Native trout		Stocked trout	
	1987 (28)	1988 (12)	1987 (12)	1988 (10)	1987 (16)	1988 (15)
Surface insects	1	0	3	4	22	20
Zooplankton	0	0	1	2	2	3
<i>Eurycercus lamellatus</i>	3	11	33	31	41	37
<i>Gammarus lacustris</i>	75	82	39	36	12	13
Mollusca	17	4	0	0	0	0
Other zoobenthos	3	3	23	23	23	25
Others	<1	0	1	4	0	2

Table 3. Number of *E. minnow*, native brown trout and stocked brown trout with different stomach fullness caught in Lake Tansbergfjorden in August 1987 and 1988. N = number of stomachs examined.

Fish category	Stomach fullness						N
	0	1	2	3	4	5	
<i>E. minnow</i>	0	2	4	21	8	5	40
Native trout	0	1	5	14	2	0	22
Stocked trout	0	2	5	20	4	0	31

There was no difference in stomach fullness between native and stocked trout ($G=0.55$, $df=3$, $P>0.05$, Table 3). *E. minnow* had a higher stomach fullness than brown trout, however, the difference was not significant ($G=7.07$, $df=4$, $P>0.05$).

Discussion

European minnow caught in Lake Tansbergfjorden fed extensively on *G. lacustris*. For juvenile native trout (mainly age 1+), *G. lacustris* and *E. lamellatus* were of equal importance as food, while stocked trout (age 1+) utilized *G. lacustris* to a small extent. In accordance with this, the *E. minnow* stayed close to the bottom (0-0.5 m) where access to *G. lacustris* is expected to be best. Native brown trout and especially stocked brown trout occurred more frequently in higher water strata. Allopatric juvenile brown trout caught on gillnets of 10 mm mesh size in Lake Tesse were all obtained between 0-0.5 m from the bottom (Hegge et al. 1992), indicating that the vertical distribution of brown trout in Lake Tansbergfjorden was influenced by the presence of *E. minnow*. This suggests that young brown trout are subjected to exploitative competition from *E. minnow* in the littoral zone. Brown trout are known to compete aggressively for territories in both mono- and multispecific fish communities (Kalleberg 1958, Jenkins 1969, Nilsson 1963, Bachman 1984). However, in sympatry with dense populations of *E. minnow*, brown trout might be affected by interference as well as exploitative competition (cf. Nilsson 1963, 1965).

Several studies report severe reductions in densities of *Gammarus* when exposed to heavy fish predation (Straskraba et al. 1966, Langeland 1978). In several Norwegian lakes, the abundance of *G. lacustris* seems to be related to the presence of *E. minnow* (Brittain et al. 1988). In Lake Øvre Heimdalsvatn, the introduction of *E. minnow* caused a drastic decline in the density of *G. lacustris*, which is now almost eliminated as food for brown trout in the lake (Lien 1978, Lien 1981, Bruun 1988). There was also a marked decline in the condition factor of brown trout in the lake following the introduction of *E. minnow* (cf. Jensen 1977, Bruun 1988).

Hatchery reared brown trout released in Lake Tansbergfjorden occurred in higher water strata, feeding less on *G. lacustris* and more on surface insects than did native trout of similar size. However, Johnsen and Ugedal (1986, 1989) found that the diet of hatchery reared brown trout released in natural waters only differs from that of naturally recruited individuals shortly after release. The difference in resource utilization found between these two categories in Lake Tansbergfjorden may be due to interactive segregation because wild salmonids seem to be more aggressive than hatchery reared fish in a low density situation (cf. Fenderson and Carpenter 1971), which is the case in Lake Tansbergfjorden. However, hatchery reared fish are generally more aggressive than wild conspecifics (Swain and Riddell 1990). There might also be adaptive differences in feeding preferences between hatchery reared and wild trout. Such differences have been found in sympatric species of both brown trout (Ferguson 1986, Cawdery and Ferguson 1988) and other salmonids (Malmquist et al. 1992).

The introduction of *E. minnow* in Lake Tansbergfjorden probably reduced the feeding conditions for brown trout through reduced density of *G. lacustris*. Hence, the existence of *E. minnow* magnifies the competition between native and stocked brown trout for this food resource. However, larger trout in Lake Tansbergfjorden probably consume *E. minnow*, which to some extent would counteract the competition effect from *E. minnow* on juvenile brown trout.

Acknowledgments

We would like to thank Reidar Gran for assistance in the test-fishing, Åslaug Viken for stomach analysis, Amy Lightfoot for linguistic assistance, and Odd Terje Sandlund and two anonymous reviewers for valuable comments on this paper. This study was financially supported by The Royal Norwegian Council for Scientific and Industrial Research (NTNF) as a part of the research program "Environmental effects of water regulation schemes".

References

- Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. - *Trans. Amer. Fish. Soc.* 113: 1-32.
- Borgstrøm, R. 1973. Dispersal of minnows. - *Jakt-Fiske-Friluft*. 102: 28-29. (In Norwegian.)
- Brittain, J.E., Å. Brabrand, S.J. Saltveit, T. Bremnes and E. Røsten. 1988. The biology and population dynamics of *Gammarus lacustris* in relation to the introduction of minnows, *Phoxinus phoxinus*, into Øvre Heimdalsvatn, a Norwegian subalpine lake. - *Rapp. Lab. Ferskv. Økol. Innlandsfiske* 109: 1-30.
- Brown, L. and P.B. Moyle. 1981. Impact of squawfish (*Ptychoccheilus* spp.) on salmonid populations: a review. - *N. Am. J. Fish. Mgmt* 1: 104-111.
- Bruun, P.D. 1988. Population characteristics and diet of brown trout in Lake Øvre Heimdalsvatn: Effects of increased population density and introduction of minnows. - *Cand. Scient. Thesis, University of Oslo, Norway*. 51 p. (In Norwegian.)
- Cawdery, S.A.H. and A. Ferguson. 1988. Origins and differentiation of three sympatric species of trout (*Salmo trutta* L.) in Lough Melvin. - *Polsk. Arch. Hydrobiol.* 25: 267-277.
- Fenderson, O.C. and M.R. Carpenter. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (*Salmo salar* L.). - *Anim. Behav.* 19: 439-447.
- Ferguson, A. 1986. Lough Melvin - a unique fish community. - *Occ. Pap. Irish Sci. & Tech. Royal Dublin Soc.* 1: 1-17.
- Hansen, H. 1988. Food habits of minnows, *Phoxinus phoxinus* (L.) in Lake Øvre Heimdalsvatn, and possible changes in the zooplankton community due the introduction of minnows. - *Cand. Scient. Thesis, University of Oslo, Norway*. 62 p. (In Norwegian with English summary.)
- Hegge, O., T. Hesthagen and J. Skurdal. 1992. Vertical distribution and substrate preference of brown trout in a littoral zone. - *Env. Biol. Fish.* (In press).
- Hesthagen, T. and J. Skurdal. 1989. Lake stockings of one-summer-old hatchery - and pond reared brown trout. - *Miljøvirkninger av vassdragsutbygging, MVU-Report A18: 1-13.* (In Norwegian with English summary.)
- Huitfeldt-Kaas, H. 1918. Ferskvandsfiskenes utbredelse og invandring i Norge med et tillæg om krebsen. - *Centraltrykkeriet, Kristiania*. 106 p. (In Norwegian.)
- Jenkins, T.M. Jr. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. - *Anim. Behav. Monogr.* 2: 57-123.
- Jensen, K.J. 1977. On the exploitation of the population of brown trout, *Salmo trutta* L., in Lake Øvre Heimdalsvatn, southern Norway. - *Rep. Inst. Freshw. Res., Drottningholm* 56: 18-69.
- Johnsen, B.O. and O. Ugedal. 1986. Feeding of hatchery-reared and wild brown trout, *Salmo trutta* L., in a Norwegian stream. - *Aquacult. Fish. Mgmt* 17: 281-287.
- Johnsen, B.O. and O. Ugedal. 1989. Feeding by hatchery-reared brown trout, *Salmo trutta* L. released in lakes. - *Aquacult. Fish. Mgmt* 20: 97-104.
- Kalleberg, H. 1958. Observation in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). - *Rep. Inst. Freshw. Res., Drottningholm* 39: 55-98.
- Langeland, A. 1978. Fish studies in lakes in Sanddøla watershed in Nord-Trøndelag, 1976-1977. - *K. norske Vidensk. Mus. Rapp. Zool. Ser. 7: 1-27.* (In Norwegian.)
- Lien, L. 1978. The energy budget of the brown trout population of Øvre Heimdalsvatn. - *Holarct. Ecol.* 1: 279-300.
- Lien, L. 1981. Biology of minnow *Phoxinus phoxinus* and its interactions with brown trout *Salmo trutta* in Øvre Heimdalsvatn, Norway. - *Holarct. Ecol.* 4: 191-200.
- Lillehammer, A. and S.J. Saltveit. 1979. Stream regulation in Norway. p. 201-213. - In: Ward J.W. and J.A. Stanford (eds.). *The ecology of regulated streams*. Plenum Press, New York.
- Malmquist, H.J., S.S. Snorrason, S. Skúlason, B. Jonsson, O.T. Sandlund and P.M. Jónasson. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. - *J. Anim. Ecol.* 61: 21-35.
- Nilsson, N.-A. 1963. Interactions between trout and char in Scandinavia. - *Trans. Amer. Fish. Soc.* 92: 276-285.
- Nilsson, N.-A. 1965. Food segregation between salmonid species in north Sweden. - *Rep. Inst. Freshw. Res., Drottningholm* 46: 58-78.
- Nilsson, N.-A. 1967. Interactive segregation between fish species. p. 323-331. - In: Gerking S.D. (ed.) *The biological basis of freshwater fish production*. John Wiley, New York.
- Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. p. 294-337. - In: Pitcher T.J. (ed.) *The behaviour of teleost fishes*. Croom Helm London & Sydney.
- Saltveit, S.J. and Å. Brabrand. 1991. Ecology and distribution of minnows, *Phoxinus phoxinus*, in Norway: a literature review. - *Rapp. Lab. Ferskv. Økol. Innlandsfiske* 130: 1-21. (In Norwegian.)
- Schoener, T. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. - *Ecology* 49: 704-726.
- Sokal, R.R. and F.J. Rohlf. 1969. *Biometry*. - W.H. Freeman & Company, San Francisco. 776 p.
- Straskraba, M., J. Chiar, S. Frank and V. Hruska. 1966. Contribution to the problem of food competition among the sculpin, minnow and brown-trout. - *J. Anim. Ecol.* 35: 303-311.
- Swain, D.P. and B.E. Riddell. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. - *Can. J. Fish. Aquat. Sci.* 47: 566-571.

Low Temperature Growth Potential of Arctic Charr and Rainbow Trout

EVA BRÄNNÄS and BO-SÖREN WIKLUND

Swedish University of Agricultural Science Department of Aquaculture, S-901 83 Umeå, SWEDEN

Abstract

The growth potential of farmed Arctic charr (*Salvelinus alpinus* L.) at 3 temperatures (0.3, 5 and 10 °C) was studied. We used a rainbow trout (*Onchorhynchus mykiss*) strain, selected for production as reference. Growth rate of Arctic charr was measured at three additional, extremely low temperatures. The charr had a significant faster weight increase than trout at the two lowest temperatures. At 10 °C the result was reversed with a significant faster weight increase for trout than for charr. The result suggests that the growth potential of farmed salmonids has generally been underestimated in low temperatures. Of the two compared species, Arctic charr is the more northern and consequently seem to have a higher growth potential at temperatures close to zero. Therefore small scale production of charr is feasible also in ice-bound farms, in particular if stratified winter water can be utilized on these locations.

Introduction

Growth data of salmonids in very low temperatures are general lacking. For aquaculture in sub-arctic areas, such information is important. Specially, for a cold water species like the Arctic charr (*Salvelinus alpinus*) that will mainly be reared in northern areas due to a low tolerance for high summer temperatures (Alanära 1990). For farms situated at northern latitudes the winter temperatures range between 0-4 °C for as long as 5-8 months. In practice, feeding are often kept at minimum during this period since no growth is expected.

One of the proposed special qualities of Arctic charr in aquaculture, is a considerable growth capacity also during natural winter conditions (Reinsnes and Wallace 1985). In experimental conditions, growth rates of Arctic charr have been reported equivalent to other salmonids (Jobling 1983). Jobling (1983) described a growth model for Arctic charr with the relationship between temperature, growth rate and initial fish weight. This model serves as a valuable tool when predicting growth rates for a particular stock. However, Jobling's model was based on empirical growth

data for fish kept in temperatures above 2 °C, and when extrapolated to temperatures below this the model predicts no growth in temperatures close to zero. Growth data collected from Swedish Arctic charr farms corresponds in 50% of the cases to the theoretical values predicted by Jobling's model in summer temperatures. Among the remaining farms, the growth rates were lower than predicted. But generally, in lower temperatures, the growth rates were higher than the theoretical values (Alanära 1990). These low temperature growth data were, however, calculated from mean temperatures on the site of the fish farm and may fluctuate between 0.5 -3 °C depending on currents.

This paper deals with the growth potential of Arctic charr in controlled temperatures between 0.3 and 10 °C. Emphasis is made to the lowest temperatures within that range. To evaluate the relative advantage of Arctic charr, a comparison was made with rainbow trout which is the most common species in Swedish aquaculture. The purpose was to contribute with growth data, as well as to suggest utilizing of the growth potential during the long winter which may improve the farm economy.

Material and Methods

Growth data are collected from a series of experiments at the Norrby laboratory, University of Umeå (63°35'N, 19°50'E). The laboratory is supplied with heated 10 °C, as well as naturally tempered brackish water (3 parts per thousand) which is constant 0.3 °C during 4 winter month. In our experiments, desired temperatures were obtained by mixing the cold and heated water. The Arctic charr originated from hatchery reared progeny from a wild caught population of Lake Hornavan, 350 km northwest of Umeå. Hornavan charr have, in comparison with three other Arctic charr populations, the highest growth potential (Wiklund and Eriksson 1986). A selected farming strain (Gloria) of rainbow trout from the national breeding programme was used for comparison. There was no difference in pretreatment of the two species. The experimental tanks were 1 m in diameter and 0.5 m high and the water was exchanged by 8 L min⁻¹. The fish were stocked at densities of 20-30 kg m⁻³. Automatic disc feeders controlled by a microcomputer were used for presentation of food. The feeders ran every 20 min during the light period with the largest portion (40%) at dawn + dusk. All treatment groups were fed "in excess" with dry pellets (EWOS AC 43), approximately 2-3.5% day⁻¹ depending on temperature.

First, growth data in 0.3 °C and 5 °C of charr and trout were collected. Each species was represented by three tanks with 40 individuals, summing up to 6 experimental units. The tanks were exposed to incandescent lighting on a 12-h-L (including 1 hour dawn and 1 hour dusk): 12-h-D cycle periods (L=light, D=dark). The initial mean weights were 161.9g (SD±21.53) and 111.75g (SD±22.75) for the charr and the trout, respectively. Every 2-3 weeks live weight was measured on each fish, starting with 3 sampling occasions in 0.3 °C. The temperature was then increased to 5 °C and the growth rate was measured on the same set of fish twice every 4 weeks.

Secondly, we extended the comparison by including growth data in 10 °C from a different experimental set-up with a photoperiod of 18-h-L: 6-h-D. The issue was originally to determine the effect of long-day compared to short-day (6-h-L:

18-h-D) conditions on growth rate, using the same populations. These comparing growth data are relevant since light regime had no significant effect on growth for neither charr, nor trout. The initial mean weights were 123.5g (SD±14.2) and 92.6g (SD±14.0) for charr and trout, respectively. Here, 80 fishes of the two species were distributed into 2 tanks each. Weight data were then collected twice with a 4 weeks interval. In all other aspects, the experimental set-up and conditions were identical of those described above.

Thirdly, the growth rate of Arctic charr was measured at three temperatures below 5 °C; 0.3, 2.4, and 4.5 °C. Another stock of Hornavan charr was used with a mean weight of 129.3g (SD±54.2). Two groups of 40 fishes were kept at each temperature and weight data were collected at the start of the experiment and after 4 weeks. These tanks were exposed to a incandescent 12-h-D: 12-h-D lightning cycle. including dawn and dusk and other experimental conditions were as described above.

Comparison of growth was done by the following regressionmodel were the hypothesis $\beta_1 = \beta_2$ is tested:

$$y_i = \alpha_1 D_i + \alpha_2 (1 - D_i) + \beta_1 t_i D_i + \beta_2 t_i (1 - D_i) + \epsilon_i,$$

where y = weight (g), α = the point where the regression line crosses the y-axis, β = the slope of the regression line. Here D_i , which is a dummy variable, = 1 (β_1 and α_1) for charr and $D_i=0$ (β_2 and α_2) for trout, t = time (days) and ϵ_i is the random disturbance term. No compensation was made for initial size. The growth rate G (% day⁻¹) was calculated from

$$G = 100(\ln W_i - \ln W_0) / t$$

where W_i = weight at day i , W_0 = weight at day 0, and t = number of days between measurements.

Results

Weight increase of rainbow trout and Arctic charr at 0.3, 5, 10 °C is presented in Fig. 1. The mean weights of the replicates are pooled since no

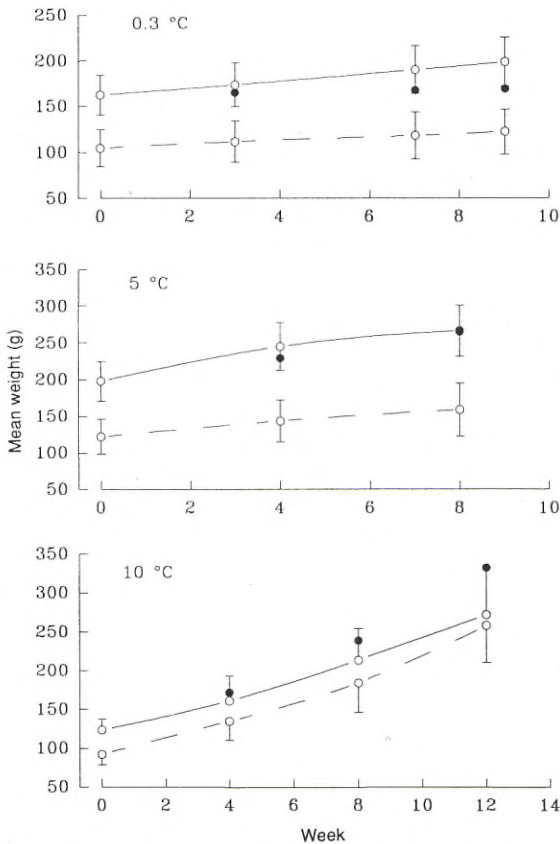


Fig. 1. Mean growth with standard errors (95%) of Arctic charr (solid line) and Rainbow trout (dotted line) in three temperatures. The theoretical growth of Arctic charr (estimated Jobling model) is indicated as filled circles.

significant difference was found (t -test, $P < 0.5$). The growth rate in 0.3 °C of charr was significantly higher than that of trout (0.32 and 0.25 % day⁻¹) (Table 1). During the first four weeks at 5 °C Arctic charr grew faster than trout, while the case was reversed during the second period. Totally, however, charr grew faster than trout at 5 °C (Table 1 and 2). At 10 °C the trout always grew faster than charr (1.26 % day⁻¹ and 0.97% day⁻¹, respectively, Table 1 and 2). For charr, the correspondence between actual and calculated weight according to an estimation from Jobling's model gave the best agreement at 5 °C (Fig 1). Growth rates found in this study were higher than predicted in 0.3 °C and lower in 10 °C.

Table 1. Growth rate (% day⁻¹) for Arctic charr and rainbow trout in three different temperatures.

Weeks	°C	n	Arctic charr	Rainbow trout
0-3	0.3	120	0.30	0.29
3-7	"	"	0.33	0.20
7-9	"	"	0.34	0.26
Total period	"	"	0.32	0.25
0-4	5	120	0.71	0.53
4-8	"	"	0.60	0.72
Total period	"	"	0.67	0.59
0-4	10	80	0.98	1.39
4-8	"	"	1.03	1.15
8-12	"	"	0.89	1.23
Total period	"	"	0.97	1.26

In the third experiment the Arctic charr increased their mean weight by about 15 g in 0.3 °C during 4 weeks and almost 40 g or 80 g in 2.4 and 4.5 °C, respectively (Table 3). Specific growth rates (Fig 2) in these temperatures were much

Table 2. Comparison of growth between Arctic charr₁ and rainbow trout₂ by means of regression analysis where the hypothesis $\beta_1 = \beta_2$ is tested. α = the lines intersection with the y-axis (weight), β = slope of the lines.

Parameter	Temp °C	Value	t
α_1	0.3	161.17	87.40
α_2	"	105.16	57.01
β_1	"	0.54	12.90
β_2	"	0.26	6.06
$r^2 = 0.69 P < 0.001$			
α_1	5	197.09	71.17
α_2	"	121.27	43.61
β_1	"	1.58	17.42
β_2	"	0.81	8.96
$r^2 = 0.74 P < 0.001$			
α_1	10	117.89	33.47
α_2	"	85.71	24.40
β_1	"	1.78	25.92
β_2	"	1.95	28.64
$r^2 = 0.69 P < 0.001$			

Table 3. Mean weight (SD) in two groups of Arctic charr before and after 28 days at three levels of temperatures.

Temp (°C)	Initial (g)	Final weight (g)
0.3	118.8 (56.1)	140.5 (64.5)
	142.0 (57.1)	157.3 (62.8)
2.4	126.4 (53.0)	170.1 (72.7)
	127.7 (55.7)	171.2 (81.0)
4.5	123.1 (54.6)	208.5 (95.5)
	137.5 (57.6)	216.6 (98.1)

higher than predicted from the estimated Jobling's model. The agreement of growth rates between this and the first experiment was best in 0.3 °C. In the first comparative study the growth rate was considerably lower in 5 °C compared to the values found in 4.5 °C.

Discussion

According to this study, Arctic charr have a higher potential for growth in temperatures close to zero, compared to rainbow trout. Of the two species,

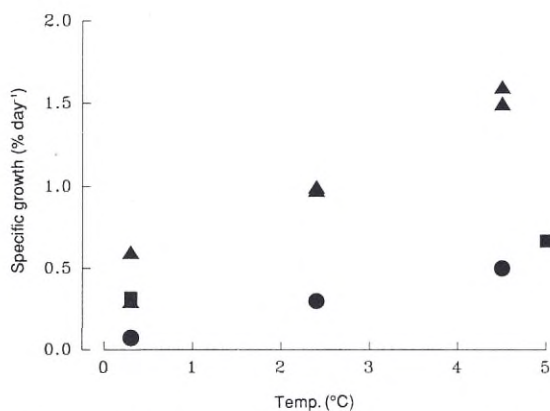


Fig. 2. The found specific growth (% day⁻¹) of Arctic charr during four weeks in three temperatures is defined as filled triangles. The result from figure 1 in 0.3 and 5 °C is included as filled squares. The theoretical growth rate (estimated Jobling model) is indicated as filled circles.

Arctic charr have the most northern distribution with a temperature optimum of 14°C (Swift 1964, Jobling 1983) compared to 16 °C or higher for trout (Hokansson et al. 1977, Austreng et al. 1987). The rainbow trout in this study had a lower initial weight which in this comparison has a positive effect for trout since growth rate decreases with increasing size (Elliot 1975, Jobling 1983). In our calculation we made no correction for higher specific growth rates. The stock of Arctic charr used in our study exhibited a lower growth rate in 10 °C than trout and were lower than predicted by Jobling's growth model for charr and there was also a discrepancy between the two different sets of results from 4.5 and 5 °C. Both in practice rearing (Alanära 1990) as well as in laboratory environment (unpubl. results), the growth rate may vary even if rearing conditions are identical, specially when temperatures exceed 5 °C. Such variations may result from different growth potential of the stocks used although they originated from the same population.

High growth rates were also reported for Atlantic salmon when kept in winter temperatures between 1 and 3 °C (Sutterlin et al. 1981, Saunders et al. 1983). In spite of modest feeding, the caged-reared salmon grew as well as or even better to free-ranging salmon with the same initial size during winter months. Wild salmon are, according to available evidence, found in water warmer than 4 °C during this period of time (Redding 1985). This together with our study gives evidence that farmed salmonids can make use of the abundance of high quality food. In contrast to their free-ranging conspecifics they can utilize the feed without spending much energy to capture it (Saunders 1986). The rainbow trout also showed a considerable growth potential (0.25% in 0.3 °C). This indicates that the winter growth of salmonids in cold environments has generally been underestimated (Saunders et al. 1983). Growth data from low temperatures therefore need to be sampled and existing growth models properly adapted. A considerable production potential can be utilized provided that feeding cost can be kept at the lowest possible level. Therefore, an important task is to gain more information of daily and diel variation

in feeding behaviour, as well as food conversion efficiency at low temperatures. Also, the best biochemical composition of food in low temperatures needs to be tested. Such information should facilitate the salmonid aquaculture industry in subarctic regions.

References

- Alanärä, A. 1990. Evaluation of the growth of Arctic charr in Swedish fishfarms 1985-88. - Swedish University of Agricultural Sciences. Dep. Aquacult. Rep. 6. 20 p. (In Swedish)
- Austreng, E., T. Storebacken and T. Åsgård. 1987. Growth rate estimates for cultured Atlantic salmon and rainbow trout. - *Aquaculture* 60: 157-160.
- Elliot, J.M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. - *J. Anim. Ecol.* 44(3): 805-821.
- Hokanson, K.E.F., C.F. Kleiner and T.W. Thorsland. 1977. Effects of constant temperature and diel fluctuations on growth, mortality, and yield of juvenile rainbow trout. *Salmo gairdneri* (Richardson). - *J. Fish. Res. Board Can.* 34: 639-648.
- Jobling M. 1983. Influence of body weight and temperature on growth rates of Arctic charr, *Salvelinus alpinus* (L.). - *J. Fish Biol.* 22: 471-475.
- Redding, D.G. 1985. Atlantic salmon (*Salmo salar* L.) to the east of the Grand Bank of Newfoundland. - *J. N.W. Atl. Fish. Sci.* 6: 157-164.
- Reinsnes, T. and J.C. Wallace. 1985. Rapport nr. 1 fra sjørøye prospect. Innfisking og settefiskstadiet. - Inst. Fisheries, Univ. Tromsø, Ser. B: Ressursbiol., 2/85. 62 p. (In Norwegian.)
- Saunders, R.L. 1986. The thermal biology of Atlantic salmon: Influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. - *Rep. Inst. Freshw. Res., Drottningholm* 63: 77-91.
- Saunders, R.L., E.B. Henderson, B.D. Glebe and E.J. Loudenslager. 1983. Evidence of a major environmental component in determination of the grilse: larger salmon ratio in Atlantic salmon (*Salmo salar*). - *Aquaculture* 33: 107-118.
- Sutterlin, A.M., E.B. Henderson, S.P. Merrill, R.L. Saunders and A.A. Mackay. 1981. Salmonid rearing trials at Deer Island, New Brunswick, with some projections on economic viability. - *Can. Tech. Rep. Fish. Aquat. Sci.* 1011. 28 p.
- Swift, D.R. 1964. The effect of temperature and oxygen on the growth rate of the Windemere char (*Salvelinus alpinus willughbii*). - *Comp. Biochem. Physiol.* 12: 179-183.
- Wiklund, B.-S. and L.-O. Eriksson. 1986. Individual growth and maturation pattern of four net-pen reared Arctic char populations. - *Rep. Inst. Freshw. Res., Drottningholm* 63. p. 117.

Shelter Selection in YOY Crayfish *Astacus astacus* under Predation Pressure by Dragonfly Larvae

ANDERS JONSSON

Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden

Abstract

Second stage young-of-the-year (YOY) crayfish (*Astacus astacus*) showed a strong preference for using artificial shelters rather than maternal protection in a laboratory experiment. If no alternative shelters were provided, the YOY sought protection under the female. The predatory impact of larvae of the dragonfly *Aeshna grandis* decreased whenever the crayfish young had access to maternal protection and/or access to artificial shelters. However, a change in behaviour of the females led to maternal predation on YOY crayfish without access to artificial shelters. The females started to prey upon their offspring sometime during the period 10 through 18 days after the first moult of the YOY crayfish.

Introduction

To escape predation features such as cryptic coloration, crypsis, Batesian mimicry, aposematism and chemical repellents etc. have evolved (Alcock 1991, Begon et al. 1990). Many species have also developed behaviour patterns that decreases the risk of predation even further (Sih 1987). The property of being able to appreciate quality differences between substrates and shelters is one example. This applies to hermit crabs who can select shells by assessing a number of shell features (Kuris and Brody 1976) such as the shell's internal dimension (Kinosita and Okajima 1968), weight and shape (Conover 1978). Eggleston and Lipcius (1992) proposed for the spiny lobster *Panulirus argus* that social condition and the scaling of lobster size to shelter size jointly regulate the choice patterns. Several authors have demonstrated that juvenile crayfish can choose between a variety of shelters and substrates under different circumstances (Mason 1970a, Stein 1975, Klosterman and Goldman 1983). Stein and Magnuson (1976), and Stein (1977) showed that individuals of *Orconectes propinquus* selected substrates affording most protection in the presence of a predator. Mason (1979) showed that access to shelters is important to reduce mortality caused by predation and cannibalism.

Young-of-the-year (YOY) crayfish, *Astacus astacus*, become mobile after their first moult. Initially these second stage YOY congregate under the mother. Non-ovigerous females eat YOY crayfish whereas ovigerous or brooding females do not (Little 1976, Munkhammar et al. 1989). However, with time the mother's behaviour in certain species changes, and she preys upon her offspring (Little 1976). Burba (1983) found that YOY crayfish seeking shelter preferred to use crayfish exuviae as refuge rather than maternal protection when the exuviae were larger than the females. Blake and Hart (1992) showed for *Pacifastacus leniusculus* that egg bearing females selected substrates rendering suitable shelters for adults but poor protection against predators for YOY crayfish. Thus, the risk is high for YOY crayfish to enter the world in areas where effective shelters are scarce with exception for the mother who is likely to turn into a predator in the near future.

This experiment was initiated to see if second stage YOY *A. astacus* are able to choose between maternal protection and artificial shelters, and, to assess whether the presence of a predator would affect the selection between shelters. Larvae of *Aeshna grandis*, one of the most common and abundant dragonflies in Sweden and which larvae use the same habitat as *A. astacus* (Sahlén 1985) was chosen as predator.

Material and methods

The study was carried out at the Department of Aquaculture, Askö laboratory, northern Gotland (58 °N), Sweden. In early June, egg-carrying *A. astacus* females were collected by scuba-diving from a pond and kept in chilled water (8 °C) in the laboratory since the hatching had to be delayed for two weeks for technical reasons. The *A. grandis* larvae (mean length 39.8±3.8 mm, range 26-45 mm) were collected in mid-July from the same pond and put in a storage basin provided with shelters (bricks, *Chara sp.*, and stones) as well as plants of *Iris sp.* The alkaline water flowed by gravity from the Lake Bästeträsk and the water temperature varied between 18-21 °C during the experiment. The tubes regulating water exchange served as platforms for the emergence for the dragonfly larvae. Aquaria (bottom surface: 40 x 40 cm²; volume 27.3 L; flow rate: 0.21 L min⁻¹; substrate: sand; shelters: one brick with >35 holes, diameter 7mm) were stocked with 25 YOY crayfish one day after their first moult. Since hatching was unsynchronized between broods (July 13-21), the start of the experiments varied between July 22-29. Female crayfish were removed from those aquaria where the brood was to be without maternal protection. The mean weight (g) of females used in treatment "A" was 26.5 ± 6.7, in "B" 25.9 ± 4.0, in control "a" 28.8 ± 12.3, and, in "b" 36.7 ± 9.4. At the start of the experiment one dragonfly larva was added to four of the treatments. These groups are denoted with capital letters whereas groups without predators are named in small letters (controls), e.g., "a" is control to treatment "A". The experimental design is described in Table 1. The number of replicates varied due to the lack of egg-carrying females. This is also the reason why the control to treatment "C" is missing.

The number of surviving YOY crayfish, corpses, and, the number of YOY sitting under female crayfish and in the bricks were counted daily. As counting of the YOY crayfish receiving maternal protection was impossible to carry out without lifting up the females, the bricks were picked up also during observations in order to equalize the experimental treatment.

Table 1. Design of the experiment concerning dragonfly larvae predation on YOY crayfish with or without access to maternal protection (female), and, in the presence or absence of artificial shelters (shelters).

Exp.	No. of YOY	Dragon-fly	Female	Shelters	Number of replicates
A	25	+	+	-	4
B	25	+	+	+	3
C	25	+	-	+	5
D	25	+	-	-	4
a	25*	-	+	-	3
b	25	-	+	+	3
d	25	-	-	-	3

* one aquarium in exp. "a" contained 22 YOY crayfish

The female crayfish were fed daily with different kinds of fish. The cladoceran *Bosmina sp.* and a diet of *Mysis sp.* and oatmeal were given to the juvenile crayfish. The dragonflies were not fed during the experiment.

Dead or emerged Aeshnids were replaced. No *Aeshna* was used in more than one aquarium. The manual handling of the dragonfly larvae, i.e., lifting up from the water, weighing and measuring, before being stocked into the aquaria, did not seem to affect their predatory behaviour negatively. Some larvae killed and began to consume their first YOY crayfish within ten seconds after being put into the aquaria. No signs of damage were ever visible on *Aeshna* larvae that had been used in the test.

Arcsin transformed percentage values for the number of YOY crayfish seeking shelter in the bricks or under the females were used in the statistical analysis. The total mortality from the beginning of the experiment through day 17 was assessed for each aquarium. These values were divided by 17, or, by the number of days it took for the *Aeshna* larvae to kill all the YOY crayfish if this happened prior day 17. Since the control to treatment "C" was missing no multiple ANOVA analysis could be used. To compare the difference in mortality between controls "a" (female only) and "d" (unprotected) the course of the experiment was divided between two periods. The first period was between the test start until day 8, the second between days 9 through 17. One-way ANOVA was used as statistical test unless stated otherwise.

Results

During the first part of the experiment, the YOY crayfish took cover under their mother if no alternative shelters were provided (Fig. 1). When given access to bricks as well as to maternal protection, they showed a very clear preference for using the shelters (Fig. 2). This preference was significant already on the first day in treatment "B" (dragonfly, female, shelter; $P < 0.01$) and in control "b" (female, shelter; $P < 0.01$), pooled groups $P < 0.001$. The presence of dragonfly larvae did not affect the choice of shelter of the YOY *A. astacus* ($P = 0.85$; Figs. 1 and 2). From day 6 and onwards, signifi-

cantly more YOY crayfish used the artificial shelter in treatment "C" (dragonfly, shelter) compared to the number of YOY using maternal protection in treatment "A" (dragonfly, female) (on day 6; $P < 0.01$; Fig 1).

The highest crayfish mortality was recorded in aquaria containing dragonfly larvae and unprotected YOY crayfish. The mortality rate in this group ("D") was significantly higher compared to all other groups ($P < 0.05$, Tukey's multiple-range test; Fig. 3; Table 2). In treatment "D" the mean number of dead YOY crayfish per day was 18.5 ± 7.2 the first day and 2.6 ± 2.7 from the second day to the end of the experiment. In one of the aquaria

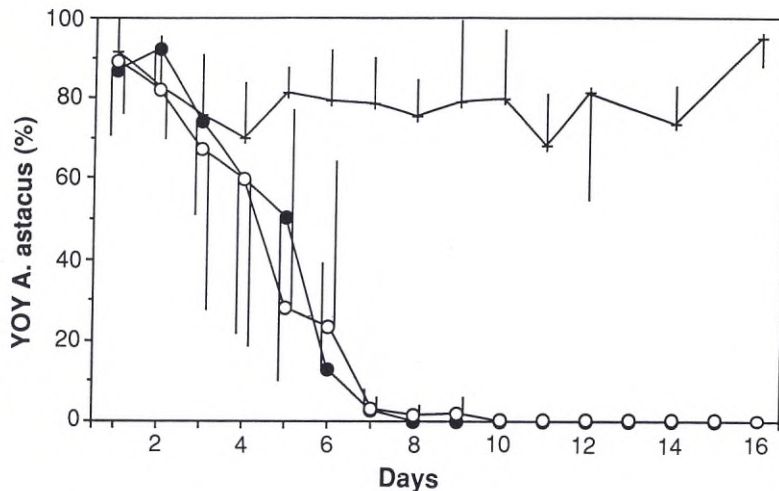


Fig. 1. Percentage (mean + SD) of YOY crayfish in the shelters in the presence of dragonfly larvae (+, treatment "C"), under the females in the presence of dragonfly larvae (●, treatment "A"), and under the females in the absence of dragonfly larvae (○, control "a").

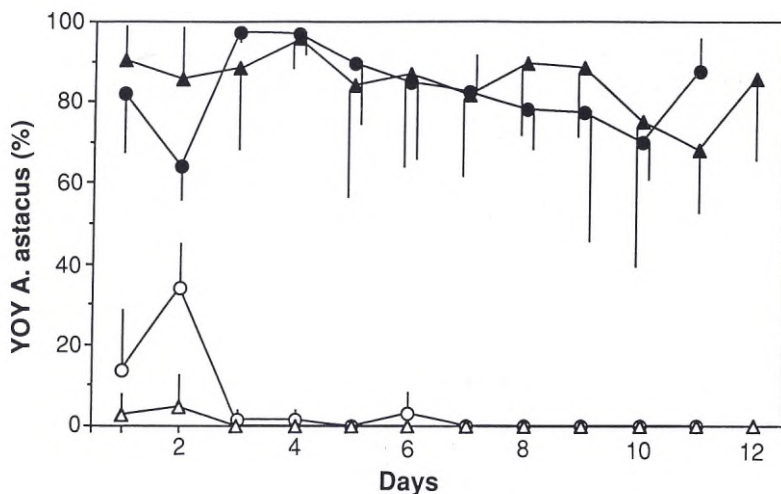


Fig. 2. Selected site of shelter by YOY crayfish (mean \pm SD) with access both to maternal protection and shelters in the presence (treatment "B", ▲ in brick, △ under female) versus in the absence (control "b", ● in brick, ○ under female) of dragonfly larvae.

Table 2. Mean number (\pm SD) of dead YOY crayfish per day after the first moult until day 17 and mean number of *Aeshna* larvae per aquarium used in the different treatments.

	TREATMENTS				CONTROLS		
	"A"	"B"	"C"	"D"	"a"	"b"	"d"
	Dragonfly Female	Dragonfly Female Shelter	Dragonfly Shelter	Dragonfly	Female	Female Shelter	Control
Mortality rates	1.9 \pm 1.2	1.7 \pm 0.9	1.1 \pm 0.7	13.2 \pm 9.1	1.0 \pm 0.7	0.7 \pm 0.5	0.5 \pm 0.4
Mean no. dragonfly /aquarium	1.3	1.7	2.0	1.2	-	-	-
Total mean no. dragonfly/aquarium	1.6 \pm 0.6						

all 25 YOY crayfish were dead within 24 hours, and, fifteen of these had been consumed by the *Aeshna* larvae.

Of the 25 *A. grandis* used in the study 8 (32%) died and 2 (8%) emerged during the course of the experiment. Since both the dead and the emerged

Aeshna larvae stopped foraging several days prior their "departures", treatments "A", "B", "C" and "D" suffered from high variances in mortality data. There was no correlation between size of dragonfly larvae and mortality of unprotected YOY crayfish.

The number of surviving YOY crayfish after 17 days tended to be lower in aquaria with the mother present compared with groups without the presence of a female, however, not significant at the 95% level (Fig. 3). One of the females in control "a" (females only) did not eat anything, i.e., neither fish given to her or YOY crayfish. Excluding this aquarium from the data, the mortality in control "a" where there were females present was signifi-

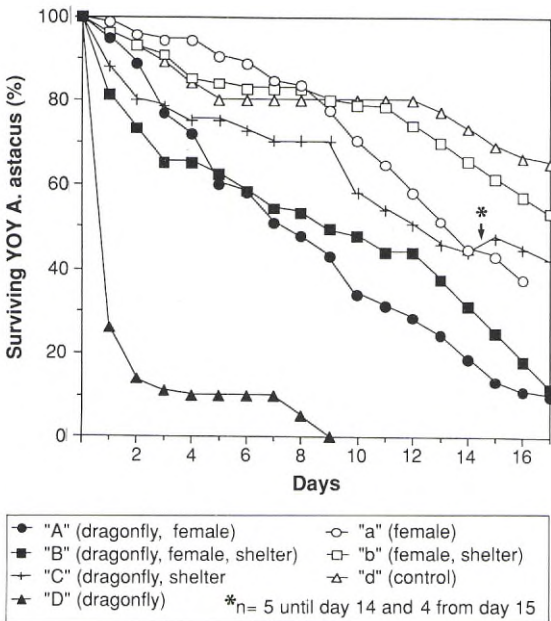


Fig. 3. Percentage of surviving YOY crayfish over time. One aquarium in treatment "C" was excluded as no undamaged replacement to the deceased *Aeshna* larvae was left in the dragonfly storage basin.

Table 3. Mean number of dead YOY crayfish per day (\pm SD) for different periods in control "a" where the YOY were together with their mother, and in control "d" where the YOY were alone and without access to shelters. No dragonfly larva was present in any of these aquaria.

Exp.	Mortality rates during days		P value
	0-8	9-17	
"a"	0.625 \pm 0.53 n=2	2.0 \pm 0.5 \rightarrow n=2	$P < 0.05$
"d"	0.625 \pm 0.54 n=3 \downarrow	0.4 \pm 0.3 \rightarrow n=3 \downarrow	ns
P value	ns	$P < 0.05$	

cantly higher compared to control "d" between days 8 through 17 ($P < 0.05$; Table 3). Including the non-foraging female in control "a" in the analysis, P value was 0.14. The females also consumed corpses of YOY crayfish, *Aeshna* larvae when they had the opportunity, as well as some *Aeshna* fecal pellets. Dead YOY crayfish were not eaten by the *Aeshna* larvae.

Discussion

It is possible that the delayed hatching of the eggs might have affected the behaviour of the female. However, the delayed hatching can be regarded as a simulation of a colder year, or, of a more northern located area. According to Abrahamsson (1972) the time of hatching (July 13-20) is similar to the hatching time in rivers in the middle of Sweden (63°N). Because of the delayed hatching of the eggs, the YOY crayfish may have moulted into their second juvenile stage at a time when some dragonfly larvae in early metamorphosis were no longer foraging. Corbet *et al.* (1960) suggested that the mortality of dragonfly larvae in metamorphosis can be as high as 50%. However, none of the *Aeshna* larvae that died in the experiment proved to be near the moment of emergence.

The strong preference for artificial shelters shown by the YOY crayfish in the presence of females was unexpected. It is possible that the daily disturbance of the females, which reduced contact between the female and her offspring, may have shortened the period of maternal protection. However, it is unlikely that this effect should appear as soon as the first day of the experiment. Even at this point there was a significant difference in the selection of shelters in treatment "B" (dragonfly, female, shelter) and in control "b" (female, shelter) where the young had access to both brick shelters as well as to maternal protection (Fig. 2). In groups where the YOY crayfish had access to maternal protection only, the number of YOY seeking maternal protection was less than 50% on the fifth day and less than 3% after day seven.

In nature ovigerous females hide in excavated dens or under rocks or similar retreats during the brooding period (Mason 1970b). Since there is a

correlation between refuge size and body size of crayfish (Foster 1992) it may be assumed that shelters at the brooding sites are not always suitable in size for YOY crayfish (Blake and Hart 1992).

The lack of suitable shelters for YOY crayfish may be the ultimate explanation for the existence of a brooding attractant but it cannot explain why the young choose a better shelter whenever provided. All movements and behaviour of second stage YOY *A. astacus* are believed to be innate (Cukerzis 1986). If there exists genetic variation in response to a brooding attractant versus artificial shelters, the adaptive shelter-selective behaviour in YOY crayfish can be selected for. If survival in YOY crayfish that hide in suitable shelters is higher than in YOY that have maternal protection, the positive response to the brooding attractant of female crayfish might be selected against in populations where suitable shelters for YOY crayfish are available. Another condition that might select against the response to the brooding attractant is the transformation of the protective mother into a predator. YOY crayfish responding most strongly to the attractant would then be the closest to the female when she loses her reluctance to eat YOY crayfish. If suitable shelters are available, YOY crayfish that cease to have a preference for the brooding attractant when the change in female occurs will be selected for.

It seems that the YOY *A. astacus* did not recognize dragonfly larvae as potential predators as they did not seek shelter more actively in the presence of *Aeshna* larvae. Stein (1977), and Stein and Magnuson (1976) concluded the opposite, i.e., that the presence of a fish predator made crayfish select substrates affording most protection. Unprotected YOY crayfish did not escape the predacious *Aeshna* larvae. It is possible that the average mortality in treatment "D" (dragonfly only) would have been even higher if the predation rate had not been reduced as a direct function of the decrease in abundance of the YOY crayfish. Several observations were made in which YOY crayfish escaped the attacks of *Aeshna* larvae. Injuries on such occasions may have led to death, which may explain some of the corpses that were scattered in the aquaria and rejected as food by the Aeshnids.

The significant difference in mortality between controls "a" (females only) and "d" (unprotected) between days 9 through 17 indicates that maternal predation exists in the crayfish *A. astacus*. However, because of the artificial circumstances typical of laboratory experiments and of the small number of replicates it is difficult to determine when this change in behaviour of the females occurred.

The results of this study indicate that second stage YOY prefer using artificial shelters rather than maternal protection and that access to suitable shelters as well as maternal protection is important in reducing predation on YOY *A. astacus*. The YOY crayfish did not display any greater urge to seek shelter if there was an *Aeshna* larva present. The results also suggest that maternal predation exists in the crayfish *A. astacus*.

Acknowledgment

I thank Professor Hans Ackefors, Dr. Magnus Appelberg and Mr. Russell James for critically reviewing the manuscript. I am also indebted to Mr. Peter Westin and Dr. Lars Westin for their practical assistance at the Ar laboratory. Parts of the study were financed by the A.E.W. Smitts fund, as well as by grants from the Swedish Royal Academy of Science (Hierta-Retzius' fund for scientific research).

References

- Abrahamsson, S.A.A. 1972. Fecundity and growth of some populations of *Astacus astacus* Linné in Sweden. - Rep. Inst. Freshw. Res., Drottningholm. 52: 23-37.
- Alcock, J. 1991. Animal behavior: an evolutionary approach. - Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts. p 596.
- Begon, M., J.L. Harper and C.R. Townsend. 1990. Ecology: individuals, populations and communities. - Blackwell Scientific Publications, Oxford. p 945.
- Blake, M.A. and P.J.B. Hart. 1992. Habitat preferences and survival of juvenile signal crayfish (*Pacifastacus leniusculus*) - the influence of water depth, substratum and predatory fish. - Oral presentation at the 9th symposium for Astacology April 5-10, Reading University, UK.
- Burba, A. 1983. Chemical regulation in crayfish behaviour during post embryonic development, p. 451-458. - In: Goldman C. R. (ed.) Freshwater Crayfish 5. Davis, California.
- Conover, M.R. 1978. The importance of various shell characteristics to the shell selection behaviour of hermit crabs. - J. Exp. Mar. Biol. Ecol. 32: 131-142.
- Corbet, P.S., C. Longfield and N.W. Moore. 1960. Dragonflies. - New Nat. 41, p 260.
- Cukerzis, J.M. 1986. Behaviour of crayfish juveniles during early stages of ontogenesis. p. 75-86. -In: Brink P.(ed.) Freshwater Crayfish 6. Lund, Sweden.
- Eggleston, D.B. and R.N. Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. - Ecology 73(3): 992-1011.
- Foster, J. 1992. The relationship between refuge size and body size in the crayfish *Austropotamobius pallipes* (Lereboullet). Poster presentation at the 9th symposium for Astacology April 5-10, Reading University, UK.
- Klosterman, B.J. and C.R. Goldman. 1983. Substrate selection of the crayfish *Pacifastacus leniusculus*. p. 254-267. - In: Goldman C.R. ed.) Freshwater Crayfish 5. Davis, California.
- Kinosita, H. and A. Okajima. 1968. Analysis of shell searching behavior of the land hermit crab, *Coenobita rugosus*. - J. Fac. Sci. Tokyo 11: 293-358.
- Kuris, A. and M.S. Brody. 1976. Use of principal component analysis to describe the snail shell resource for hermit crabs. - J. Exp. Mar. Biol. Ecol. 22: 69-77.
- Little, E.E. 1976. Ontogeny of maternal behavior and brood pheromone in crayfish. - J. Comp. Physiol. 112 (2): 133-142.
- Mason, J.C. 1970a. Maternal-offspring behaviour of the crayfish *Pacifastacus trowbridgii* (Stimpson). - Am. Midl. Nat. 84: 463-473.
- Mason, J.C. 1970b. Egg-laying in the western North American crayfish, *Pacifastacus trowbridgii* (Stimpson) (Decapoda, Astacidae). - Crustaceana 19: 37-44.
- Mason, J.C. 1979. Effects of temperature, photoperiod, substrate, and shelter on survival, growth, and biomass accumulation of juvenile *Pacifastacus leniusculus* in culture. p. 73-82. - In: Laurent P.J. (ed.) Freshwater Crayfish 4. Thonon-les-Bains, France.
- Munkhammar, M., R. Gydemo, L. Westin and H. Ackefors. 1989. Survival of noble crayfish (*Astacus astacus* L.) larvae alone and in the presence of females. - Aquaculture 409-414.
- Sahlén, G. 1985. Sveriges trollsländor (Odonata). Fältbiologerna, 151 p. (In Swedish.)
- Sih, A. 1987. Predators and prey life-styles: an evolutionary and ecological overview. p. 203-224. - In: Kerfoot W.C. and A. Sih (eds.) Predation: direct and indirect impacts on aquatic communities. University Press of New England.
- Stein, R.A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. - Ecology 58: 1237-1253.
- Stein, R.A. and J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. - Ecology 57: 751-761.

NOTES AND COMMENTS

Effects of Different Preservation Methods on Total Length and Weight of Larval Vendace (*Coregonus albula* (L.))

JUHA KARJALAINEN

University of Joensuu, Karelian Institute, Saimaa Research, P.O. Box 111, SF-80101 Joensuu, Finland

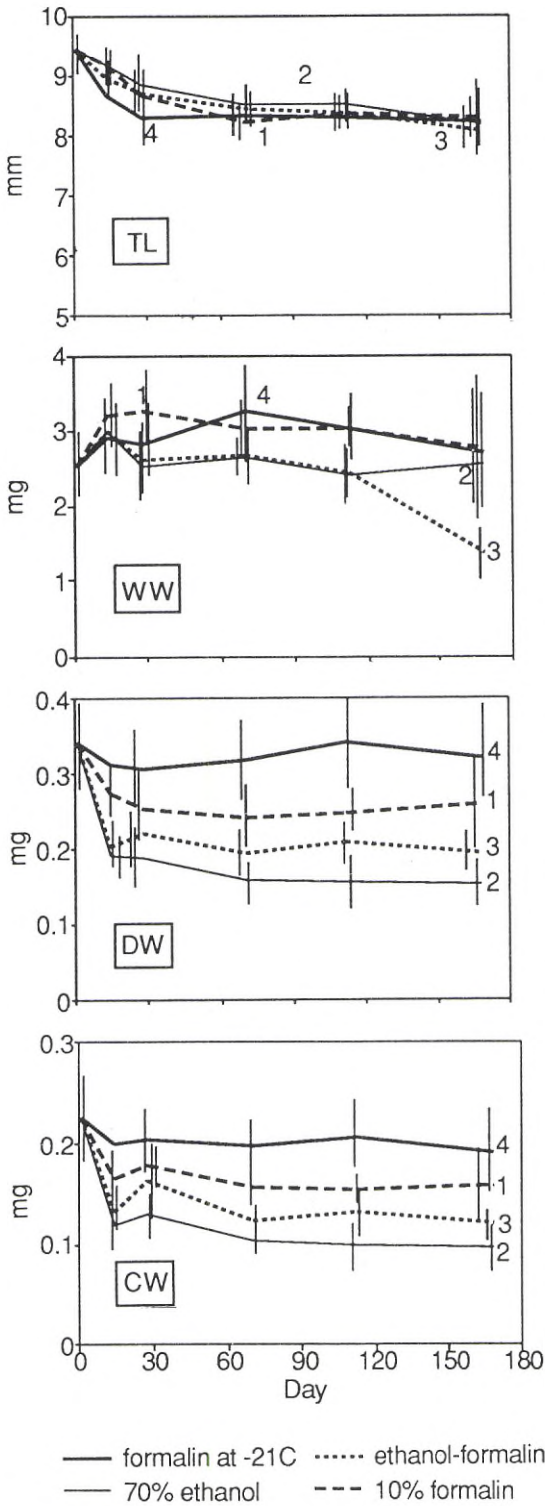
In numerous studies a considerable length reduction or change in biomass of different organisms has been demonstrated during preservation (Schnack and Rosenthal 1978, Hay 1981, Dabrowski and Bardega 1982, Geffen 1982, Salonen and Sarvala 1980, 1985). All kinds of preservation methods (alcohols, formalin, freezing) affect the dimensions and biomass of animals. Due to preservation, biomass estimates, especially dry and carbon weight, could decrease up to 50-60% of the values for live freshwater invertebrates (Salonen and Sarvala 1985). Body shrinkage is dependent on the size of larvae, and death itself may be the cause of shrinkage (Radtke 1989). The effects of different fixation methods on body shrinkage of fish larvae have been studied frequently, but studies of the change in biomass of larvae during preservation are rare.

Length of fish larvae is routinely measured to estimate their age, growth, condition and mortality (e.g. Rice et al. 1987). Biomass estimates are used in growth and food consumption studies as well as for constructing energy budgets of fish. Due to different fixation methods and duration of storage, comparisons between different studies can be considerably biased. In this experiment, the effects of four different preservatives on total length, wet weight, dry weight and carbon weight of vendace larvae (*Coregonus albula* (L.)) were compared during 6 months storage. The average change in length and weight were calculated to correct length and weight values of preserved larvae to that of fresh larvae.

The newly hatched vendace larvae were reared in cylindrical, plastic tanks (13-L), for two weeks. The larvae were fed on live zooplankton at 12 °C. The 8-10 mm long larvae were randomly divided into five groups. The larvae in the first group (0) were anaesthetized with MS 222 and total length ($TL \pm 0.1$ mm), wet weight ($WW \pm 0.1$ mg), dry weight ($DW \pm 0.01$ mg) and carbon weight ($CW \pm 0.01$ mg) were measured (Day 0). After anaesthetizing larvae were preserved in four different preservatives: (1) 10% formalin neutralized with hexametylenetetramin (4% formaldehyde), (2) 70% ethanol, (3) a solution of 70% ethanol and 1% neutralized formalin (1:1) and (4) freezing in 10% neutralized formalin at -21 °C (Salonen and Sarvala 1980, 1985).

The samples in preservatives 1, 2 and 3 were stored at room temperature for 14, 28, 70, 112 or 168 days. Before measuring total length and wet weight, the larvae were carefully flushed and kept in distilled water for 15 minutes. Dry weight was measured after drying for 24 h at +60 °C in pre-burned aluminium foil cups. Immediately after the measurement of dry weight, carbon weight was determined by high temperature combustion (Salonen 1979).

All preservatives caused a significant reduction of the vendace larvae length (ANOVA $p < 0.001$). The reduction of the larvae lengths were correlated to the duration of the storage (Fig. 1). After 28 days, total length remained nearly stable. Dabrowski and Bardega (1982) showed that maximal reduction of body length of vendace larvae was



reached 40 days after preserving in formalin. The average reduction in length of larvae preserved in formalin was 11.0% (range 2.5-12.7%), in ethanol 9.6% (2.5-14.9%), in a mixture of ethanol and formalin 10.9% (5-15%) and in formalin at -21 °C 12.1% (11.7-12.6%) (Fig. 1). The mean values were calculated for the period from 28th day to 168th day of the storage. The average length reduction of formalin preserved vendace larvae was very similar to that found by Dabrowski and Bardega (1982) for vendace larvae and by Schnack and Rosenthal (1978) for herring larvae.

Preservation in formalin increased the wet weight of the larvae. Wet weight of preserved larvae was significantly higher than for fresh larvae (ANOVA $p < 0.001$). The average increase of wet weight was 21.5% in 10% formalin and 17.0% in 10% formalin at -21 °C (Fig. 1). The best preservatives for wet weight samples were ethanol and ethanol-formalin. The difference between fresh and preserved larvae was -4.0% in ethanol and -2.0% in ethanol-formalin. The mean value of ethanol-formalin was calculated for the period from 28th to 112th day of storage. The advantage of a mixture of ethanol and formalin was that the larvae kept straight. The larvae preserved in ethanol bended during the storage, which made them more difficult to handle. However, ethanol-formalin solution was too dilute for a long period of storage. After 16 weeks the wet weight of the larvae was considerably reduced.

All preservation methods, except freezing in 10% formalin, caused significant decreases of dry and carbon weight of larvae compared to fresh fish ($p < 0.001$). The major change occurred within 2

Fig. 1. Changes in total length (TL mm), wet weight (WW mg), dry weight (DW mg) and carbon weight (CW mg) of vendace larvae preserved in (1) 10% neutralized formalin, (2) 70% ethanol, (3) a mixture of 70% ethanol and 1% neutralized formalin and (4) freezing in 10% neutralized formalin at -21 °C. Vertical lines represent standard deviation (SD). At the beginning of the experiment 10 to 29 live larvae and after preserving 9 to 15 larvae preserved in each preservatives were measured.

weeks after the fixation (Fig. 1). This period could be shorter, probably only some days (Salonen and Sarvala 1980). After two weeks the change was insignificant. The dry weight and carbon weight of the larvae preserved in 10% formalin at -21 °C was similar to that of fresh fish; the average decrease in dry and carbon weight was 6.0% and 11.1%, respectively. The average reduction of the dry weight of larvae preserved in formalin was 25.7%, in ethanol 50.5% and in a mixture of ethanol and formalin 40.4%. Similarly, the loss of carbon was 28.1%, 51.2% and 40.4% in formalin, in ethanol and in a solution of ethanol and formalin, respectively.

All preservation methods changed total length and biomass estimates of the preserved larvae as compared with the values of fresh larvae. The effects of all preservatives on total length were at the same level. The biomass estimates were influenced more by the fixation. Formalin preservation increased wet weight of the larvae. After flushing with distilled water, wet weight of the larvae preserved in ethanol or in a solution of ethanol and formalin was similar to that of fresh larvae. Freezing in formalin is a suitable method for preserving dry or carbon weight samples. As discussed by Salonen and Sarvala (1985) the loss of carbon in aldehyde preservation is partly counter balanced by an increase due to aldehyde carbon, and freezing seems to reduce the loss of body carbon. After an initial change of the total length or weight of vendace larvae, the increase or decrease was near-

ly stable in all preservatives. Thus, it was possible to correct the values for preserved larvae to those of fresh larvae.

References

- Dabrowski, K. and R. Bardega. 1982. The changes of fish larvae dimensions due to fixation in different preservatives. - *Zool. Jb. Anat.* 108: 509-516.
- Geffen, A.J. 1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. - *Mar. Biol.* 71: 317-326.
- Hay, D.E. 1981. Effects of capture and fixation on gut content-sand body size of Pacific herring. - *Rapp. Cons. Int. Explor. Mer.* 178: 395-400.
- Radtke, R.L. 1989. Larval fish age, growth, and body shrinkage: information available from otoliths. - *Can. J. Fish. Aquat. Sci.* 46: 1884-1894.
- Rice, J.A., L.B. Crowder and M.E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. - *Trans. Amer. Fish. Soc.* 116: 703-718.
- Salonen, K. 1979. A versatile method for rapid and accurate determination of carbon by high temperature combustion. - *Limnol. Oceanogr.* 24: 177-183.
- Salonen, K. and J. Sarvala. 1980. The effect of different preservation methods on the carbon content of *Megacyclops gigas*. - *Hydrobiol.* 72: 281-285.
- Salonen, K. and J. Sarvala. 1985. Combination of freezing and aldehyde fixation, a superior preservation method for biomass determination of aquatic invertebrates. - *Arch. Hydrobiol.* 103: 217-230.
- Schnack, D. and H. Rosenthal. 1978. Shrinkage of Pacific herring larvae due to formalin fixation and preservation. - *Meeresforschung* 26: 222-226.

Research on Biochemical Genetics of Salmonids - A Review of Contributions from the former Soviet Union

TIIT PAAVER (Ed.)

Academy of Sciences of Estonia, Vanemuise St. 21, 202400 Tartu, Estonia

Introduction

The former Soviet Union has large fish resources which have always had an important place in the Soviet economy. There has been a continuous interest in the population biology of fishes from both the theoretical and applied points of view. The problem of distinguishing isolated populations and revealing intraspecies structure has been central to research projects of several institutes of academic and applied sciences.

Rather simple and cheap techniques of protein electrophoresis were quickly applied in these studies by more advanced laboratories. However, in contrast to western science PAAG, not starch electrophoresis, became the main tool of this research. Hydrolyzed starch was not produced in the USSR or eastern block countries. The Hungarian Company "Reanal" supplied the Soviet Union with kits of chemicals for polyacrylamide gel electrophoresis. Attempts to prepare starch for electrophoresis in home conditions did not give a stable quality product and so from the beginning of the 1970s all studies on fish biochemical genetics in the Soviet Union were based on PAAG electrophoresis. Since then numerous scientists have collected a large quantity of information about the genetics of salmonids and have achieved significant success in understanding their population genetics.

Research on biochemical genetics of salmonids has been concentrated at the central institutes situated in large cities such as Moscow, or in the institutes of scientific centers on the Pacific coast, Vladivostok and Magadan, and Petropavlovsk on Kamtschatka. The main objects of these studies have been the valuable, commercially important Pacific salmon species - pink, chum and sockeye salmon. They have proven to be extremely

interesting subjects for serious theoretical investigations of the evolutionary processes and factors determining population structure. Simultaneously, the urgent need to reveal their population structure in order to improve the management of salmon stocks has resulted in the financial support of these studies. An excellent review of all genetic research carried out on Pacific salmon has been published by prof. V.S. Kirpitschnikov (1990). Unfortunately this Russian publication is not available for western scientists. The research on other groups of salmonids has been sparse with only a few scientists working on them.

Priority in the studies of genetics of salmonids belongs to a group of scientists from Vladivostok headed by Y. Altukhov. They started with the analysis of genetic variability of polymorphic proteins from Pacific Salmon and used these as markers to distinguish populations, to study the population structure of chum and pink salmon and to estimate the effect of transplantations of eggs and fry between rivers. These investigations were continued at the Institute of General Genetics later on when dr. Altukhov and some other members of the group moved to Moscow. One of the most discussed developments of this group has been the concept of fluctuating stocks of pink salmon. The investigations of population structure and dynamics of allele frequencies of sockeye salmon was initiated by prof. V. Kirpitschnikov at the Institute of Cytology in St. Petersburg to reveal the roles of different evolutionary factors, primarily selective forces and genetic drift. These studies included biochemical analyses of isoenzyme activity and attempted to estimate the fitness of different genotypes in experimental and natural conditions. The most extensive studies of biochemical genetics of salmonids of the Pacific region were initiated by group of geneticists from the Institute of Biologi-

cal Problems of Northern Territories (Magadan) headed by R. Viktorovsky. This included not only pacific salmon, but also charrs and coregonids. Research on biochemical genetics of coregonids was also carried out in St. Petersburg, Institute of Lake and River Fisheries Research by A. Lokshina 1979-87. Besides the estimates of genetic variability and systematic relationships, the data on biochemical genetics were used in selective breeding of *Coregonus peled* (project leader M. Andriasheva). Population structure of Atlantic salmon has been studied by V. Slynko and S. Semyonova from the Institute of General Genetics and S. Titov from the Institute of Lake and River Fisheries Research. The main goal of these authors has been to reveal genetic substructuring of the species in north-west of Soviet Union. A. Osinov (Moscow University) has studied systematics and evolution of several salmonid species concentrating mainly on the intraspecies systematics of brown trout *Salmo trutta*. From the very beginning of application of biochemical methods into fish genetics in Soviet Union besides protein electrophoresis some attention has been paid to DNA studies. B. Mednikov

was pioneer in these studies followed by some people in recent years.

Almost all of the results of these authors have been published only in Russian (except a few abstracts or proceedings of international conference papers). Yet some of the most important Russian scientific journals (Genetics; J. of Ichthyology) are translated into English and are available in western countries. We should like to encourage our colleagues to use this information. However, far from all the data is published in these journals. We have compiled this overview of activities of Soviet scientists in salmonid genetics to give people in this field of research all over the world a chance to exchange information.

The review articles were written by the authors themselves, our task as editors was to collect and revise the papers, to translate from Russian to English in certain cases and to make them look more or less uniform. Unfortunately some of the important results are still missing (e.g. most of the groups of R. Viktorovsky and V. Kirpitschnikov, S. Titov and A. Lokshina). But list of references in the end of this review can also give some overview of the results of these groups.

Studies of Mitochondrial and Repetitive Nuclear DNA in Salmonid Fish

L.K. GINATULINA and A.A. GINATULIN

Institute of Biology and Pedology, Far East Division of the Russian Academy of Sciences, 690022 Vladivostok, Russia

The mtDNA heterogeneity was tested in 6 populations from Primorye at intervals of 150-300 km (along the coastal line) and in 4 populations from Sakhalin along the south-west and south-east coasts. Samples from different generations were studied in several populations.

The polymorphic cleavage patterns of chum salmon *Oncorhynchus keta* mtDNA were produced by 4 endonucleases (XbaI, EcoRI, BamHI,

Eco 81I) from the 21 endonucleases tested. The latter pair turned out to be the most informative for conducting the intra- and interpopulational studies. With BamHI and Eco 81I, eight clonal lines of the mitochondrial genotypes were found in *O. keta*.

Recently we have found 5 other endonucleases (VapI, Eco91I, CfrI, Cfr10I, Eco147I) which reveal the *O. keta* mtDNA polymorphism.

The main results of the studies of mtDNA from chum Salmon can be summarized as follows:

1. The genetic structure of 3 natural populations of the south, middle and north regions of Primorye is stable in time. However, frequencies of clones in samples from 3 generations differed greatly in the population from south-east Sakhalin (Naiba River) which for some years was replenished at the cost of artificial reproduction, accompanied repeatedly by the delivery of fish eggs from the other regions.

2. The hatchery populations of the south-west Sakhalin are characterized by an absolute uniformity of the genetic composition whereas genetic variability is higher in the population from the south-east. On the whole the South Sakhalin stocks of *O. keta* which are artificially reproduced look less heterogeneous than the natural stocks of Primorye. They differ qualitatively from Primorye stocks in the absence of one of the mtDNA cleavage patterns revealed by the Eco81I which is common to all the Primorye populations studied.

3. Primorye populations appear to be well differentiated genetically. Even using only two "polymorphic" endonucleases we succeeded in establishing 4 variants in genetic structure which differed in the number of clones and their proportion in the populations.

4. The geographical distribution of the frequencies of the polymorphic mtDNA variants and the clonal lines from south to north on the coast of Primorye has the clinal U-shaped dependence upon the distance between populations.

In addition to tissues from the adult fishes the use of materials from fry which can be kept alive for more than 20 days are needed for large scale geographic analysis, due to difficulties with the transportation of samples from remote areas to the laboratory.

A search has been carried out for restriction endonucleases which can split off fragments of a discrete length from repetitive nuclear DNA. These fragments are revealed as electrophoretic bands after under going fluorescent staining. With the help of these fragments the specificity of the struc-

ture of one or another genome could be estimated.

Although numerous endonucleases were tested on the salmon DNA, only 11 satisfy these requirements. Interspecific analysis of DNA from 6 *Oncorhynchus* and 2 *Salvelinus* species was performed using endonuclease Pvu II. The set of Pvu II-fragments of *O. keta* DNA included 13 fragments from 370 to 3800 base pairs (bp) in length. In similar length fragments from other species the sets also contained fragments which displayed themselves as genus and species-specific. For instance, the fragment 570 bp typical of all *Oncorhynchus* was not observed in *Salvelinus*. The amount of DNA in fragments varies greatly from species to species. The fragment 2340bp long is absent from *O. keta*, but it is quantitatively well represented in *O. gorbuscha*, - 4% of the total genome. In *O. nerka* it forms 1%, in *O. masu*, *Salvelinus malma* and *S. leucomaenis* - 0.1%, whereas in *O. kisutsch* and *O. tshawytscha* this fragment is revealed only after hybridization with the radioactive probe.

The radioactive probe was prepared from PvuII-fragment 370 bp of *O. keta* DNA cloned in pUC 19-*E. coli* JM106 system. Salmon DNA was digested with PvuII, electrophoresed, transferred to a filter and hybridized with a labelled probe. Fluorescent analysis showed the genus and species-specificity in distribution of PvuII-repetitions. At the same time comparison of the hybridization and fluorescent bands confirms the presence of some repetitive families cut off by PvuII in salmon genomes.

The total content of the DNA stretches which are homologous to the probe was estimated by dot hybridization. The total DNA from all the species mentioned as well as the DNA of the related taxa *Osmerus mordax* and *Clupea pallasii* were applied on to the filter in this case. It was shown that genome stretches homologous to the cloned repeats of DNA from *O. keta* were specific only for Salmonidae and they varied in quantity from species to species. Preliminary results also revealed double differences in the level of hybridization with DNA from *O. keta* from Kamchatka and South Primorye.

Biochemical Polymorphism, Population-Genetic Structure, Speciation and Phylogenetical Relationships between Fishes of Subfamily Salmonidae

ALEXANDER G. OSINOV

Department of Ichthyology, Faculty of Biology, M.V.Lomonossov, Moscow State University,
119899 Moscow, Russia
phone: 939-13-33

In most cases the level of genetic variability was estimated on the basis of 29-35 enzyme loci. In spite of significant interpopulation differences in the level of genetic variability within a species. Species (forms) with high (*Salmo trutta*, *S. gairdneri*/*Oncorhynchus mykiss*, sharp-snouted form of *Brachymystax lenok*), intermediate (*Salmo salar*, *Hucho taimen*) and low (*Salmo ischchan*, blunt-snouted form of *B. lenok*, *Parahucho perryi*) levels of average heterozygosity could be distinguished. In some cases the low level of genetic variation results from the specific history of the population (founder, or more probably, bottleneck effect). Such events probably took place during different periods in the genesis of Sevan trout, *S. ischchan* (Osinov, 1989a, 1990a), trouts, *S. trutta*, from the Vahsh and the Kafirnigan river basins (Tadjikistan, USSR) (Osinov, 1990b), *P. perryi* (Osinov, 1991) and blunt-snouted form of lenok (Osinov et al., 1990).

Electrophoretic data confirm that in regions of sympatry the two forms of lenok are genetically isolated, though restricted gene flow obviously takes place. The low levels of average heterozygosity ($H=0.000-0.002$) and genetic differentiation ($D=0.000$ between all forms) in Sevan trout indicates a recent bottleneck, which took place before the beginning of their ecological differentiation (Osinov, 1989a, 1990a). Based on data of genetic differentiation of brown trout and lenok populations from different parts of their distribution range, the hypothesis of their genesis and dispersal is discussed (Osinov, 1984, 1988, 1990b, Osinov et al., 1990). There are species with different levels of genetic divergence in the genus *Salmo* (*S. ischchan*-*S. trutta*, $D=0.008-0.041$; *S.*

trutta-*S. salar*, $D=0.333-0.375$), but they form only two species groups, or subgenera (according to Vladykov, 1963). All representatives of the Atlantic group (*S. trutta*, *S. salar*, *S. ischchan*) have similar level of genetic divergence from the representative of *Parasalmo* - *S. gairdneri*/*O. mykiss* ($D=0.856-1.066$) (Osinov, 1989b).

From a phylogenetic point of view the genetic similarity ($D=0.335-0.107$) of Siberian taimen and lenok and the considerable genetic divergence by both of them from Sakhalin taimen ($D=0.755-0.179$ and $0.891-0.203$ accordingly), it can be presumed that Sakhalin taimen could be turn out to be the separate genus *Parahucho* (Osinov, 1991).

At the present time we are carrying out the investigation of the evolutionary relationships between species in the genera *Salvelinus* and *Oncorhynchus* and the phylogenetic relationships of Salmoninae species as a whole. In collaboration with researchers from the Limnological Institute of the Siberian Branch of the Russian Academy of the Sciences we are studying the population-genetics structure of *Coregonus* species of Lake Baikal.

Main publications (all in Russian)

- Osinov, A.G. 1984. Zoogeographical origins of brown trout, *Salmo trutta* (Salmonidae): data from biochemical genetic markers. - *J. Ichthyol.* 24(1): 11-24.
- Osinov, A.G. 1988. Brown trout *Salmo trutta* (Salmonidae) of Black and Caspian sea basins: population-genetic analysis. - *Genetica (USSR)* 24(12): 2172-2186.
- Osinov, A.G. 1989a. The low level of genetic variability and differentiation of ecological forms of Sevan trout *Salmo isohchan* Kessler. - *Genetica (USSR)* 25(10): 1827-1835.

- Osinov, A.G. 1989b. Genetic divergence between species and some phylogenetical problems in the genus *Salmo*. p. 97-107. - In: Kirpichnikov, V.S (ed.) Genetics in aquaculture. St. Petersburg, Nauka.
- Osinov, A.G. 1990a. On the origin of the Sevan trout *Salmo ischchan* Kessler: population-genetic approach. - J. General Biology 51(6): 817-827.
- Osinov, A.G. 1990b. Genetic variability and differentiation of brown trout (*Salmo trutta* L.) populations of Tadjickistan. - Proc. Moscow Univ. Ser. 16., Biol. (1): 37-41.
- Osinov, A.G. 1991. Genetic divergence and phylogenetical relationships between lenoks of genus *Brachymystax* and huchens of genera *Hucho* and *Parahucho*. - J. Ichthyol. 31(3). (In press.)
- Osinov, A.G., I.I. Ilyin, S.S. Alexeev. 1990. Forms of lenoks (*Brachymystax*, Salmoniformes, Salmonidae) in the light of population-genetic analysis. - J. Zool. 69(8): 76-90.

Comparative Biochemical Genetics of Species within Coregonidae, Salmonidae and Thymallidae

LUIDMILA N. ERMOLENKO

Institute of Biological Problems of the North, Russian Academy of Sciences, Far East Division,
K.Marx Str. 24, 685010 Magadan, Russia
phone 29724

1. Population genetics of coregonid fishes from the river basins of North-East Asia: Samples from populations of 11 species of the Coregonidae family from the Yenisei, Chaun, Anadyr, Amur and Uda rivers were studied by electrophoresis. The genetic variability in this taxonomic group was estimated (P-99% criterion varied between 4% and 48%, H-0.2% and 11%). Genetic distances (D) between 9 species of the genus *Coregonus* ranged from 0.01 to 0.33. *C. lavaretus pidschian*, *C. muksum* and *C. ussuriensis* constitute a closely related group within the genus *Coregonus*. Four genetically distinct species (*C. tugun*, *C. autumnalis*, *C. peled*, *C. nasus*) were evident. This is perhaps connected to an earlier origin of the specified ciscoes as independent species.

Interpopulation genetic differences of *C. lavaretus pidschian*, *C. sardinella* and *C. nasus* from the Yenisei, Chaun and Anadyr rivers were analyzed. Peculiarities of allele frequency distributions allow one to predict the method and succession of coregonids in river systems of North-East Asia.

2. Comparative electrophoretic analysis of biochemical loci within the families Coregonidae, Salmonidae and Thymallidae including 23 species from 10 genera have been studied (*Coregonus*, *Stenodus*, *Prosopium*, *Oncorhynchus*, *Salmo*, *Parasalmo*, *Salvelinus*, *Hucho*, *Brachymystax* and *Thymallus*). On the basis of the collected data, the evolutionary stability of some biochemical loci was estimated. Polymorphic loci, which have not differentiated during evolution of studied taxonomic groups, were described.

Genetic variability of *Hucho taimen* and *Brachymystax lenok* (two forms) from the Uda river was examined. These phylogenetically related genera also exhibit close genetic relationship.

3. Population genetics of pacific salmon of North-East Asia: Population genetic studies of pacific salmon are continuing. The present objects of study are chum salmon (*Oncorhynchus keta*) from the river basins of Kamchatka

Genetic Variability and Differentiation in Salmonid Fish

YURI KARTAVTSEV

Institute of Marine Biology Far East Science Center, Russian Academy of Sciences
690022 Vladivostok 690022, Russia

1. Population genetic structure, allozyme and morphological variability in some commercially valuable marine invertebrates and salmonid fish were investigated. The results obtained, allow insight into the stock problems for those species and permit interpretation of the micro spatial allozyme heterogeneity in terms of natural selection (Kartavtsev, 1979, Kartavtsev et al., 1985, Kartavtsev, 1986). It was shown that under certain conditions the allozyme heterozygosity influences morphological homeostasis (Kartavtsev, 1989, 1990).

2. Literature data and our own results (Kartavtsev et al., 1983, Kartavtsev and Mamontov, 1983) on genetic differentiation measured in genetic distance scale have been summarized. A study of genetic distance between animal taxa using a representative sample of allozyme loci, has shown that conspecific populations have, as a rule, the least genetic differences ($D=0.01-0.05$). Subspecies and semi species ($D=0.2$), species and genera ($D=0.5$) form a sequence of rising levels of differentiation. However, many exceptions among salmonids (Ryman et al., 1979, Kartavtsev et al., 1983 and others) allow us to conclude that reproductive isolation of newly-formed species can be created even by very few genome changes comparable to those known for conspecific populations. The differences in level and pattern of isozyme activity between tissues suggest that regulatory gene divergence takes place in early stages of species formation and may be larger than the structural gene divergence.

Main Papers on salmonid fish genetics

- Kartavtsev, Yu.P. 1979. An estimation of balance nature of biochemical polymorphism. p. 36-40. - In: Biochemical and population genetics of fishes. Inst. of Cytol., Acad. Sci. St. Petersburg, USSR. (In Russian.)
- Kartavtsev, Yu.P. and A.M. Mamontov. 1983. Electrophoretic study of protein variability and similarity of *Coregonus autumnalis*, two forms of whitefish (Coregonidae) and grayling (Thymallidae) from the Baikal Lake. - *Genetica* 19(11): 1895-1902. (In Russian.)
- Kartavtsev, Yu.P., M.K. Glubokovsky and I.A. Chereshev. 1983. Genetic variability and differentiation of two sympatric trout species (*Salvelinus*, Salmonidae) from the Chukotka. - *Genetica* 19(4): 584-593. (In Russian.)
- Kartavtsev, Yu.P., N.E. Polyakova and A.I. Karpenko. 1985. Inheritance, qualitative and quantitative variability of allozymes of malate dehydrogenase, malic enzyme and lactate dehydrogenase in chum salmon, *Oncorhynchus keta*. - *Genetica* 21(5): 845-853. (In Russian.)
- Kartavtsev, Yu.P. 1986. Biology and genetics of salmon species from the Primorie and the Sakhalin regions in a connection with the problems of their natural and artificial reproduction. - Vladivostok: Sci. Rep., State Registration No 81,090,861, v. 1-2. (Manuscript in Russian.)
- Kartavtsev, Yu.P. 1989. Allozyme variability and morphological homeostasis in pink salmon *Oncorhynchus gorbuscha* (Pisces: salmonidae). - VINITI Deposits, No 847-B89, 08.02.89. 33 p. (Manuscript in Russian, also prepared for Evolution, USA.)
- Kartavtsev, Yu.P. 1990. Allozyme heterozygosity and morphological homeostasis in pink salmon *Oncorhynchus gorbuscha* (Pisces: salmonidae). - *Genetica*. (In press, in Russian.)

Main Problems and Results from Studies of Biochemical and Population Genetics of Salmonid Fish

YURI P. ALTUKHOV and YELENA A. SALMENKOVA

Laboratory of Population Genetics, Institute of General Genetics, Russian Academy of Sciences
Gubkin st.3, Moscow B - 333, 117809 Moscow, Russia

1. Genetic variability of enzymes and quantitative estimates of its level in populations of Pacific salmon: Studies of inter- and intraspecies genogeographic variation and genetic differentiation of chum and pink salmon populations in Soviet Far East region have been carried out. Populations of chum from Sakhalin and Iturup Islands, the Amur river, and the Primorye coast have been screened for 18-23 loci, of which eight are polymorphic. Together with the Institute of Biological Problems of the North (Magadan), populations from the Okhotsk sea, Eastern Kamtschatka and the Anadyr River have been analyzed. Proportions of inter-population components from the total gene diversity is 7%. 10 loci (7 polymorphic) have been analyzed in populations of pink salmon from Sakhalin, Iturup and Western Kamtschatka. Gene diversity between population forms differ by 2.2%. This consists mainly of genetic differences between samples from odd and even years.

2. Investigations of mechanisms which maintain allozyme polymorphism in populations of Salmonid fish: Long-term data on the biology and distribution of allele frequencies in loci Pgm and Ldh 4 in subdivided spawning populations of sockeye salmon in Lake Azabach (Kamtschatka) allows one to estimate the contribution of different evolution any factors to the formation of the genetic structure of stocks and to estimate the fitness of different genotypes. Differences in the effect of natural selection on the distribution of genotypes of these loci can be shown.

The heterozygosity of some loci was higher in many of the later generations of pink salmon spawners as compared to fry. This feature can be estimated as evidence of cyclic balancing selec-

tion, acting on populations of pink salmon against heterozygotes in the early stages of life history, but favouring heterozygotes in later stages. The similarity of allele frequencies over large parts of the distribution area characteristics of pink salmon can be explained by similar selection coefficients affecting these loci.

3. Studies of connections between allozymic variability and variation in quantitative traits of adaptive significance: Connections have been found between the level of heterozygosity in single loci and sexual-age structure in populations of sockeye salmon. Average heterozygosity of several loci has an effect on viability and growth rate of pink salmon on early life stages.

4. Studies on the influence of selective fishery on biological and genetic structures of populations: Significant changes of sex-size composition and decline in the level of genetic variability due to the exclusive selection of large spawners for artificial propagation during several generations have been shown in pink salmon.

5. Analysis of the effects of transfer of chum Salmon eggs between hatcheries in the Sakhalin - Kuril islands - Amur region: Due to significant genetic differences between the populations of chum, extremely poor results of such transfers of eggs could be shown by population genetic analysis.

6. Analysis of population origins of fish caught in regions of coastal fisheries: The origins of immature chum salmon caught during the pink salmon fishery in the south from the Tatar strait and chum caught in the region of Rybnovsk, (North Sakhalin) has been shown.

Investigations of Genetic and Epigenetic Variability of Proteins of Salmonid Fish

VLADISLAV I. SLYNKO¹ and SERAFIMA K. SEMYONOVA²

¹ Institute of Biotechnology, Nauchnyi proyezd 8, 117246 Moscow, Russia

² Institute of Biology of Gene, Russian Academy of Sciences, Vavilov St. 34/5, 117984 Moscow, Russia

1. The intraspecies population structure of pink salmon consists of spawning groups which are linked by space (the very exact translation "mutually connected by territory"). The isolation between them is not so rigid in space and time as in other salmonid fish. By means of MDH-A phenotype frequencies genetic heterogeneity can be shown on three levels of interspecies structure: 1) within a generation 2) between subsequent generations within a river population 3) between populations of different rivers. To some extent this subdivision can also be described in MDH-B phenotype distribution, however, AGPDH variation only reveals the differences between odd and even year generations within a river. The populations of chum salmon are isolated more by space than by time, this can also be followed in the distribution of protein phenotypes.

The homology of Mdh electrophoretic patterns was detected for all species of genus *Oncorhynchus* excluding masou salmon. The latter having greater resemblance to fish of the genus *Salmo* or *Salvelinus*. Different susceptibility of MDH isozymes to ions of heavy metals have been described in pink and chum salmon. There are also differences between species regarding this feature.

2. A biochemical marker which is linked to sex has been described in Atlantic and pink Salmon. This nonspecific blood esterase is monomorphic in males and females of Atlantic salmon and females of pink salmon, but polymorphic in male pink salmon.

3. Fertile interspecies hybrids have been found in sympatric populations of Atlantic salmon and brown trout as well as in chum and pink salmon. There have also been fertile backcrosses in the

case of the latter pair. The proportion of hybrid salmon x trout in natural and hatchery populations ranges between 0-3% on the Baltic Sea coast and 31.4% in the Narva river. The proportion of hybrid chum x pink fluctuated in some spawning groups between 0 and 7%. The viability of hybrid progeny was lowered.

4. Using biochemical genetic markers the young of natural and hatchery populations of all salmonid fish can be monitored alive. Interspecies hybrids can be detected and reveal the changes in the genetic structure of a population.

5. The subdivision of populations of Atlantic salmon into two groups (Kola Peninsula and Baltic Sea - Lake Onega - Petschora River) was revealed on the basis of distribution of EST-D phenotypes. The alleles of this enzyme are species specific for Atlantic salmon and brown trout. The other marker enzymes (ME, PER, CK, AGP) permit one to distinguish three groups in the populations of salmon (Kola, Baltic and Onega-Petschora), but exhibit common alleles for salmon and trout.

6. Comparative electrophoretic studies of esterases, malic enzyme and creatine kinase were carried out for 28 species from 7 genera of the suborder Salmonoidei. The influence of phosphorus, chlororganic compounds and heavy metals on the kinetics of esterases of salmon and trout was estimated.

7. Whitefish forms from geographically isolated and ecologically unique Lake Seidozero have been shown to differ from whitefish of Lake Imandra and the Rivers Tuloma and Lotta in the electrophoretic patterns of hemoglobin, AGPDH, ME, MDH, LDH, EST, EST-D.

Genetic Variability of Proteins in the Populations of Vendace (*Coregonus albula*) and least Cisco (*Coregonus sardinella*). (Project was finished in 1988.)

ANDREI A. PERELYGIN

Institute of Cytology, Russian Academy of Sciences, St. Petersburg

Variability of enzymes in populations of vendace from Lakes Ladoga, Onega, Peipus and populations of least cisco from three regions in the Ob River basin were investigated by means of PAAG electrophoresis. Inheritance of variability in LDH-3*, ME-4* and SOD-1* was tested in 12 individual crosses. They proved not to be linked with each another. Variation was described at the following loci: AAT-1,2*, CK-1,2*, GPDH-2*, PGI-1,2*, PGI-3*, IDH-1*, IDH-4*, LDH-5*, ME-1,2*, ME-3,4*, PGM-2* and SOD-1* in vendace, as well as at AAT-1,2*, CK-1,2*, GPDH-1*, GPDH-2*, PGI-3*, IDH-4*, LDH-5*, G6PDH-1*, PGM-2*, SOD-1* in least cisco. Level of heterozygosity was similar in both species ranging from 0.066-0.069. The proportion of polymorphic loci ranged from 0.37-0.42. The level of differentia-

tion between large and small vendace in lakes Ladoga and Onega, which are described as different subspecies or species, was insignificant. The genetic distance between these forms was 0.0018 in Lake Ladoga and 0.0024 in Lake Onega while distances between local populations were 0.0016 in Lake Ladoga and 0.0005 in Lake Onega. Loci which could be used to show the genetic differentiation of populations were ME* and SOD* in Lake Ladoga and Idh and Pgi in Lake Onega.

Qualitative differences could only be revealed between species of cisco in the patterns of CK*. There were also significant differences between them in the allele frequencies of SOD-1*, PGM-2*, and AAT-1,2* too. The genetic distance between vendace and least cisco was 0.104

References to scientific publications written in russian and not mentioned in review papers (The names of journals are translated into English.)

- Althukov, Yu.P. 1989. Genetic processes in populations. - Second editon. Moscow, Nauka. p. 328.
- Althukhov, Yu.P. and N.V. Varnavskaya. 1983. Adaptive genetic structure and its connections with intrapopulation differentiation for sex, age and growth rate in sockeye salmon, *Oncorhynchus nerka* (Walb.). - *Genetica* 19(5): 796-807.
- Althukov, Yu.P., S.V. Mezherin, Y.A. Salmenkova and V.T. Omelchenko. 1989. Effect of selective hatchery on adaptive genetic and biological structure of pink salmon *Oncorhynchus gorbuscha* (Walb.) population. - *Genetica* 25(10): 1843-1853.
- Althukhov, Yu.P., A.Yu. Novoselskaya, E.A. Salmenkova, G.D. Ryabova, A.A. Goncharova, S.M. Konovalov, V.I. Ilyin, A.G. Shevlyakov and Yu.I. Novoselsky. 1983. Factors of differentiation and integration of genetical structure of a native system of *Oncorhynchus nerka* Walb. (Pisces) subpopulations in Lake Azabachye (Kamchatka). - *J. Gen. Biol.* 44(3): 316-331.
- Althukov, Yu.P., E.A. Salmenkova, V.T. Omelchenko, G.A. Rubtzoza and Yu.E. Dubrova. 1987. Balancing selection as a possible factor maintaining uniformity of allele frequencies of enzyme loci in populations of pacific pink salmon *Oncorhynchus gorbuscha* (Walb.). - *Genetica* 23(10): 1884-1896.
- Althukov, Yu.P., E.A. Salmenkova, V.T. Omelchenko and V.N. Yefanov. 1983. Genetic differentiation and population structure of pink Salmon of Sakhalin - Kuril Islands region. - *Marine Biology* 2: 46-51.

- Althukov, Yu.A., E.A. Salmenkova, G.D. Ryabova and N.I. Kulikova. 1980. Genetic differentiation of chum salmon *Oncorhynchus keta* (Walb.) populations and effectiveness of some acclimatization measures. - *Marine Biology* 3: 23-38.
- Andryasheva, M.A. 1989. Studies of polymorphic protein loci and quantitative traits in fish. Genetics in Aquaculture. - Proceedings of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 29-47.
- Andryasheva, M.A. and A.B. Lokshina. 1987. Population-genetic approach to selection of peled (*Coregonus peled* Gm.). I. A method for increasing stock heterozygosity for enzyme loci. - *Genetica* 23(12): 2085-2097.
- Chebanov, N.A., N.V. Varnavskaya and V.S. Varnavskij. 1983. Estimation of the success of participation in spawning of male chum salmon belonging to different hierarchical ranks with the help of genetic-biochemical markers. - *J. Ichthyol.* 23(5): 774-778.
- Chernov, V.M. and S.N. Borkhsenius. 1987. Quantitative estimation of homology between genomes of two species of pacific salmon genus *Oncorhynchus* and intraspecies forms of sockeye salmon. - Proceedings of all-union research institute of lake and river fisheries 261: 84-91.
- Chernov, B.M. and S.N. Borkhsenius. 1989. Determination of polygenetic relationships between pacific salmon of genus *Oncorhynchus* by method of molecular hybridization of DNA. - *Marine Biology* 2: 23-29.
- Ermolenko, L.N. 1989. Genetic variability and interpopulation differences of whitefish of *Coregonus lavaretus* group. - *Genetica* 25(5): 886-893.
- Ermolenko, L.N., S.P. Pustovoyt, A.N. Makoedov and R.M. Viktorovsky. 1987. Genetics of lactate dehydrogenase isoenzymes in Salmonid fish. - *Genetica* 23(2): 344-354.
- Ermolenko, L.N. and E.A. Rudminaitis. 1984. Multiple allelism of isoenzymes of esterase D in salmonid fish. - *Genetica* 20(7): 1205-1210.
- Gagalchy, N.G. 1985. Biochemical polymorphism of the Kamchatka pink salmon *Oncorhynchus gorbuscha* (Walb.). I. Allelic frequencies of polymorphic loci in odd generation. - *Genetica* 21(5): 854-860.
- Gagalchy, N.G. 1986. Biochemical polymorphism in Kamchatka pink salmon *Oncorhynchus gorbuscha* (Walb.). II. Allelic frequencies of polymorphic loci in even generation. - *Genetica* 22(12): 2839-2846.
- Glubokovsky, M.K. and L.A. Zhivotovsky. 1989. Population structure of pink salmon: facts and models. Genetics in Aquaculture. - Proceedings of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 47-67.
- Glubokovsky, M.K., L.A. Zhivotovsky, R.M. Viktorovsky, A.M. Bronevsky, K.J. Afanasyev, V.V. Efremov, L.N. Ermolenko, B.A. Kalabushkin, V.G. Kovalyev, A.W. Makoedov, T.V. Malinina, S.P. Pustovoyt and G.A. Rubtzova. 1989. Population structure of pink salmon. - *Genetica* 25(7): 1275-1285.
- Ilyina, L.V. 1987. Influence of some abiotic factors on genotypic and allelic rates of lactate dehydrogenase B1 locus in the sockeye fry. - *Genetica* 23(7): 1284-1289.
- Kaukoranta, M., B.M. Mednikov, V.A. Maksimov and K.A. Savvaitova. 1982. Genetic divergence of charrs of the genus *Salvelinus* (Salmonidae, Salmoniformes). - *J. Zool.* 61(9): 1372-1379.
- Kirpichnikov, V.S. 1986. The state and aims of pink salmon population-genetic investigations. Genetics in Aquaculture. - Proceedings of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 87-97.
- Kirpichnikov, V.S. 1987. Genetics and selection of fish. - 2 edition. Leningrad, Nauka. p. 520.
- Kirpichnikov, V.S. 1990. Genetic studies of pacific salmon. - *J. Gen. Biol.* 51(1): 15-35.
- Kirpichnikov, V.S., G.A. Muske and A.D. Scholl-Engberts. 1987. Population genetics of Kamchatka salmon genus *Oncorhynchus*. I. Frequency dynamics of the alleles of lactate dehydrogenase (LDH) and phosphoglycomutase (Pgm) loci in sockeye salmon (*O. nerka* (Walb.)) of the Dalneye Lake. - *Genetica* 23(7): 1299-1310.
- Lokshina, A.B. 1980. Comparative electrophoretic analysis of some proteins of Coregonid fish. - Proceedings of all-union research institute of lake and river fisheries 153: 46-57.
- Lokshina, A.B. and M.A. Andryasheva. 1981. Methods and results of selective breeding of *Coregonus peled*. Communication II. Change of genetic structure under the influence of selective breeding. - Proceedings of the all-union research institute of lake and river fisheries 174: 77-80.
- Lokshina, A.B., M.A. Andryasheva and E.V. Chernyaeva. 1987. Connections of heterozygosity with some components of fitness in *Coregonus peled*. - Proceedings of all-union research institute of lake and river fisheries 261: 40-50.
- Lokshina, A.B. and L.A. Polyakova. 1985. Analysis of level of variability of albumine 2 locus in the spawners of peled of first gynogenetic generation. - Proceedings of all-union research institute of lake and river fisheries 228, 45-47.
- Makoedov, A.N., L.N. Ermolenko, S.P. Pustovoyt, L.T. Bachevskaya and V.G. Kovalyov. 1989. Esterase D polymorphism in salmonids. - *Marine Biology* 4: 55-59.
- Mamontov, A.M. and V.M. Yakhnenko. 1987. Biochemical polymorphism of Arctic cisco ("omul") from Lake Baikal. - "Morphology and ecology of fish" Novosibirsk. p. 9-19.
- Matzak, E.A. 1989. Genetic analysis of sockeye salmon *Oncorhynchus nerka* (Walb.) population from Lake Kurilskoye, Kamchatka. Genetics in Aquaculture. - Proceedings of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 87-97.
- Omelchenko, V.T. 1975. The use of electrophoregrams of proteins in systematics of species of genus *Salvelinus*. - *Marine Biology* 4: 76-79.
- Omelchenko, V.T. and G.P. Vyalova. 1990. Pink salmon population structure. - *Marine Biology* 1: 3-13.
- Osinov, A.J. 1984. Some additional data on origin of the recent range of the sea trout *Salmo trutta* L. (Salmonidae), based on biochemical markers. - *J. Ichthyol.* 24(1): 11-24.
- Osinov, A.G. 1988. Brown trout *Salmo trutta* (Salmonidae) of Black and Caspian Sea basins: population-genetic analysis. - *Genetica* 24(12): 2172-2186.

- Osinov, A.G. 1989. Genetic divergence between species and some phylogenetical problems in the genus *Salmo*. Genetics in Aquaculture. - Proceeding of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 97-107.
- Osinov, A.G. 1989. The low level of genetic variability and differentiation of ecological forms of Sevan trout *Salmo ischchan Kessler*. - *Genetica* 25(10): 1827-1835.
- Osinov, A.G. 1990. Genetic variability and differentiation of brown trout (*Salmo trutta* L.) populations of Tadzhikistan. - Proc. of Moscow University. Ser. 16. Biol. 1: 37-41.
- Perelygin, A.A. 1988. Population genetic analysis of european cisco *Coregonus albula*. Differentiation of sympatric small and large cisco from Lake Ladoga. - *Cytology and Genetics* (Novosibirsk) 22(1): 50-53.
- Polyakova, N.E. and A.G. Oleinik. 1988. Isozymes of esterase D in *Oncorhynchus masu*. - *Genetica* 24(6): 1130-1131.
- Salmenkova, E.A., Yu.A. Althukov, R.M. Viktorovsky, V.T. Omelchenko, L.T. Batchevskaya, L.N. Ermolenko, E.A. Rudminaitis and B.A. Semenov. 1986. Genetic structure of chum salmon populations spawning in rivers of the Far East and the North East of the USSR. - *J. Gen. Biol.* 47(4): 529-549.
- Salmenkova, E.A., V.T. Omelchenko and Yu.S. Roslyi. 1989. Differences in the genetic structure of summer and autumn races on Amur Chum Salmon. Genetics in Aquaculture. - Proceedings of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 80-86.
- Semyonova, S.K. and V.I. Slynko. 1988. Polymorphism of proteins in population of Atlantic salmon (*Salmo salar* L.), brown trout (*S. trutta* L.) and their hybrids. - *Genetica* 24(5): 548-555.
- Shubin, P.N. and A.B. Zakharov. 1984. Hybridization of European grayling *Thymallus thymallus* (L.) and arctic grayling *Thymallus arcticus* (Pallas) in the secondary contact zone of the species. - *J. Ichthyol.* 24(3): 502-504.
- Shubina, E.A. and B.M. Mednikov. 1986. The repetitive sequences families in salmon fishes DNA of the genus *Oncorhynchus*. - *Molec. Biol.* 20: 947-956.
- Skurikhina, L.A., B.M. Mednikov and P.Ya. Tugarina. 1985. Genetic divergence of graylings (*Thymallus*) of Eurasia and "species network". - *J. Zool.* 64(2): 245-251.
- Skurikhina, L.A., P.Ya. Tugarina and B.M. Mednikov. 1986. On the situation in the system Thymallidae (Salmoniformes) in the light of DNA X DNA molecular hybridization data. - *J. Ichthyol.* 26(1): 56-60.
- Slynko, V.I. and S.K. Semenova. 1978. Esterase as a character connected with the sex in Salmonidae. - *Scientific papers of Acad. Sci. USSR* 234(1): 224-225.
- Titov, S.F. and R.V. Kazakov. 1989. The use of genetic analysis of Atlantic salmon *Salmo salar* L. in improvement of artificial salmon populations. Genetics in Aquaculture. - Proceedings of 3 all-union conference of genetics, selection and hybridization of fishes, Tartu, 1986. Leningrad. p. 179-186.
- Varnavskaya, N.V. 1984. Distribution of Ldh-B1 and Pgm gene frequencies in sockeye salmon (*Oncorhynchus nerka* Walb.) populations preferring different types of spawning grounds. - *Genetica* 20(1): 100-106.
- Varnavskaya, N.V., V.S. Varnavsky, I.I. Vetsler and K.Ya. Nepomnyashchii. 1988. Peculiarities of genetic spatial differentiation of sockeye salmon (*Oncorhynchus nerka* Walbaum) populations of Nachiki, Dalneye, Blichneye, Dvuyurtochnoye lakes (Kamchatka). - *Genetica* 24(4): 723-731.
- Varnavskaya, N.V., V.S. Varnavsky and O.N. Saravansky. 1988. Peroxidase polymorphism in sockeye salmon *Oncorhynchus nerka* (Walb.) populations of Kamchatka. - *Genetica* 24(10): 1866-1872.
- Viktorovsky, R.M., L.T. Batshevskaya, L.N. Yermolenko, E.A. Rudminaitis, G.D. Ryabova, A.N. Makoyedov, N.G. Schevtshenko and L.I. Gutin. 1986. Genetic structure of chum salmon populations in the North East of the USSR and the problems of rational management of its stock. - *Marine Biology* 2: 51-59.
- Zhivotovsky, L.A., K.J. Afanasiev and G.A. Rubtzova. 1987. Selective processes on enzyme loci in pink Salmon. - *Genetica* 23(10): 1876-1883.
- Zhivotovsky, L.A. and M.K. Glubokovsky. 1989. The role of migrations and selection in the genetic differentiation of pink salmon. - *Scientific papers of Acad. Sci. USSR* 308(5): 1235-1240.
- Zhivotovsky, L.A., M.K. Glubokovsky, R.M. Viktorovsky, A.M. Bronevsky, K.I. Afanasyev, V.V. Efremov, L.N. Ermolenko, B.A. Kalabushkin, V.G. Kovalyev, A.N. Makoyedov, T.V. Malinina, S.P. Pustovoyt and G.A. Rubtzova. 1989. Genetic differentiation in pink salmon. - *Genetica* 25(7): 1261-1274.

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, with the original manuscript.

Authors are recommended to keep their papers short.

Fifty offprints are supplied free of charge. An additional number may be ordered at cost. Price list and order forms for offprints 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 figures or figure captions. A variable divided with another variable should be noted as the following example L per min is $L \text{ min}^{-1}$.

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	$^{\circ}\text{C}$
hour	h
(spell out for diel time)	
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)	$^{\circ}$
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)	$P\beta$	per mille (per thousand)	‰	age-class (n.)
radian	rad	siemens	S	age-group (n.)
sample size	N	tesla	T	aquaculture (n.)
second (angular)	"	trihydroxymethyl-		Arctic char (n.)
standard deviation	SD	aminomethane	tris	brackish water (n.)
standard error	SE	volt	V	brackish-water (adj.)
variance	V or var	watt	W	chi-square (n., adj.)
		weber	Wb	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.)
Physics and Chemistry		General (some are restricted)		
all atomic symbols		compass directions (maps and coordinates): east	E	
alternating current	AC	north	N	
ampere	A	south	S	
becquerel	Bq	west	W	
candela	cd	et alii	et al.	
chemical acronyms listed in Webster's dictionaries (DDT, EDTA, etc.)		et cetera	etc.	
coulomb	C	filial generation	F	
dextro	D	for example	e.g.,	
direct current	DC	international unit	IU	
electron volt	eV	months (tables, figures): first three letters (Feb, Jun, etc.)		
equivalent	eq	ploidy	n	
farad	F	sex (tables, figures, hybrid crosses): female	♀	
gray	Gy	male	♂	
hertz	Hz	that is	i.e.,	
hydrogen ion activity (negative log of)	pH	United Kingdom	UK	
joule	J	United States (adjective)	U.S.	
levo	L	United States of America (noun)	USA	
lumen	lm			
lux	lx			
molar	M			
mole	mol			
newton	N			
normal	N			
ohm	Ω			
ortho	o			
para	p			
pascal	Pa			
		Word List		
		The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:		

Contents

Tom G. Northcote	Migration and Residency in Stream Salmonids - some Ecological Considerations and Evolutionary Consequences _____	5-17
Martin-A. Svenning Astrid Smith-Nilsen Malcolm Jobling	Sea Water Migration of Arctic Charr (<i>Salvelinus alpinus</i> L.) Correlation between Freshwater growth and Seaward Migration, based on back-calculation from Otoliths _____	18-26
Björn Malmqvist	Stream Grazer Responses to Predator Odour - an Experimental Study _____	27-34
Anders Klemetsen Harald Muladal Per-Arne Amundsen	Diet and Food Consumption of Young, Profundal Arctic Charr (<i>Salvelinus alpinus</i>) in Lake Takvatn _____	35-44
Carl Folke Håkan Olsén Svante Winberg Rickard Bjerselius Lars Karlsson	Differences in Rheotactic Response and Attraction to Population - Specific Odours in Baltic Salmon (<i>Salmo salar</i> L.) Parr _____	45-51
Odd Terje Sandlund	Differences in the Ecology of two Vendace Populations separated in 1895 _____	52-60
Erik Degerman Berit Sers	Fish Assemblages in Swedish Streams _____	61-71
Trygve Hesthagen Ola Hegge Jostein Skurdal	Food Choice and Vertical Distribution of European Minnow, <i>Phoxinus phoxinus</i> , and Young Native and Stocked Brown Trout, <i>Salmo trutta</i> , in the Littoral Zone of a Subalpine Lake _____	72-76
Eva Brännäs Bo-Sören Wiklund	Low Temperature Growth Potential of Arctic Charr and Rainbow Trout _____	77-81
Anders Jonsson	Shelter Selection in YOY Crayfish <i>Astacus astacus</i> under Predation Pressure by Dragonfly Larvae _____	82-87
	Notes and Comments _____	88-101

